

A TAXONOMIC MONOGRAPH OF THE MOSS GENUS *CODRIOPHORUS* P. BEAUV. (GRIMMIACEAE)

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HALINA BEDNAREK-OCHYRA

W. SZAFER INSTITUTE OF BOTANY, POLISH ACADEMY OF SCIENCES KRAKÓW 2006 A taxonomic monograph of the moss genus *Codriophorus* P. Beauv. (Grimmiaceae) Suggested abbreviation: *Taxon. Monogr. Codriophorus*

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Chapter 1

INTRODUCTION

The traditionally conceived genus Racomitrium Brid. is a relatively large genus of acrocarpous mosses of the family Grimmiaceae. Its species are medium-sized or large plants growing in tufts or extensive mats and are common in the cold, cool and temperate zones of both hemispheres, while in the tropics they are restricted to montane and altimontane elevations. Although they have generally been readily distinguishable, the genus itself suffered a bad reputation as one of the most difficult amongst mosses. This was due to the exceptional variation of some species which constituted taxonomically difficult complexes, for example the R. canescens and R. heterostichum groups, which were variously interpreted by different bryologists. Detailed taxonomic study of the R. canescens group (Frisvoll 1983a) revealed that it actually consisted of eight well-defined and sharply separated species on the basis of characters which had formerly been largely ignored, but which proved to be exceptionally stable and valuable for characterisation of the species. Among others these were the structure of the costa and leaf hair-point, the papillosity of the laminal cells, and the form of alar and supraalar cells.

Taxonomic studies revealed a similar situation in the Racomitrium heterostichum complex in the Northern Hemisphere (Frisvoll 1988). These resulted in the description of several new species and the resurrection of other neglected ones, often on the basis of largely neglected or forgotten characters. An analogous situation has long existed in the R. crispulum complex in the Southern Hemisphere. A large number of austral Racomitrium species had been lumped with R. crispulum (Hook.f. & Wilson) Hook.f. & Wilson (Clifford 1955) and this concept was perpetuated to some extent by Lawton (1973). However, subsequent taxonomic studies have clearly shown that at least in the western part of the austral region many species had been incorrectly considered conspecific with R. crispulum and were actually distinct and unmistakable species on their own right (Roivainen 1955; Bell 1974; Deguchi 1984, 1987; Bednarek-Ochyra et al. 1999; Ochyra et al. in preparation). Preliminary researches in the Subantarctic and Australasia have revealed a similar situation and have shown that R. crispulum itself is a narrow endemic of two New Zealand islands in the cool temperate zone, Auckland and Campbell Islands (Ochyra et al. in preparation).

Likewise, global research on the variability of *Racomitrium lanuginosum* (Hedw.) Brid. showed that in fact it was a complex of two well-defined species and one subspecies (Vitt & Marsh 1988). Shortly afterwards a third distinct species, *R. patagonicum* Bednarek-Ochyra & Ochyra, was added to this group (Bednarek-Ochyra & Ochyra 2003).

The taxonomic problems existing in the aforementioned complexes of Racomitrium strongly suggested that other groups of this genus might be aggregations of closely related but otherwise distinct species. Especially promising were R. aciculare and R. fasciculare which had usually been described as polymorphic species. Though in Europe they had been considered malleable but otherwise well-defined species, elsewhere they had neither been satisfactorily treated nor thoroughly studied. Noguchi (1974), in his revision of Racomitrium in Japan, stated that "R. fasciculare is exceedingly variable in many respects" and recognised four varieties within it. Unfortunately, it was only a local treatment and some widely distributed species required detailed study on a worldwide scale. Also, preliminary studies of North American populations of R. aciculare showed it was a critical complex containing some distinct entities which deserved recognition as separate species, among them R. aduncoides Bednarek-Ochyra (Bednarek-Ochyra 1999a) and R. norrisii Bednarek-Ochyra & Ochyra (Bednarek-Ochyra & Ochyra 2000). These strongly indicated the necessity of a global revision of these species and the present taxonomic monograph is the result of these investigations. In order to resolve properly all taxonomic problems associated with the species concerned, it was necessary to lectotypify the oldest names which refer to the core species of these complexes.

Although *Racomitrium* was a fairly large genus by muscological standards, containing about 80 species, its infrageneric classification had been totally neglected until the mid-1990s. Then an infrageneric classification of this genus was procuded and based largely on peristome structure, shape of the perichaetial leaves and papillosity of the laminal cells (Bednarek-Ochyra 1995). *Racomitrium* was divided into four subgenera, namely *Racomitrium* subg. *Racomitrium*, *R.* subg. *Cataractarum* Vilh., *R.* subg. *Niphotrichum* Bednarek-Ochyra and *R.* subg. *Ellipticodryptodon* (Vilh.) Bednarek-Ochyra & Ochyra. These corresponded well to the four unranked groups recognised within this genus by Kindberg (1898), namely Lanuginosa, Papillosa, Canescentia and Laevifolia respectively, which were subsequently given the status of sections by Noguchi (1974). Subsequent studies have shown that Racomitrium was an artificial genus and these subgenera did in fact represent natural and well-established taxa which are easily distinguishable from one another. Therefore these subgenera were raised to the rank of independent genera by Bednarek-Ochyra & Ochyra (in Ochyra et al. 2003), namely Racomitrium s. str., Codriophorus P. Beauv., Niphotrichum (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra and Bucklandiella Roiv. They are distinctive taxa through various combinations of unique or otherwise presumably advanced characteristics for the Grimmiaceae such as the presence of pellucid alar cells, variously papillose laminal cells, papillosity of seta and calyptra, torsion of seta, shape of peristome teeth, anatomy of costa, and shape of hair-point.

Racomitrium aciculare and *R. fasciculare* clearly belong within the genus *Codriophorus* which corresponds to *Racomitrium* subg. *Cataractarum*. The aim of this study is to obtain a better understanding of the genus. It includes the circumscription of *Codriophorus* and a worldwide, monographic revision of its all species based on morphological studies of herbarium material.

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Chapter 2

HISTORICAL PERSPECTIVE

A HISTORY OF THE GENUS

The history of the generic name *Codriophorus* has been presented in detail by Bednarek-Ochyra *et al.* (2001). The name was published posthumously in the final work of the French bryologist A. M. F. J. Palisot de Beauvois (1752–1820), *Muscologie ou traité sur les mousses* (Palisot de Beauvois 1822*a*, *b*) which was intended to be a revised version of his *Prodrome des cinquième et sixième familles de l'aethéogamie. Les mousses. Les lycopodes* (Palisot be Beauvois 1805). The manuscript was prepared for printing by Arsène Thiébaut de Berneaud who served as a secretary of the Société Linnéenne de Paris (Ochyra & Lamy 2004). He was not a bryologist and could not eliminate numerous errors and inconsistencies which were present in the work.

This work appeared in the first volume of *Mémoires de la Société Linnéenne de Paris* (Palisot de Beauvois 1822*a*) and as a separate with independent pagination reprinted from the journal (Palisot de Beauvois 1822*b*). It is impossible to establish now which version was published first and therefore for the sake of convenience both the original publication and the reprint are considered to have been simultanenously published. There have been some discrepancies regarding the effective date of publication of *Muscologie*. Margadant (1968) and Stafleu & Cowan (1983) indicated 1823 as the year of publication of this work but the letter from Jean-Baptiste Mougeout dated 30 October 1822 to Thiébaut de Berneaud in which he heavily criticised this paper clearly indicate that it was published in 1822, not 1823 (Lamy 1990).

The strong critique of *Muscologie* by Mougeout in his letter to the editor prompted Augustin-Niçaise Desvaux, a disciple of Palisot de Beauvois, to publish a short article in which he corrected many errors and inconsistencies occurring in *Muscologie* (Desvaux 1824). Among other things, he found that the generic name *Codriophorus* was misspelled and correctly should have read *Codonophorus*. He was certainly right because the handwritten 'codono' may be easily misinterpreted as 'codrio' and, additionally, in Greek the word 'codrios' does not exist. Moreover, Palisot de Beauvois certainly referred to a moss bearing conical-mitrate or bell-shaped calyptrae. Although correct from the linguistic point of view, the name *Codonophorus* is nomenclaturally illegitimate because it bears the type of an earlier validly published name. At most *Codonophorus* may be considered only as an orthographic variant of *Co-driophorus*.

Codriophorus was described, with the serial number 16, as a member of the second section Ectopogones. It was placed in the group having divided peristome teeth and specifically in its subgroup with cucullate calyptrae, along with the genera *Fissidens*, *Cecalyphum* (= *Dicranum*), *Didymodum* (= *Didymodon*), *Swartzia* (= *Distichium*), *Trematodum* (= *Trematodon*) and *Dicranum*. In the brief French diagnosis the author characterised this genus as having frequently lobed calyptra, conic-subulate operculum, cylindrical to ovoid and straight to slightly curved capsule, straight or rarely arcuate setae, which are variable in length, and oblong exserted vaginula.

Palisot de Beauvois (1822*a*, *b*) provided a relatively broad taxonomic discussion in support of his decision to recognise *Codriophorus* as a new genus which was considered to occupy an intermediate position between *Dicranum* and *Trichostomum*. Unfortunately, no species were mentioned in the protologue and the author stated only that the genus comprised terrestrial plants growing epiphytically on tree trunks.

The text of Palisot de Beauvois' (1822*a*, *b*) paper is accompanied by eleven plates with illustrations of selected genera and species. The legends to the plates are published on separate, unnumbered pages. The third plate consists of drawings of six species, including two species of *Codriophorus*, namely *C. acicularis* (Hedw.) P.Beauv. and *C. pulvinatus* (Hedw.) P.Beauv. It should be noted that in the legend the masculine gender of the generic name is changed to the neuter gender *Codriophorum* and the species accordingly have the names *C. aciculare* and *C. pulvinatum*.

In modern moss taxonomy these species refer to two separate genera, *Racomitrium* and *Grimmia* as, respectively, *R. aciculare* (Hedw.) Brid. and *G. pulvinata* (Hedw.) Sm. Both species are saxicoles and this ecological preference contradicts markedly the statement in the protologue that *Codriophorus* consists of epiphytic species. Possibly, Palisot de Beauvois intended to include more species in this genus. This assumption appears to be confirmed by his comment on the label of the type material of his *Trichostomum obtusifolium* P. Beauv. in the Bridel herbarium at B which reads: "Trichostomum obtusifolium j'en fais un nouveau genre avant les Dicranum aciculare, pulvinatum et autres espèces à dents fendues" (Bednarek-Ochyra 2001). This species is currently considered to be identical to *Anomodon minor* (Hedw.) Lindb. which is predominantly an epiphyte, although it may also grow on calcareous rocks.

The taxonomic status of the genus *Codriophorus* has been obscure since its inception and the name has therefore fallen into disuse. In the bryological literature of the 19th century it was mentioned only by Léman (1825) who considered both *Codriophorus* and *Codonophorus* to be congeneric with *Trichostomum* Hedw. However, both names, *Codriophorus* and *Codonophorus*, appear in *Index muscorum* (Wijk *et al.* 1959, 1969) where they are considered to be synonyms of *Racomitrium*. Nevertheless, the relevant entries in this opus are largely incorrect and the errors occur in the bibliographic data, author citation, typification and taxonomic conclusions. They have been corrected by Bednarek-Ochyra *et al.* (2001).

Codriophorus originally consisted of two species and therefore lectotypification of this name was required as correctly pointed out in the Index nominum genericorum (plantarum) (Farr et al. 1979). The generic characters mentioned in the protologue are very general and can be easily applied either to C. acicularis or C. pulvinatus. Bednarek-Ochyra et al. (2001) chose C. acicularis as lectotype and made Codriophorus synonymous with Racomitrium. However, when the traditional genus Racomitrium was split into four segregates, Codriophorus was the only name for a genus comprising species classified into Racomitium subg. Cataractarum (Ochyra et al. 2003). It is worth noting that selection of the second species of the genus, Codriophorus pulvinatus, as lectotype would have had far-reaching nomenclatural consequences because then the generic name Dryptodon Brid. published four years later (Bridel 1826), would have been endangered. Dryptodon is a widely used name for a distinct grimmialean genus which has usually been considered monotypic, consisting of only D. patens (Ochyra et al. 1988). However, after splitting the large and heterogeneous genus Grimmia Hedw. (Ochyra et al. 2003), Dryptodon has become the largest segregate and home of numerous species traditionally placed in Grimmia subg. Rhabdogrimmia Limpr. Accordingly, this would have necessitated many more nomenclatural changes in Dryptodon than in Codriophorus in its present circumscription unless Dryptodon would had been conserved against Codriophorus, but then a completely new name would have had to have been coined for the segregate of *Racomitrium* comprising species of the R. aciculare-R. fasciculare complex.

Vilhelm (1926) recognised the separate subgenus *Racomitrium* subg. *Cataractarum* to accommodate *R. aciculare* and *R. aquaticum*. The name of this subgenus derives from the Latin substantive *cataracta* = waterfall and refers to the wet habitats occupied by these species. In selecting the name *Cataractae*, this author was certainly inspired by the specific epithet of *R. cataractarum*, one of the synonymous names of *R. aquaticum*. Vilhelm (1926) used the name *Cataractae* for this subgenus which, ac-

cording to the current Code (Greuter *et al.* 2000), should be construed as a noun in the genitive singular and in the spirit of the provision of Art. 21.2 be corrected to *Cataractarum*, not *Cataracta* as suggested by Bednarek-Ochyra (1995), because the derivation of the latter word as a subgeneric name is unknown. *Cataracta* is a feminine noun for cataract and it does not agree with *Racomitrium*.

Codriophorus is a natural and easily distinguished genus that is primarily recognised by the presence of large, flat papillae distributed over the longitudinal cell walls and covering the major part of the lumina, very much resembling those in the genus Racomitrium s. str. However, in contrast to *Racomitrium*, the calyptra in *Co*driophorus is densely papillose, a character also unique to the genus, the costa often ends well below the leaf apex, the innermost perichaetial leaves are epilose, the setae are smooth and twisted to the right on drying. Moreover, in the majority of species hyaline leaf hair-points are absent and, if present, they are denticulate to nearly smooth, not strongly papillose as in Racomitrium s. str. and the capsules are never ventricose at the base. Codriophorus has mostly shorter peristome teeth which are divided to the middle or below, and only rarely to the base, into two or three prongs.

A HISTORY OF THE SPECIES AND INFRASPECIFIC TAXA

Within the two centuries and more of the history of modern bryology 80 names have been proposed for the taxa which are currently placed in the genus Codriophorus or have otherwise been associated with the names of its principal species, comprising 42 species, 25 varietal and 13 form names (Table 1). The overwhelming majority of these taxa, 61, were originally described under the generic name Racomitrium Brid. A further seven were described under Grimmia Hedw., five under Trichostomum Hedw., four under Dicranum Hedw. and one each under Bryum Hedw., Orthotrichum Hedw. and Codriophorus itself. Of these, only two taxa currently belong within different genera, namely Dicranum aciculare var. pumilum Turner, which is identical to Bucklandiella obtusa (Brid.) Bednarek-Ochyra & Ochyra (Frisvoll 1988), and Trichostomum obtusifolium P.Beauv. which was reduced by Arnott (1825) to an unranked infraspecific taxon within Trichostomum aciculare and subsequently considered identical to Anomodon minor (Hedw.) Lindb. (Bednarek-Ochyra 2001). The identities of eleven taxa could not be definitely established because the relevant type collections have not been located or made available for investigation, but they refer exclusively to infraspecific taxa (for detailed discussion of these see Chapter 8, p. 249).

ACCEPTED SPECIES

As a result of a taxonomic revision of all available type collections as well as a great number of non-type specimens it was found that the genus *Codriophorus* cur-

No.	Year of publications	Taxon name	Region	Current identity				
VALIDLY PUBLISHED NAMES								
		Pioneer period						
1.	1801	Trichostomum fasciculare (Schrad.) ex Hedw.	Europe	Codriophorus fascicularis				
2.	1801	Dicranum aciculare Hedw.	Europe	Codriophorus acicularis				
3.	1801	Bryum lutescens Dicks.	Britain	Codriophorus fascicularis				
4.	1803	Trichostomum aquaticum (Brid.) ex Schrad.	Europe	Codriophorus aquaticus				
5.	1804	Dicranum aciculare var. fluitans Turner	Ireland	?				
6.	1804	D. aciculare var. gracile Turner	Ireland	Codriophorus aquaticus				
7.	1804	D. aciculare var. pumilum Turner	Ireland	Bucklandiella obtusa				
8.	1805	Trichostomum obtusifolium P.Beauv.	N America	Anomodon minor				
9.	1825	T. fasciculare var. secundum Ahnf.	Sweden	?				
10.	1827	Racomitrium cataractarum Brid.	Germany	Codriophorus aquaticus				
11.	1827	Orthotrichum submarginatum Brid.	Newfoundland	Codriophorus acicularis				
12.	1830	Trichostomum protensum A.Braun ex Duby	France	Codriophorus aquaticus				
13.	1845	Racomitrium aciculare var. denticulatum Bruch & Schimp.	Europe	Codriophorus acicularis				
		American period		·				
14.	1851	<i>R. aciculare</i> var. <i>aquaticum</i> Poech	Czechia	?				
15.	1861	R. fasciculare (Hedw.) Brid. fo. rivulare J.E.Zetterst.	Norway	Codriophorus fascicularis				
16.	1864	Grimmia varia Mitt.	British Columbia	Codriophorus varius				
17.	1868	Racomitrium depressum Lesq.	California	Codriophorus depressus				
18.	1869	Grimmia laevigata Mitt.	Tierra del Fuego	Codriophorus laevigatus				
19.	1871	Racomitrium virescens Lindb.	Europe	Codriophorus fascicularis				
20.	1872	R. brevisetum Lindb.	Sakhalin	Codriophorus brevisetus				
21.	1873	Grimmia nevii Müll.Hal.	Oregon	Codriophorus acicularis				
22.	1884	Racomitrium canescens (Hedw.) Brid. var. lutescens Lesq. & James	California	Codriophorus varius				
23.	1884	R. fasciculare (Hedw.) Brid. fo. gracile Boulay	France	?				
24.	1887	R. fasciculare var. nigricans Warnst.	Greenland	Codriophorus fascicularis				
25.	1888	R. oreganum Renauld & Cardot	Oregon	Codriophorus varius				
26.	1890	Grimmia speciosa Müll.Hal.	British Columbia	Codriophorus varius				
27.	1890	Grimmia willii Müll.Hal.	South Georgia	Codriophorus laevigatus				
28.	1892	Racomitrium microcarpon (Hedw.) Brid. var. palmeri Kindb.	Bering Sea	Codriophorus fascicularis				
29.	1893	<i>R. fasciculare</i> var. <i>haplocladon</i> Kindb.	Bering Sea	Codriophorus fascicularis				
30.	1893	R. aciculare var. brachypodium Besch.	Japan	Codriophorus carinatus				
31.	1894	<i>R. papeetense</i> Besch.	Society Islands	Codriophorus fascicularis				
32.	1895	<i>R. aciculare</i> var. <i>angustifolium</i> Höhn.	Spain	?				
33.	1896	<i>R. tenuinerve</i> Kındb.	Bering Sea, British Columbia	Codriophorus fascicularis				
		Far East Asian period						
34.	1903	R. aciculare fo. falcatum Jaap	Germany	Codriophorus acicularis				
35.	1903	R. protensum fo. robustum Loeske	Germany	Codriophorus aquaticus				
36.	1904	R. aciculare var. falcatum Grav.	Belgium	Codriophorus acicularis				
37.	1905	R. canaliculatum Mitt. ex Cardot	Japan	Codriophorus anomodontoides				
38.	1907	R. aciculare var. angustifolium Röll	Germany	?				
39.	1907	R. loriforme Dusén	Chile	Codriophorus laevigatus				
40.	1908	R. molle Cardot	Japan	Codriophorus mollis				
41.	1908	<i>R. fauriei</i> Cardot	Japan	Codriophorus carinatus				
42.	1908	<i>R. fauriei</i> to. <i>irrigatum</i> Cardot	Japan	?				
43.	1908	<i>R. sudeticum</i> (Funck) Bruch & Schimp. var. <i>subellipticum</i> Cardot	Japan	Codriophorus carinatus				
44.	1908	<i>R. fasciculare</i> var. <i>brachyphyllum</i> Cardot	Korea	Codriophorus anomodontoides				
45. 46	1908	<i>K. jasciculare</i> (Hedw.) Brid. var. <i>orientale</i> Cardot	Korea, Japan	Codriophorus brevisetus				
40. 47	1908	<i>K. jasciculare</i> var. <i>atroviriae</i> Cardot	Japan	Coariophorus Jascicularis				
47.	1908	K. anomodontoldes Cardot	Japan, Korea	Coartophorus anomodontoides				
4ð. 40	1908	R. carinaium Cardot	Korea	Coartophorus carinatus				
49.	1909	K. sawaaae Cardot	Japan	Couriophorus brevisetus				

TABLE 1. A list in chronological order of accepted and synonymous names proposed for taxa belonging to or placed in *Codriophorus*. Names printed in boldface refer to currently accepted species.

No.	Year of publications	Taxon name	Region	Current identity
50.	1910	R. fasciculare fo. nigrescens H. Winter	Norway	Codriophorus fascicularis
51.	1910	R. fasciculare fo. submersum H.Winter	Norway	Codriophorus fascicularis
52.	1910	R. fasciculare fo. validius H.Winter	Norway	Codriophorus fascicularis
53.	1911	R. fasciculare fo. excurrens Mönk.	Denmark	?
54.	1913	R. aciculare fo. purpurascens Zodda	Sicily	?
55.	1913	Grimmia fascicularis (Hedw.) Müll.Hal. fo. subsimplex Arnell	Yakutia	Codriophorus corrugatus
56.	1916	R. aciculare var. radiculosum Guim.	Portugal	Codriophorus acicularis
57.	1926	<i>R. aciculare</i> fo. <i>humile</i> Vilh.	Central Europe	Codriophorus acicularis
58.	1926	<i>R. aciculare</i> fo. <i>fluviatile</i> Vilh.	Central Europe	Codriophorus acicularis
59.	1927	R. fasciculare var. erosum Broth.	Hawaiian Islands	Codriophorus anomodontoides
60.	1927	R. fasciculare var. perrobustum Broth.	Hawaiian Islands	Codriophorus anomodontoides
61.	1934	R. dichelymoides Herzog	Colombia	Codriophorus dichelymoides
62.	1936	R. plicatum Herzog	Chile	Codriophorus laevigatus
63.	1937	R. bandaiense Sakurai	Japan	Codriophorus anomodontoides
64.	1937	R. nipponicum Sakurai	Japan	Codriophorus anomodontoides
65.	1937	R. papillosum Sakurai	Japan	Codriophorus brevisetus
66.	1937	R. hedwigioides Sakurai	Japan	Codriophorus anomodontoides
67.	1937	R. formosicum Sakurai	Taiwan	Codriophorus anomodontoides
68.	1937	R. yakushimense Sakurai	Japan	Codriophorus anomodontoides
69.	1937	R. hypnoides Lindb. fo. chrysophyllum Sakurai	Japan	Codriophorus brevisetus
70.	1937	R. canescens var. yezoalpinum Sakurai	Japan	Codriophorus brevisetus
71.	1939	R. bandaiense var. ramosum Sakurai	Japan	Codriophorus anomodontoides
72.	1942	R. hedwigioides var. chrysophyllum Sakurai	Japan	Codriophorus anomodontoides
73.	1946	R. scabrifolium E.B.Bartram	Tierra del Fuego	Codriophorus laevigatus
		Revisionary period		
74.	1960	R. breutelioides Dixon	Tristan da Cunha	Codriophorus laevigatus
75.	1974	R. fasciculare var. hayachinense Nog.	Japan	Codriophorus brevisetus
76.	1995	R. hespericum Sérgio, J.Muñoz & Ochyra	Spain	Codriophorus acicularis
77.	1999	R. aduncoides Bednarek-Ochyra	N America	Codriophorus aduncoides
78.	2000	R. ryszardii Bednarek-Ochyra	N America	Codriophorus ryszardii
79.	2000	R. norrisii Bednarek-Ochyra & Ochyra	N America	Codriophorus norrisii
80.	2004	Codriophorus corrugatus Bednarek-Ochyra	Asia, Alaska	Codriophorus corrugatus
		NOMINA NUDA		
1.	1825	Trichostomum aciculare var. acutifolium Arn.	Scotland	?
2.	1837	Racomitrium aciculare var. viride Hampe	Germany	?
3.	1857	R. fasciculare var. minus Mitt. & Wilson	Sikkim	Bucklandiella himalayana
4.	1880	R. brevipes A.Jaeger	Japan	Codriophorus anomodontoides
5.	1916	<i>R. aciculare</i> var. <i>brevicaule</i> Meyran	France	?

rently consists of 15 species. The European species of the genus are quite common and abundant in some areas and because of their fairly large size they readily attracted the attention of collectors. Therefore it is hardly to be wondered at that they have been known to botanists since the earliest times, long before the publication of Species plantarum by Linnaeus (1753) and even the Historia muscorum of Dillenius (1741), who is generally considered to be the father of bryology. The earliest description of a species of Codriophorus is that of Muscus aquaticus pileis acutis published by Petiver (1695) which was subsequently adopted in the works of Ray (1696, 1704), Morison (1699) and Vaillant (1727). There are some discrepancies in the interpretation of this species by the last author in his Botanicon parisiense and Bridel (1798) considered Vaillant's plants to be Codriophorus aquaticus in the modern sense, whereas Lindberg (1863) believed that the drawing of the fertile plant represented the present-day *C. acicularis* while the sterile plant was *Philonotis fontana* (Hedw.) Brid. The second oldest species of *Codriophorus* is *C. acicularis* which was described by Ray (1724) who used the polynomial phrase-name for this species, *Bryum hypnoides erectum montanum, erectis capitulis acutis.*

Dillenius (1741) accepted the two above-mentioned species of *Codriophorus* and provided their descriptions and illustrations, designating them by the phrase-names *Bryum hypnoides aquaticum, calyptris nigris acutis* (*C. aquaticus*) and *Bryum montanum hemiheterophyllum, operculis acutis* (*C. acicularis*). Moreover, this author added a third species, *Bryum hypnoides, hirsutie virescens, fasciculare alpinum*, which refers to the modern *C. fascicularis*. Of these, only *C. acicularis* was approved by

Linnaeus (1753) who proposed for it the binomial name '*Bryum aciculare* L.'. *C. fascicularis* was admittedly accepted by Linnaeus (1753) but as an unnamed variety β within his '*Bryum hypnoides* L.', whereas *C. aquaticus* was completely ignored by him. All Dillenian *Codriophorus* species were widely accepted in numerous Floras of the second half of the 18th century and were given the binomial names '*Trichostomum fasciculare* Schrad.' (Gmelin 1791), '*Dicranum aciculare* Hedw.' (Hedwig 1782) and '*Trichostomum aquaticum* Brid.' (Bridel 1798).

In the history of the currently accepted *Codriophorus* species four distinct periods can be recognised which, for practical reasons, consist of fifty-year partitions. Interestingly, in each period except the first, four species were discovered and described.

(a) Pioneer period (1801–1850) — This period is actually limited to the first three years when the three Dillenian species of the genus were validated. Hedwig (1801) validly published *Codriophorus acicularis* as *Dicranum aciculare* and *C. fascicularis* as *Trichostomum fasciculare*, while *C. aquaticus* was validated in 1803 in an anonymous review of Bridel's (1798) *Muscologia recentiorum* which was most probably completed by H. A. Schrader, editor of *Journal für Botanik* in which the review was published. In the subsequent years of the first half of the 19th century several species and infraspecific taxa were described, all of which were, however, identical to the three oldest species of the genus.

(b) American period (1851-1900) — This period is so-named because three of the four Codriophorus species recognised in it were described from North and South America. Actually, all these species had been described by 1872. The first was described by Mitten (1864) as Grimmia varia from material from British Columbia and this species was subsequently transferred to Racomitrium as R. varium (Mitt.) A.Jaeger by Jaeger (1874). Four years later Lesquereux (1868) described Racomitrium depressum from California, and a year later Mitten (1869) distinguished Grimmia laevigata from the Tierra del Fuego archipelago in southern South America from the specimen collected by J. D. Hooker during his famous Antarctic voyage of 1839-1843. Jaeger (1874) moved this species to Racomitrium as R. laevigatum A.Jaeger, retaining the specific epithet laevigatum, although under Grimmia it was unavailable, being a later homonym of G. laevigata (Brid.) Brid. of 1826. Finally, Lindberg (1872) described the fourth species, Racomitrium brevisetum, from material collected in Sakhalin in the Russian Far East.

(c) Far East Asian period (1901-1950) — At the beginning of the 20th century the French bryologist J. Cardot studied the large collection of mosses from the Far East, including Korea and Japan, made by the French missionary Faurie. The results were published in several articles (Cardot 1904, 1905, 1908*a*, 1909) in which he described a great number of new taxa of the genus *Racomitrium*. No fewer than ten of them fit the concept of the genus *Codriophorus* and three species, *Racomitrium molle*, *R. carinatum* and *R. anomodontoides*, all described in 1908, are currently accepted as good species. The fourth species distinguished by Herzog (1934) in this period, *Co-driophorus dichelymoides*, originates from the Andes of Colombia in South America.

(d) Revisionary period (1951 onwards) — Critical taxonomic studies on the *Racomitrium aciculare*, *R. aquaticum* and *R. fasciculare* complexes resulted in the discovery and description of four distinct new species. These were *R. aduncoides* from eastern North America (Bednarek-Ochyra 1999a), *R. ryszardii* and *R. norrisii* from western North America (Bednarek-Ochyra 2000; Bednarek-Ochyra & Ochyra 2000) and *Codriophorus corrugatus* from East Asia and Alaska (Bednarek-Ochyra 2004c).

'SUNK' TAXA

This group consists of 65 taxa whose names have been reduced to synonymy of accepted species names. Thirtyone of these have been proposed as new heterotypic synonyms in the present monograph. Moreover, the original material for one *nomen nudum*, *Racomitrium brevipes* A.Jaeger, was located and studied and this name proved to be a new synonym of *Codriophorus anomodontoides*. 'Sunk taxa' are also discussed in the same four periods used for the group of accepted species.

(a) Pioneer period (1801–1850) — Only eight taxa, including four species, were described in this period in addition to the three accepted species. All taxa but one were described from European material, only Orthotrichum submarginatum being based upon a specimen from Newfoundland in North America. For two varieties, Dicranum aciculare var. fluitans and Trichostomum fasciculare var. secundum, no original materials have been located and another varietal name, Racomitrium aciculare var. denticulatum, was lectotypified by an illustration. Two names, Trichostomum obtusifolium and Dicranum aciculare var. gracile, refer to taxa definitely excluded from Codriophorus.

(b) American period (1851–1900) — Altogether 16 taxa were described in this period, including nine from North and South America and Greenland, thus confirming nomenclatural accuracy. For two European varieties and one form no type materials have been located. Seven taxa were described as species, including five from North and South America, but it is worth noting that two of these were originally described as varieties, *Racomitrium microcarpon* var. *palmeri* and *R. aciculare* var. *brachypo-dium*, both subsequently raised to species rank, *R. palmeri* (Kindb.) Kindb. and *R. brachypodium* (Besch.) Cardot.

(c) Far East Asian period (1901–1950) — This was the most prolific period for distinguishing new *Codriophorus* taxa and in total 36 were described, comprising 12 species, 12 varieties and 12 forms. Only for two varieties and one form has no type material been located. Of these, 19 taxa were described from Arctic Siberia, Japan, Korea, and Taiwan in East Asia, a figure which again confirms the correctness of the choice of name. All was mainly the result of the activity of J. Cardot who described eight taxa (in addition to the three accepted species) and the Japanese bryologist K. Sakurai who, as a typical splitter, proposed ten new taxa from Japan and Taiwan (Sakurai 1937a, b, 1939, 1942) but none has been accepted in modern bryology and all names have been reduced to synonymy. Interestingly, no new taxa were described from

North America in this period and only three new species were described from southern South America all of which proved to be conspecific with *Codriophorus laevigatus*.

(d) Revisionary period (1951 onwards) — Only two new species from Tristan da Cunha and Spain and one variety from Japan were described as new in this period in addition to the four new and accepted species. Such a situation is typical for modern bryophyte taxonomy when new taxa are described on the basis of a thorough assessment of a large amount of material and environmental modifications are not given any taxonomic recognition.

Chapter 3

MATERIAL AND METHODS

HERBARIUM MATERIAL

The present study was mostly based on the examination of herbarium specimens, although living material of three European Codriophorus species was collected from Poland. In the course of this study approximately 11,000 dried herbarium specimens were examined from the following 68 institutional herbaria: AAS, ALTA, B, BA, BCB, BISH, BM, BP, BR, BRNM, C, CANM, CAS, COLO, DUKE, E, F, FH, FLAS, G, GJO, GZU, H, HAL, HBG (only Codriophorus fascicularis), HIRO, ICEL, JE, KRABG, KRAM, KYO, LBL, LD, LE, LISU, M, MA, MAK, MAINE, MICH, MO, NICH, NMW, NY, O, OSC, OXF, PAMP, PC, POZG, PR, PRC, ROST, S, SOM, SOSN, TENN, TNS, UC, UPS, US, VIT, W, WAW, WRSL, WTU, WVA and ZAMU. The herbaria acronyms are standardised according to Index herbariorum (Holmgren et al. 1990) and Bryological herbaria (Iwatsuki et al. 1976). In addition, the private herbaria of Dr U. Drehwald (Göttingen), Prof. Dr R. Düll (Duisburg), Dr J. Eggers (Schönfeld), Dr A. P. Dyachenko (Yekaterinburg), Dr A. Erdag (Aydýn), Professor J.-P. Frahm (Bonn) Dr M. O. Hill (Huntingdon), Dr D. T. Holyoak (Camborne), Dr V. Hugonnot (Varennes), Drs E. A. and M. S. Ignatovs (Moscow), Dr Monika Koperski (Bremen), Dr M. Lüth (Freiburg), Dr J. Muñoz (Madrid), Dr M. Privitera (Catania) and Dr G. Uyar (Incivez) were consulted. Unfortunately, several requests to borrow the herbarium holdings of Codriophorus species from British Columbia and coterminous territories deposited at UBC, from China housed in IFSBH and C. acicularis and C. aquaticus from HBG remained unanswered.

I have tried to see type material of all names proposed in the genus, including the specific, varietal and form names, and also the original material of the invalid names. I was able to locate and study the type or original material of 69 names (86%) including the type of all species names, whereas the type or original material of 11 varietal and form names (14%) could not be studied. I have assumed that the unlocated types refer to modifications of no taxonomic importance. In the cases of two varietal names the relevant type specimens have not been located and these names have been lectotypified by illustrations accompanying original descriptions. Also, the two earliest species names in the genus *Codriophorus, C. aquaticus* and *C. fascicularis* are lectotypified with the relevant illustrations in *Historia muscorum* of Dillenius (1741) with a simultaneous selection of epitypes, i.e. interpretative types.

TREATMENT OF TAXA

Morphological and anatomical research was carried out according to common practice in bryology. Specimens were investigated dry for determining habit, leaf arrangement, seta and shape of capsule and calyptra. They were moistened in warm water for habit and leaf stance in wet condition which often differ significantly from those in dry condition. However, shape of the capsule was found not to differ much when moistened, so this is not included in the descriptions. Overall measurements of plants as well as setae and capsule length were made from dry material under the stereomicroscope and are given in centimetres or millimetres, whereas all microstructures were measured under the compound microscope and are given in microns (μ m).

The shape of leaf cells is given in surface view and the location of measured cells is shown diagrammatically (Fig. 1). Cell measurements include the lumen and walls of the measured cell. Plant sizes and the lengths of stems are given in centimetres. Three informal categories of plant size have been used, namely small (not exceeding 1.5 cm), moderately sized (1.5–5.0 cm) and large (more than 5.0 cm). Unless indicated otherwise, the leaf features given in the descriptions refer to leaves that are situated in the middle parts of the stem or branches to which they are attached.

Sporophyte and calyptra features were obtained by examination of mature sporophytes, unless otherwise stated. Shapes and sizes given for capsules do not include lids, which are described separately. Lengths of the peristome teeth were measured from the capsule mouth.

The descriptions follow a standard scheme and include the following headings which are italicised in the text: plants, stems, rhizoids, axillary hairs, leaves, leaf apex, leaf margins, costa, laminal cells (including basal, alar and supra-alar cells), perigonia, perichaetial leaves, seta, capsule, operculum, annulus, exothecial cells, stomata, peristome, spores and calyptra. All these characters were investigated in detail in several dozens of specimens of



FIGURE 1. Leaf dimensions and measured cells location. AC - alar cells; AP - leaf apex; BC - basal cells; HPL - hair-point length; L - length; LC - lower cells; MC - mid-leaf cells; SC - supra-alar cells; UC - upper cells; W - width.

each taxon. These specimens were selected to cover variation along both ecological and geographical gradients.

Each species is illustrated with line drawings, usually assembled on two or more plates, and for some species SEM micrographs of various details are also presented. The plates with line drawings always show all morphological and anatomical details and in the case of variable species full spectra of the most variable characters, including leaf shapes, leaf apices and transverse sections of the costa are given.

The description of each species is accompanied by relevant additional material in which variation, reproduction, habitat, taxonomy and nomenclature as well as geographical distribution are discussed. Details of all features which are of value in identifying a particular species are given under the subtitle 'Diagnostic characters and differentiation' immediately following the overall species description. In order to determine what the taxonomically significant characters were, every possible structure had to be examined and a record kept of what was found for each individual species. In addition to the enumeration of the diagnostic characters of a species, included here is a discussion of other species that might be confused with the one under consideration and how they can be most readily distinguished from it.

The range of variation on a worldwide scale is described for each species with consideration of the most interesting aberrations not dealt with in the general description. The reproductive capacity of the species concerned is calculated on the basis of the frequency of sporophyte production in the total amount of material examined. The ecological data are given here as accurately as possible but, as noted above, the treatment of *Codriophorus* is based upon the examination of herbarium specimens with familiarity in the field limited to the European species. Therefore the treatment of 'Habitat' is mostly taken from information on herbarium labels which often contain insufficient or ambiguous information. In some cases information from reliable floristic and ecological treatments has also been used.

One of the most important aspects of a taxonomic revision or monograph which significantly differentiates it from a floristic work is the nomenclatural treatment. The taxonomist must try to deal with all validly published names in the group concerned and to establish the correct names for the taxa recognised in the treatment. The nomenclatural studies are of fundamental importance since they should lead to nomenclatural stability. Hence special attention was paid to unravel nomenclatural problems and to explain and clarify historical and taxonomic confusion. Names are arranged in groups of homotypic synonyms which are subsequently arranged in order of priority and chronology, whereby the group that includes the correct name is given first, and is followed by groups of taxonomic synonyms. Names within a group of homotypic synonyms are similarly ordered, with the basionym given first. The first group of homotypic synonyms in a series of taxonomic synonyms is obviously shown below the correct name of the taxon involved.

The nomenclature was consistently checked from the original literature. Valid names are immediately followed by citation of the publication in which they were originally published and are given in chronological order. Abbreviations of authors follow Brummitt & Powell (1992) and abbreviations of journals and books are as given by Crosby (2003). Various comments on types and lectotypifications as well as a taxonomic history are given for each taxon.

The distribution of individual species has been presented on maps which are entirely drawn up on the basis of the specimens examined and no literature data has been included. These are eventually discussed in the descriptive part of the 'Geographical distribution' entry. For widely distributed species dot maps are completed for each continent or geographical region. Additionally, the global range of such species is presented on a separate map using continuous lines and dots.

The distribution maps are accompanied by lists of the specimens examined. These are preceded by specimens distributed in exsiccati which are listed in alphabetical order of editor name(s). For rare and less frequent species all specimens are cited, whereas for common species a representative selection of the specimens examined is given. The localities of the individual species are arranged alphabetically by continent (Macaronesia is treated as the equivalent of a continent) and within continents by countries and within countries by administrative or geographical units.

Chapter 4

TAXONOMIC CHARACTERS

The broadly conceived genus Racomitrium s. lato, like other large genera of the Grimmiaceae, including Schistidium and Grimmia s. lato, has always been considered to be one of the most difficult and complex amongst mosses, no less intricate than such genera as Pohlia Hedw., Bryum Hedw., Drepanocladus (Müll.Hal.) G.Roth and Hypnum Hedw. Some critical groups within this genus which now, after splitting, lie within particular segregates, for example the Bucklandiella heterosticha complex, the Niphotrichum canescens complex and Racomitrium s. str. itself, had acquired the bad reputation of being school textbooklike examples of taxonomic chaos which could not be described or properly arranged using the traditional methods of classical taxonomy (Anderson 1963). The main reason for this state of affairs was perceived as twofold. Firstly, there was considerable phenotypic plasticity and malleability of some characteristics that were considered to be of high taxonomic importance, for example branching pattern, colour and robustness of plants and leaf shape. Secondly, clones or pure lines whose individuals were similar or identical genotypically had become established owing to common asexual reproduction which had led to the fixation of some combinations of characters. Because these often tended to be fairly uniform throughout a single population, there was a strong temptation, especially for former generations of taxonomists, to recognise various phenotypes as separate species or at least infraspecific taxa. Such activity simply added to the chaos which already existed and hampered the correct circumscription and determination of taxa.

Subsequent taxonomic studies, for instance in the *Niphotrichum canescens* complex (Frisvoll 1983*a*), the *Bucklandiella heterosticha* complex (Frisvoll 1988), the *B. crispula* complex (Deguchi 1984), the *Schistidium apocarpum* group (Blom 1996) and the *Racomitrium lanuginosum* group (Vitt & Marsh 1988; Bednarek-Ochyra & Ochyra 2003), challenged the pure-line hypothesis and showed it to be a rather speculative concept. This was mainly because many taxa of these complexes, including often the most variable species, reproduce readily sexually and freely produce mature sporophytes. Furthermore, some character states, including the branching pattern, coloration of plants, presence and form of hair-points and stratosity of the laminal cells have no or limited diagnostic value. Of course these characters are obvious and easily

observed but at the same time are subject to considerable variability induced by changing environmental conditions. In contrast, some less conspicuous characters are very stable and constant or modifiable to a narrow extent, and these proved to be of great taxonomic value although hitherto they had been largely ignored by taxonomists. Of these the most important in *Codriophorus* are the anatomical structure of the costa, leaf margin and areolation, supra-alar cells and innermost perichaetial leaves. In contrast to other groups of mosses, sporophyte characters are generally less important taxonomically in this genus, although sometimes the size and shape of the capsule, the peristome teeth and the shape of the exothecial cells have some importance for the circumscription of individual species.

Several characters of *Codriophorus* species are strongly modified environmentally and climatically. The variability shows a trend common to all taxa but its degree for a particular character varies markedly among the taxa and also between sections and subsections. Costa width for instance varies freely from medium-broad to broad or very broad in species of the type section of *Codriophorus*, whereas it is either relatively narrow to mediumbroad or broad and varies within narrower limits in taxa of sect. *Fascicularia*. The most important modifications occur along the moisture gradient and are similar to those observed in *Bucklandiella* (Frisvoll 1988), *Niphotrichum* (Frisvoll 1983*a*) and *Schistidium* (Blom 1996).

The gametophyte and sporophyte characters of Codriophorus species are reviewed below, with special consideration of their diagnostic value and taxonomic importance. The classification of character states and notes on their evolution are discussed briefly under individual characters in order to provide a basis for establishing relationships between species and the subdivision of the genus into sections and subsections. Bucklandiella is used as the comparative outgroup for the classification of character states as plesiomorphous (ancestral) and apomorphous (derived) since this genus is considered to be a more generalised group within the Grimmiaceae and has been revised for the Northern Hemisphere (Frisvoll 1988) and partly for the western part of the Southern Hemisphere (Deguchi 1984; Bednarek-Ochyra et al. 1999). Cao & Vitt (1986) used the genus Racomitrium s. lato as outgroup in their phylogenetic analysis of Grimmia s. lato and Schistidium and suggested the polarisation of character states and their structural reduction within the Grimmiaceae which paved the way for establishing a major evolutionary trend within *Codriophorus*.

GAMETOPHYTE GENERATION

Gametophyte characteristics are taxonomically the most important in *Codriophorus*. They are all observed on both the vegetative and perichaetial leaves and therefore for taxonomic studies they are the most important part of the plant. The leaves have a simple structure but their primary characteristics are combined in various ways, providing a good basis for the recognition of species. All 15 species of the genus can usually be distinguished using one or a few leaves but in the case of variable species it may be of importance to investigate a greater number of leaves from each plant or specimen.

1. Growth-form

Codriophorus species are mostly widely, loosely or, occasionally, densely caespitose plants, but most taxa growing under moist habitat conditions are mat-forming. Plants growing submerged in the rapids of streams or in waterfalls sometimes have a fruticose habit with the main stem attached to rocks by a discoid foot, for example, in *C. acicularis, C. mollis* and *C. aduncoides*.

2. Stem

The stems in Codriophorus species are erect, arcuately to curved-ascending or prostrate. They are tough, stiff, rigid and wiry in texture and only in C. mollis are the stems more flexible and pliable. The stems are usually dark brown to reddish-brown and glistening. In transverse section they are circular, oval or obtusely angled and their most peculiar feature is the lack of a central strand in all species. The cortical layer is composed mostly of 3-5 rows of small, sclerenchymatous cells with small lumina and incrassate walls that are clearly demarcated from the medullary cells which are much larger, hyaline or yellowish and thin- or thick-walled and arranged in 5-8 layers. Anatomically, the stem of Codriophorus clearly belongs to type III sensu Deguchi (1978) which is more or less equivalent to Kawai's (1965) type 'b'. In C. norrisii the cortex is fairly weak, comprising only 1-3 layers of stereid cells, whereas in C. varius the stem is very thick and consists of 10-13 layers of medullary and 3-5 rows of cortical cells. Based on generalised outgroup comparison Cao & Vitt (1986) considered the reduction of the central duct as a derived character and it is consistently absent in all genera of the Racomitrioideae.

There is great variation in stem length which is primarily correlated with habitat. The longest stems have been observed in the mat-forming plants of *C. acicularis* (20.5 cm), *C. varius*, *C. fascicularis* and *C. anomodontoides* (20.0 cm), *C. aduncoides* (17 cm) and *C. aquaticus* (16.5 cm) from moist and aquatic habitats. Also, similarly long stems reaching 20 cm have been found in *C. laevigatus* in plants forming deep, luxuriant tufts or compact wefts. The shortest measured stems were found in *C. acicularis* and *C. aquaticus* (0.5 cm). *C. norrisii* is definitely the smallest species of the genus with the stems only 2–3 cm long on average and with the longest stem reaching only 3.5 cm. Also, *C. ryszardii* and *C. brevisetus* are fairly short plants, with the stems 1–7 and 3.0–8.5 cm long, respectively.

3. Branching pattern

The mode of branching is often considered of high taxonomic importance, but actually it is very variable, even within a single species. The branches are intercalary and a monopodial pattern of branching occurs in all species of the genus. The perichaetia terminate the lateral branches and therefore Codriophorus species are cladocarpous. However, the production of a terminal sporophyte does not terminate the growth of the plant and a subapical innovation is subsequently produced which laterally displaces the terminal perichaetium. Consequently the species have a pseudo-pleurocarpous growth-form. Additional lateral branches are produced in all species of Codriophorus, apparently independently of the production of a sporophyte. All taxa can be found mostly irregularly sparingly or profusely dichotomously or fasciculately, or rarely pinnately branched, but sometimes in C. mollis, C. depressus, C. aquaticus, C. carinatus, C. fascicularis, C. brevisetus, C. corrugatus and C. varius the shoots are simple and almost unbranched. C. anomodontoides and C. ryszardii have generally sparsely branched shoots and some species of sect. Fascicularia, including C. brevisetus, C. fascicularis, C. corrugatus, C. laevigatus and C. varius, have very often numerous short, horizontal tuft-like branchlets which give the plants a pinnulate or nodose appearance.

Robustness of the plants is an unimportant taxonomic character but such species as *Codriophorus anomodontoides* and *C. laevigatus* are generally large, robust and coarse plants, whereas *C. brevisetus*, *C. carinatus* and *C. norrisii* are mostly small to moderately sized and gracile. In many species such as *C. fascicularis*, *C. acicularis*, *C. aquaticus*, *C. aduncoides* and *C. varius* plants of damp and wet sites are generally larger than those of drier habitats and particularly robust and coarse plants are found in typically rheophytic habitats. In the Arctic, epigean plants of *C. fascicularis* are considerably larger than saxicolous ones in the same area. In *C. aquaticus* and *C. fascicularis* populations from areas with a marked oceanic climate are more robust than those from areas with a continental one.

4. Plant colour

The upper parts of plants are green, yellow-green or olivaceous and the lower parts are brownish to blackishbrown. However, in various ecological situations, especially in exposed and insolated sites, secondary colours develop including orange, rusty and reddish, usually in various combinations and hues. The aquatic and submerged plants of *Codriophorus acicularis* and *C. depressus* are often blackish-green to entirely black and some plants of *C. varius* are greyish-green above due to leaf pilosity. Due to considerable infraspecific variability, the plant colour is of limited value in distinguishing taxa.

5. Axillary hairs

These occur commonly in all species in the leaf axils, at the tip of the stem or just below. They are filiform, mucilage-secreting structures (Berthier *et al.* 1974; Schofield & Hébant 1984) composed of 6–21 hyaline cells but in *Codriophorus mollis* 1–2 short basal cells are brownish pigmented. There are some differences in the length of the axillary hairs between closely related species, e.g. in *Codriophorus acicularis* they are 6–20-celled, whereas in *C. norrisii* 9–12-celled and *C. aduncoides* 18–21-celled. In general, the diagnostic value of the axillary hairs is limited in *Codriophorus* since the numbers of cells forming them markedly overlap among species, although in other moss families they are considered to be a valuable diagnostic character (Nishimura 1985; Buck 1987, 1988; Whitemore & Allen 1989; Hedenäs 1989*a*).

6. Rhizoids

These are smooth, branched, dark or reddish- to blackish-brown. They occur at the base only or in plants with prostrate stems they are scattered on the surface facing the ground. Occasionally, they are very few or even absent on some plants or are very abundant forming a dense tomentum, for example in *Codriophorus acicularis*. In the genus *Codriophorus* they have no value for distinguishing species, although in other groups of mosses, for example in the Mniaceae, Hypnaceae and Amblystegiaceae, their topography is of taxonomic importance (Koponen 1968; Tuomikoski & Koponen 1979; Crundwell 1979; Hedenäs 1987, 1989*b*, 1993).

7. Leaves

Orientation and arrangement — The leaves are arranged spirally in many rows and they are usually crowded and densely and evenly set along the stems and branches (Fig. 2). Plants from wet habitats have more distant leaves than those from drier places and in Codriophorus dichelymoides they are regularly remotely set. In species growing in permanently wet habitats the lower parts of the stems are often denuded and appear bristly due to erosion of the laminae, leaving just the persistent costae behind. The leaves are erect and appressed, usually imbricate and not altered on drying, although sometimes they are slightly crisped in C. carinatus, C. ryszardii and C. depressus. They are straight to slightly curved or falcate and sometimes they are distinctly falcato-secund to homomallous, for example in C. acicularis, C. aduncoides, C. anomodontoides and C. depressus. Only in C. dichelymoides are

the leaves strongly falcate and *C. fascicularis*, which normally possesses straight leaves, may develop falcate ones when growing in unusually wet habitats (Fig. 66.32–35).

Decurrency — The leaves are shortly decurrent in most species but longer and more distinctly decurrent and usually auriculate in species of the type subsection of *Co-driophorus*.

Shape — The leaf shape varies considerably in Codriophorus species. The commonest shape can be described as lanceolate or ovate-lanceolate but it exhibits great diversity, ranging from narrowly lanceolate to ovate- or linearlanceolate. The base may be more or less pronounced ovate or ovate- to oblong-lanceolate, not or distinctly plicate in C. varius and C. laevigatus, and the leaf gradually tapers to a short- or long acuminate, subulate point which is usually straight or slightly flexuose. In C. corrugatus the leaves are slenderly long acuminate, usually with a fine serpentine, corrugated and strongly wavy acumen (Figs 91.16-28, 92.10-15). No distinct leaf shoulders are present. This leaf shape is found in all species of the genus, except for those in subsect. Codriophorus in which lingulate, elliptical, or broadly ovate to broadly ovate-lanceolate leaves are predominantly found.

Size — In contrast to the genera Grimmia s. lato and Schistidium, the leaves in Codriophorus species are more or less of the same size along the whole stems and branches. In the majority of species they generally are 2-3 mm long on average, with occasional deviations to 1.5 and 4.0 mm (Fig. 3). C. laevigatus has markedly the largest leaves in the genus which are 3.0-4.5 mm long on stems and 4-8 mm on tuft-like branchlets. Other largeleaved species are C. depressus (3-5 mm), C. anomodontoides (3.0-4.5 mm), C. ryszardii (3.2-4.0 mm) as well as C. varius and C. dichelymoides (3-4 mm). The leaf width usually varies from 0.8 to 1.2 mm on average and as a rule is correlated with leaf length. Therefore C. laevigatus has the widest leaves (0.9–1.3 mm) followed by C. depressus (1.0-1.3 mm) and C. varius (1.0-1.2 mm) although in the last they are occasionally up to 1.5 mm wide. C. brevisetus and C. carinatus have the narrowest leaves in the genus, 0.6-0.9 mm wide, and in C. fascicularis the width varies from 0.5 to 1.0 mm, occasionally to 1.5 mm.

Profile — Most species possess concave to broadly canaliculate-concave leaves but in subsect. *Hydrophilus* the leaves are keeled to obtusely carinate in the distal half. Species of sect. *Fascicularia* have a more or less distinctly plicate leaf base, often reduced to a single fold near the costa which partly encloses the costal furrow. Concave or canaliculate-concave leaves represent a derived state, whereas keeled leaves are ancestral.

8. Leaf apex

The leaf apex is generally acute to subacute, but in species of subsect. *Hydrophilus* it is usually narrowly





FIGURE 3. Variation in leaf length within and between species. Thick bars show normal variation, thin bars show range of extreme values. — Abbreviations: ACI – *Codriophorus acicularis*; ADU – *C. aduncoides*; MOL – *C. mollis*; NOR – *C. norrisii*; AQU – *C. aquaticus*; CAR – *C. carinatus*; RYS – *C. ryszardii*; DEP – *C. depressus*; DIC – *C. dichelymoides*; FAS – *C. fascicularis*; BRE – *C. brevisetus*; ANO – *C. anomodontoides*; COR – *C. corrugatus*; LAE – *C. laevigatus*; VAR – *C. varius*.

rounded-obtuse, while in species of the type subsection it is broadly rounded-obtuse (Fig. 4). The leaf apex is generally muticous and only in *Codriophorus laevigatus* (Fig. 4.7) and in many plants of *C. varius* (Fig. 4.8) are the leaves terminated with a hyaline or yellowish-hyaline, flat, denticulate, straight or flexuose hair-point. Epilose ecads of the latter have a narrowly rounded-obtuse leaf apex (Fig. 4.9). In *C. carinatus* the leaves are either muticous or very shortly hyaline tipped. The apex is usually plane but in *C. mollis* is it sometimes cucullate and in *C. aduncoides* it is often tubular to subcucullate owing to inflexed margins.

9. Leaf margin

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Profile — Plane leaf margins occur in *Codriophorus* dichelymoides and in some phenotypes of *C. carinatus*. In the other species the margins are usually asymmetrically recurved to revolute (more broadly and often longer recurved on one side and narrowly or even plane on the other side). In species of the type section the margins are typically recurved to mid-leaf, occasionally to $\frac{2}{3}-\frac{3}{4}$ of the way up the leaf, whereas in sect. *Fascicularia* they are recurved to $\frac{2}{3}-\frac{3}{4}$ of the leaf length and often from the base nearly to the apex. Margins recurved throughout the whole length of the lamina are considered to be plesiomorphous, whereas margins shortly recurved to plane represent a derived state. It seems that the general evolutionary trend in the Grimmiaceae is from long recurved to plane or slightly recurved leaf margins (Cao & Vitt 1986).

Dentation — In most species the leaf margins are entire throughout and only eventually appear papillose-crenulate by having projecting cell papillae. In species of subsect. *Codriophorus* (except for *C. mollis*) the margins are typically irregularly remotely, coarsely, bluntly or sharply toothed, eroso-dentate to sinuate at the apex and down the margins to about $\frac{1}{5}-\frac{1}{4}$ of the way below it, whereas in *C. depressus* they are only occasionally bluntly, irregularly dentate or sinuate at the apex. Likewise, in all species of sect. *Fascicularia* (except *C. fascicularis*) the leaf apex is dentate or denticulate-cristate to cristate. However, the dentation is subject to considerable variability and it is missing on some leaves. Entire leaf margins are an ancestral type and dentate margins represent a derived state.

Stratosity — All species of Codriophorus have unistratose leaf margins, except for four species. In the majority of C. brevisetus populations of the leaf margins are bistratose in 1-2 or sometimes 3 rows of cells in the distal portion. Also in C. norrisii the margins are 2- or sometimes 4-stratose throughout in (1-)2-12(-13) cell rows, forming swollen limbidia extending from the apex to the base, being broadest distally and becoming progressively narrower towards the base. The margins are predominantly unistratose in C. aquaticus and C. acicularis but sometimes they are bistratose in the former for 1-3 rows of cells distally. In the latter they are infrequently 2-3- or even 4-stratose in 1 or 2-4 rows of cells forming swollen marginal thickenings in the upper part. A thickened leaf margin seems to be derived in *Codriophorus* as is the case in other segregates of Racomitrium and Schistidium (Blom 1996).

10. Costa

The costa is single, stout to very robust and entire to laterally spurred in the distal portion. It is entire or variously forked or bifurcate at the apex, often with one branch much longer than the other. It is brown to yellowbrown or sometimes concolorous with the laminal cells and usually well-demarcated from them in the lower part and often imperceptibly merging with them above. The costa is subpercurrent and vanishes a few cells below the leaf apex in most species but in *C. varius* it is sometimes percurrent. In *Codriophorus mollis*, *C. aduncoides* and *C. corrugatus* it typically ceases in mid-leaf or slightly above, often ending with just one branch of the bifurcate apex. In *C. anomodontoides* the costa typically extends for

FIGURE 2. SEM micrographs of leaves at shoot tips. — 1–3. Codriophorus acicularis. 4. C. mollis. 5. C. ryszardii. 6. C. fascicularis. 7. C. anomodontoides. 8. C. laevigatus. 9. C. varius. — [1 from Schofield et al. 101402, ALTA; 2 from Landals & Scotter 830, ALTA; 3 from Sérgio et al. 8296, LISU; 4 from Schofield et al. 101537, ALTA; 5 from Schofield & Vaarama 23970, DUKE; 6 from Lisowski 59922, KRAM; 7 from Musci japonici 1245, KRAM; 8 from Roivainen 1989, KRAM; 9 from Schofield 22633, KRAM].





FIGURE 5. Variation in costa width within and between species. Thick bars show normal variation, thin bars show range of extreme values. For abbreviations see Fig. 3.

 $\frac{3}{4}$ of the leaf length and in *C. brevisetus*, *C. fascicularis*, *C. laevigatus* and *C. dichelymoides* it usually reaches usually $\frac{3}{4}-\frac{5}{6}$ of the way up the leaf.

The costa is widest near the base and most often becomes gradually narrowed and weaker upwards. Nonetheless, its width is usually subject to considerable variation (Fig. 5) and because the width ranges greatly overlap among the species, this character is of limited value. The stoutest and widest costae are found in rheophytic species and plants growing in rheophytic habitats. The widest costae are known in Codriophorus depressus (100-200 µm), C. aquaticus (100-180 µm) and C. aduncoides (90-180 µm), although in the last they may occasionally reach 220 µm in width. In C. acicularis the costa width is exceedingly variable, ranging from 60 to 180 µm, but the broadest costae are found only in plants growing in the rapids of streams. In general, in species of sect. Codriophorus, the costae are the most robust and widest, including C. ryszardii (90-120 or sometimes to 135 µm), C. carinatus (85-105 µm), C. dichelymoides (85-100 µm) and C. mollis (75-100 µm). Species of sect. Fascicularia generally have weaker and narrower costae, except for C. varius in which it is 75-100 or 110 µm wide. In other species the costa width does not usually exceed 75 µm, only occasionally reaching 85 µm in C. brevisetus and C. anomodontoides, The narrowest costae are found in C. corrugatus – (30-)40-60(-70) µm and C. laevigatus - (35-)50-60(-75) μm.

In all species of *Codriophorus* except *C. dichelymoides* the costa is situated at the bottom of a groove which may be deep and narrow-angled, often partially enclosed by

the infolded leaf base in sect. *Fascicularia* and occasionally in some plants of sect. *Codriophorus*, or shallow and wide-angled in species of the type section (Fig. 6.1–2). In *C. dichelymoides* the costa is superficial and nearly as thick as the lamina, except for the extreme base. The costa is most often planoconvex being strongly convex on the dorsal side, but occasionally in some populations of *C. acicularis* it is distinctly binonvex. In *C. anomodontoides* the situation is reversed and the costa is convex on the ventral side and flattened or sometimes furrowed on the dorsal side.

The profile of the costa in transverse section is very variable and hence of limited diagnostic importance, except for *Codriophorus anomodontoides* whose costa is usually reniform, crescent-shaped or rarely semi-terete in the distal and median parts, or sometimes throughout, but most often is rectangular or lunate and strongly flattened dorsally in the proximal portion. The exposed dorsal side is usually symmetric but occasionally it is somewhat irregular.

The anatomy of the costa is a taxonomically important character, especially the number of cell layers and the number of cells in particular layers. All species of *Codriophorus* have the B-type of costa in Kawai's (1968) classification in which the distinction between the central and dorsal cells is unclear, but the distinctions between the ventral and central cells and between the ventral and dorsal cells are somewhat clearer. This is a simple type of costa with guide cells.

In sect. *Fascicularia* the costa is bistratose throughout and only sometimes at the extreme base is it tristratose. It is not differentiated anatomically and only in the basal part the dorsal row consists of small, sclerenchymatous cells that form a weak stereid band. The only exception in this section is *C. varius* in which the costa is 3–4-stratose in the proximal portion with a fairly pronounced, 2–3-layered dorsal stereid band. In contrast, in the type section, the costa is 2–4-stratose in the upper and median parts and 3–7-layered in the lower half, consisting of a single row of (3-)5-11(-15) enlarged ventral epidermal cells and a 2–6-layered dorsal stereid band of small sclerenchymatous cells with strongly incrassate walls.

11. Laminal cells

The laminal cells are unistratose in most species (Fig. 6) and only in *Codriophorus norrisii* are they variously bistratose in the distal portion. Additionally, the upper cells are bistratose in some populations of *C. ac-icularis, C. aquaticus, C. depressus* and *C. brevisetus.* The multistratosity of the laminal cells is evidently an adaptation to aquatic habitat conditions and has no taxonomic importance since the distribution of the bistratose

FIGURE 4. SEM micrographs of leaf apices. — 1–2. Codriophorus acicularis. 3. C. mollis. 4. C. ryszardii. 5. C. fascicularis. 6. C. anomodontoides. 7. C. laevigatus. 8. C. varius, plant with piliferous leaf apex. 9. C. varius, plant with muticous leaf apex. — [1 from Schofield et al. 101402, ALTA; 2 from Landals & Scotter 830, ALTA; 3 from Schofield et al. 101537, ALTA; 4 from Schofield & Vaarama 23970, DUKE; 5 from Lisowski 59922, KRAM; 6 from Musci japonici 1245, KRAM; 7 from Roivainen 1989, KRAM; 8 from Henderson 17040, KRAM; 9 from Lyford 200, KRAM].



FIGURE 6. SEM micrographs of transverse sections of the laminal cells in *Codriophorus acicularis.* — 1–2. Transverse section of the costa in the lower part showing its position at the bottom of a shallow groove. 3–4. Transverse section of the leaf lamina showing the cell papillosity. The depressions over the lumen centres are arrowed — [All from *Sérgio & Séneca 8769*, LISU].

patches and spots is irregular and random in these species. The laminal cells are transparent in all species other than *C. carinatus* in which they are distinctly opaque.

The cells are, in general, thick- and sinuose-walled in the upper and median parts, whereas the basal cells have nodulose and porose longitudinal walls. Their length and width vary greatly, even in different modifications of the same species, and the size of the cells has slight taxonomic importance and can only be taken into account when other characteristics have been used to define the species. However, features of the structure of the cells, namely the sinuosity, porosity and to some extent the papillosity and thickness of the walls in different parts of the leaf are of more value.

There are two different patterns of leaf areolation in *Codriophorus* (Fig. 7). In species of sect. *Codriophorus* (Figs 7.1–4) and in *C. brevisetus* the upper cells are predominantly isodiametric – subquadrate, rounded-quadrate, rounded-hexagonal, oval to bluntly angular or transversely rectangular. They are mostly straight-walled, 5–15 µm long and are exceptionally intermixed with short-rectan-

gular cells to 20 µm. Only in C. dichelymoides are they somewhat longer, 15-25 µm. In contrast, all species of sect. Fascicularia (except C. brevisetus) have elongate, rectangular, long to linear-rectangular upper laminal cells, 20-50 µm long on average and in individual cases extending to 60 µm (C. anomodontoides and C. laevigatus) and 90 µm (C. corrugatus) (Figs 7.5-9). The cells gradually become elongate and distinctly sinuose-walled downwards (Figs 8-9) but in most species of sect. Codriophorus and C. brevisetus they tend to be only shortly rectangular in the median and lower parts of the lamina, just 10-25 or 30 µm long. Conversely, in species of sect. Fascicularia except for C. brevisetus, as well as in C. depressus and C. dichelymoides, the cells are long to linear-rectangular in mid-leaf and below, mostly 30-60 µm long. Unlike length, the width of the laminal cells is less variable and generally ranges from 5 to 10 µm.

The areolation in the basal part of the lamina is more or less similar in all species and is composed of long rectangular cells, mostly $30-60 \ \mu m \log n$, They have strongly incrassate, nodulose and porose longitudinal walls and the

FIGURE 7. SEM micrographs of upper laminal cells. — 1–2. Codriophorus acicularis. 3–4. C. mollis. 5–6. C. anomodontoides. 7–8. C. varius. 9. C. laevigatus. — [1 from Landals & Scotter 830, ALTA; 2 from Sérgio et al. 8296, LISU; 3–4 from Schofield et al. 101537, ALTA; 5–6 from Musci japonici 1245, KRAM; 7 from Schofield 22633, KRAM; 8 from Lyford 200, KRAM; 9 from Roivainen 1989, KRAM].





lowermost 2–4 rows of cells are intensively pigmented and form a yellow, orange- or golden-brown strip along the leaf insertion.

Cells that become gradually shorter towards the leaf apex but are otherwise predominantly elongate and distinctly sinuose throughout the lamina represent a plesiomorphous state, whereas isodiametric cells and not or only slightly sinuose in the upper part of the leaf in contrast with the elongate and sinuose cells in its broadest part, represent a derived state (Vitt 1984). A similar situation is observed in *Niphotrichum* (Frisvoll 1983a), *Bucklandiella* (Frisvoll 1988) and in *Schistidium* (Blom 1996).

The cells in the majority of *Codriophorus* species are distinctly papillose in a peculiar manner with large, flat papillae distributed on both the dorsal and ventral surfaces of the leaf over the longitudinal walls and major part of the lumina, leaving only a narrow slit in the middle (Fig. 6.3–4). Such a disposition of the papillae gives a regular, but unusual appearance to the transverse leaf sections which consist of distinct depressions over the centres of the cell cavities separated by large, elevated and uniform flat or rounded thickenings over the walls and lateral parts of the lumina. The papillae are either entirely smooth, as for example in C. fascicularis and C. ryszardii, or have distinct secondary papillulae on the surfaces of the primary papillae. These are distinctly visible in *C. acicularis*, C. aquaticus, C. aduncoides and are especially prominent in C. varius. These differences in the shape of the papillae among the various species of Codriophorus have already been noted by Lawton (1972) who described the papillae in C. acicularis as paired but it is an imprecise designation because in fact the papillae are flat with more or less distinct papillulae (Figs 7.2, 4, 8). This papilla shape is exceptional in mosses and is known elsewhere only in Racomitrium s. str. In C. depressus and C. dichelymoides, as well as very rarely in some plants of C. acicularis, the laminal cells are smooth or nearly so with very low papillae seen only on the young leaves. Also, in C. norrisii, the papillosity is weak and the papillae are represented by narrow cuticular ridges distributed only over the cell walls while the lumina are not covered by papillae. The papillae are present on the cells throughout the lamina except for the base where they are less distinct and possess characteristic transverse spiral thickenings (Fig. 9.6).

12. Alar cells

The alar cells are often well-differentiated from the coterminous basal cells. They are usually broader and larger than the adjacent cells, mostly quadrate to shortly rectangular with thick to strongly incrassate walls and form a flat or somewhat swollen, auriculate and shortly decurrent, hyaline to yellow, brown or yellow-, orange- to reddish-brown group. The alar cells are especially distinct in species of subsect. *Codriophorus*, namely *C. acicularis*, *C. aduncoides*, *C. mollis* and *C. norrisii*, as well as in *C. laevigatus* but because they are variously developed, even on a single plant, they have limited value as a diagnostic character. For example, in *C. depressus* they are either similar to the adjacent basal cells or markedly larger, $40-100 \mu m \log 10-18 \mu m$ wide, with strongly incrassate, porose and nodulose walls, forming convex, decurrent and dark brown or dark yellow auricles.

13. Supra-alar cells

The supra-alar or basal marginal cells are either not differentiated and similar to or markedly different from the coterminous laminal cells. The differentiated supraalar cells are subquadrate to rectangular, mostly with esinuose and thin to moderately thick walls and hyaline to yellowish-hyaline. Because these cells are generally transparent, they are sharply set off from the laminal cells and form a distinct marginal border which consists of from 5 to 27 cells. It is composed mostly of a single row of cells but in most species of subsect. *Fasciformes* it is accompanied by a second inner row which is generally much shorter and consists of up to ten cells.

As in other genera of the Racomitrioideae, including Bucklandiella and Niphotrichum, the differentiation of the basal marginal border is an important taxonomic characteristic in Codriophorus. It is entirely absent in species of subsect. Codriophorus and in C. ryszardii of subsect. Hydrophilus, and in other species of the type section it is either not or scarcely developed or very short and composed of 2-15 short, subquadrate, thicker-walled cells. On the other hand, it is always present in sect. Fascicularia and quite often the basal marginal border is of two rows of cells, especially in species of subsect. Fasciformes and subsect. Piliferi, and is usually very long, consisting of 5-25 elongate and thin-walled cells. Only rarely is it absent or scarcely and imperfectly developed on some leaves, but then it is usually missing from one side only.

14. Vegetative reproduction

No means of vegetative reproduction is known in the genus *Codriophorus*.

SPOROPHYTE GENERATION

Fully developed sporophytes are known in all species of *Codriophorus* except *C. laevigatus* in which no mature capsules have so far been discovered. In *C. dichelymoides* only a few mature and immature sporophytes have been detected in three specimens. Some species of the genus

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FIGURE 8. SEM micrographs of mid-leaf cells. — 1–4. Codriophorus acicularis. 5. C. mollis. 6–7. C. fascicularis. 8. C. varius. 9. C. laevigatus. — [1 from Sérgio et al. 8296, LISU; 2–4 from Schofield et al. 101402, ALTA; 5 from Schofield et al. 101537, ALTA; 6–7 from Lisowski 59922, KRAM; 8 from Schofield 22633, KRAM; 9 from Roivainen 1989, KRAM].



FIGURE 9. SEM micrographs of lower cells. — 1. Codriophorus acicularis. 2. C. mollis. 3. C. ryszardii. 4. C. anomodontoides. 5. C. varius. 6. C. fascicularis. — [1 from Sérgio et al. 8296, LISU; 2 from Schofield et al. 101537, ALTA; 3 from Schofield & Vaarama 23970, DUKE; 4 from Musci japonici 1245, KRAM; 5 from Schofield 22633, KRAM; 6 from Lisowski 59922, KRAM].

are generally very prolific and usually produce sporophytes in profusion and thus makes possible detailed characterisation of the sporophytes and determination of the variability of their most important features. *C. acicularis, C. norrisii, C. ryszardii, C. varius* and *C. brevisetus* produce sporophytes abundantly throughout their ranges, but others are less fecund, for example *C. anomodontoides, C. mollis, C. aquaticus* and *C. depressus. C. fascicularis* is very prolific in areas with a temperate climate but in the severe climate of the Arctic and in high mountains its fecundity is limited and it produces sporophytes only rarely. *C. corrugatus* is frequently found with sporophytes in Japan and Alaska, but is sterile in mainland Asia. Likewise, *C. carinatus* is known to be fertile only in Japan and Taiwan, whereas in mainland Asia it is sterile. The sporophyte does not seem to offer important differentiating characteristics which can be used in an internal classification of the genus, but at species level some sporophyte characters may be taxonomically useful.

15. Sexuality

All *Codriophorus* species are dioicous but, as stated above, it does not much affect the fecundity of most species. There is no morphological difference between male and female plants in this genus. Female gametangia are terminal on the tips of lateral branches, hence *Codriophorus*, as is the case with other segregates of the former genus *Racomitrium* which is a typical cladocarpous genus. Nonetheless, owing to the presence of subterminal innovations, the sporophytes often appear lateral because the innovation continues to grow in the same direction as the preceding shoot.

16. Perigonium

As with most mosses, these are bud-like and reach 1.0-2.2 mm. They are olive-brown or brown and the outermost perigonial bracts are similar to the vegetative leaves, but smaller. The inner bracts are strongly concave, broadly ovate to almost circular, shortly and broadly obtuse to rounded with a weak costa and lax laminal cells. Antheridia are numerous, to 25, claviform on a short stalk, light brown. The bryological literature consistently states that no paraphyses are present in the perigonia in Racomitrium s. lato, which includes Codriophorus. It is untrue and filiform, light, hyaline- or yellowish-brown paraphyses reaching half the length of the antheridia occur in all species of the genus. They have also been detected in other segregates of Racomitrium s. lato, namely in Bucklandiella macounii (Kindb.) Bednarek-Ochyra & Ochyra and Niphotrichum elongatum (Frisvoll) Bednarek-Ochyra & Ochyra.

17. Perichaetium

The perichaetial leaves are very diverse in *Codriophorus* and, as is the case with *Bucklandiella* (Frisvoll 1988), they are of some importance with regard to a natural classification of the genus. This is especially true of the innermost perichaetial leaves which are of particular importance in taxonomy at infrageneric level or in the circumscription of individual species, whereas the outermost ones are similar to the vegetative leaves and do not have any diagnostic value. Only in *C. dichelymoides* are the outermost leaves lanceolate, straight, somewhat plicate and gradually acuminate, with a distinct costa ceasing well below the apex, in contrast to the straight and nonplicate cauline leaves are oblong-lanceolate, rather abruptly narrowed to a long, filiform, mostly recurved acumen.

The innermost perichaetial leaves are distinctly modified in comparison to the vegetative leaves. They are strongly concave and convolute, sheathing the seta and show great variation in shape and areolation. In the type section the innermost bracts are predominantly oblongovate to lingulate, less often oblong-lanceolate, narrowly to broadly rounded-obtuse, acute to subacute and entire or indistinctly sinuose at the apex. They are mostly hyaline, yellowish-brown or yellowish-hyaline throughout owing to their lax and thin-walled areolation, but sometimes in Codriophorus acicularis they are chlorophyllous and thick-walled in the distal half, or more often possess only a small group of chlorophyllous cells at the extreme apex as in C. acicularis, C. mollis and C. ryszardii. In C. norrisii the chlorophyllous cells consistently occupy the upper third of the lamina and are bistratose in patches 1-3 cells wide at the margins. In C. dichelymoides the laminal cells are chlorophyllous throughout, with thickand sinuose-walled laminal cells and this character state strongly supports recognition of a separate monotypic subsection, subsect. *Andicola*.

In subsect. *Fasciformes* oblong or oblong-lanceolate bracts predominate, and ovate-lanceolate bracts, hyaline or yellowish-hyaline throughout, are less frequent. Only in *C. brevisetus* are a few extreme apical cells thicker-walled. In *C. varius* and *C. laevigatus* the innermost perichaetial leaves are strongly longitudinally plicate. In the former they are entirely hyaline throughout, bluntly serrate at the apex owing to projecting cell ends and much smaller than the vegetative leaves, only 2.2–2.5 mm long, and these features, along with other peculiar gametophyte and sporophyte characters, warrant recognition of the separate subsection, subsect. *Piliferi* to accommodate *C. varius*.

As stated above, the innermost perichaetial leaves are also plicate in *C. laevigatus* but in other respects they are unique in the genus, being oblong and abruptly constricted into a short filiform acumen, or truncate and notched at the apex and, more importantly, with chlorophyllous, thick- and sinuose-walled rectangular cells throughout the lamina that are only shortly rectangular to isodiametric at the margin in the distal portion. This shape and the structure of the innermost perichaetial leaves are unique in *Codriophorus* and make the phytogeographically highly isolated *C. laevigatus* also a species strongly separated taxonomically which is, accordingly, positioned in a separate subsection, subsect. *Chrysei* within sect. *Fascicularia*.

18. Seta

The setae are mostly single per perichaetium, although in most species two or three sporophytes can be found in a single perichaetium, and in Codriophorus anomodontoides the setae are quite often geminate. In the only known specimen of C. laevigatus with immature sporophytes the setae are predominantly geminate. In all species the setae are exserted, straight or somewhat flexuous, entirely smooth, lustrous, with very long, linear and thick-walled epidermal cells which are mostly slender but in C. mollis and C. dichelymoides are fairly stout. When young, the setae are yellowish above and orange to orange-brown below but with age they become mostly blackish-brown below, reddish-brown above or brown, brownish-black to dark red throughout. In species of the type section as well as in C. varius the setae are twisted clockwise throughout, and only in C. dichelymoides and in species of subsect. *Fasciformes* is the seta dextrorse with a single torsion to the left immediately below the urn. In C. laevigatus only young setae are known and these are twisted to the right.

The absolute length of the setae (excluding the vaginula) is variable within quite broad limits (Fig. 10), even within a single population, and ranges from 3 mm in *C. carinatus* and *C. fascicularis* to 15 mm in *C. acicularis* and 20 mm in *C. varius*, but in extreme cases they may be only 1.5 mm long in *C. brevisetus* and *C. mollis* and as long as 20 mm in *C. anomodontoides* and 22 mm in *C. varius*. Most species generally have short setae,



FIGURE 10. Variation in seta length within and between species. Thick bars show normal variation, thin bars show range of extreme values. For abbreviations see Fig. 3.

averaging less than 10 mm, and the shortest ones are recorded in *C. norrisii* (4.0–4.2 mm) and *C. brevisetus* (4–6 mm), whereas *C. varius* has the longest mature setae, 12–20 mm on average. The length 3–7 mm in *C. laevigatus* refers to young immature setae and their true length can be measured only when mature sporophytes are found in this species.

19. Vaginula

The most important feature of the vaginula is its epidermal cells which are rectangular to linear and have sinuose and porose walls. This is one of the diagnostic characters of the genus *Codriophorus* as well as other segregates of *Racomitrium* and is not found in any other genera of the Grimmiaceae. The vaginula is dark or less often light brown to reddish-brown and is generally 1-2 mm long.

20. Capsule

The capsules in all species are exserted, erect, straight and symmetric being often slightly curved, gibbous and asymmetric only in Codriophorus depressus. They are usually light or dark brown to olive-, reddish- or yellowish-brown, smooth or occasionally sulcate when dry and empty in C. varius and C. anomodontoides, dull to lustrous and mostly pachydermous. The urns are ovoid, obloid, ellipsoid, obloid-cylindrical to long cylindrical, markedly narrowed towards the mouth and gradually or rapidly tapering to the seta. However, there is considerable infraspecific variation in capsule shape and size and it is difficult to demonstrate differences in these characters among the species (Fig. 11). The largest capsules, 3-4 times as long as wide, are known in C. varius and they are 3.0-4.2 mm long and 0.8-1.0 mm wide. In most species the capsule only rarely reaches 3 mm (2.0–3.1 mm



FIGURE 11. Variation in capsule length within and between species. Thick bars show normal variation, thin bars show range of extreme values. For abbreviations see Fig. 3.

in *C. aquaticus*, 1.8–3.0 mm in *C. depressus* and 2.3–3.0 in *C. ryszardii*) and usually extends only to 2.3–2.8 mm (*C. acicularis*, *C. aduncoides*, *C. dichelymoides*, *C. fascicularis* and *C. anomodontoides*). The shortest capsules are known in *C. brevisetus* (1.2–1.5 mm) and *C. corrugatus* (1.5–2.0 mm). The width of the capsule is also variable but within much narrower limits, from 0.7 to 1.0 mm with the widest urns having been observed in *C. acicularis*, to 1.1 or rarely 1.3 mm.

21. Operculum

This is conical-rostrate with a long, straight or slanted beak and its length is strictly correlated with the length of the peristome teeth. Hence, the longest operculum occurs in *Codriophorus varius*, to 1.9 mm, in which the peristome teeth are up to 1.8 mm long. In other species the operculum is shorter and the shortest one, up to 1 mm, is found in *C. dichelymoides*, but actually only a few mature capsules have been seen in this species. The length and shape of the operculum have no taxonomic importance.

22. Annulus

It is well-developed in all species and usually tardily deciduous. It is composed of 1–4 rows of large, pellucid, vesiculose, light brown to orange- to reddish-brown cells with strongly incrassate walls (Figs 12.1–2).

23. Exothecial cells

These are variable both in size and shape. As a rule, they are elongate, oblong to long or linear-rectangular, but often mixed with isodiametric, subquadrate, roundedquadrate, oval and irregularly angular to hexagonal cells. In *Codriophorus varius, C. anomodontoides* and *C. aduncoides* they are disposed in fairly regular longitudinal rows.



FIGURE 12. SEM micrographs of peristomial details. — 1. Annulus of *Codriophorus acicularis*. 2. Lower part of the outer surface of the peristome teeth and annulus in *C. varius*. 3. Peristome teeth in *C. anomodontoides*. 4. Peristome teeth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. anomodontoides*. 6. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C. acicularis*. 5. Lower part of the outer surface of the peristome tooth in *C.*

In most species they are thick-walled but in *C. norrisii* and *C. brevisetus* they are thin- to firm-walled. The midurn exothecial cells become smaller, isodiametric, mostly rounded-quadrate, oblate to transversely rectangular, thick-walled, often dark to orange-brown in 3–6 tiers, forming a distinct pigmented strip at the capsule rim. The number of differentiated cells at the capsule mouth is not particularly constant within a single species and, in general, the exothecial cells have no taxonomic importance in *Codriophorus*, in contrast to, for example, *Schistidium* in which two distinct types are known to occur (Blom 1996). The exothecium of *Codriophorus* species has a firm appearance and does not change much on drying after dehiscence, making the urn pachydermous in texture.

24. Stomata

The number of stomata varies considerably in *Codriophorus* species from six to 40. Stomata occur at the base of the urn in the area below the spore sac in most spe-





FIGURE 14. Variation in peristome length within and between species. Thick bars show normal variation, thin bars show range of extreme values. For abbreviations see Fig. 3.

cies and are arranged in 2–4 concentric rows. They are of phaneroporous type and most probably functionless, bicellular, brown to reddish-brown, rounded, with rounded or oval pori and are mostly variously oriented.

25. Peristome

The peristome in *Codriophorus* is haplolepideous and consists of 16 lanceolate teeth that are yellow, yellow-, orange- to reddish-brown or orange-reddish. In most species the teeth are deeply split nearly to the base into two regular or three irregular, terete, filiform, often fragile, free or coherent, more or less distinctly articulated branches (Figs 12.3, 13.4), sometimes only with a narrow longitudinal slit or perforations in the basal part (Fig. 13.8-9). In C. acicularis, C. norrisii and C. dichelymoides the teeth are bifid or tripartite down to the middle or for two thirds of their length (Figs 12.4, 13.1–2) and in C. aquaticus the teeth are split from the middle to the base. The teeth are generally densely covered throughout on both surfaces with spiculate or peg-like papillae (Figs 12.2, 5-6; 13.1-3, 5-7, 9) though occasionally in C. varius they are faintly papillose to nearly smooth. The teeth arise from a short to a fairly high basal membrane, 15-82 µm tall and have a distinct, fragile, hyaline preperistome which is usually as high as the basal membrane.

The length of the teeth varies considerably within and among the species of *Codriophorus* (Fig. 14). The longest are found in *C. varius* and they range from 1000 to 1800 μ m, whereas the shortest are present in *C. cari*-

natus and range from 300 to 350 μ m. The teeth are generally short in sect. *Codriophorus* and only rarely exceed 500 μ m as in *C. ryszardii* in which they are 500–650 μ m tall. In contrast, the teeth are fairly long in subsect. *Fasciformes*, ranging from 550 to 760 μ m and only in *C. brevisetus* they are 350–450 μ m tall. In *C. laevigatus* peristome teeth are unknown.

According to Cao & Vitt (1986) the entire and long peristome teeth represent a plesiomorphous state, whereas short and narrowly triangular teeth are considered to be derived.

26. Spores

The spores are globose to ellipsoid, light brown, finely papillose or nearly smooth and are $10-20 \ \mu m$ in diameter (Fig. 15.1–3).

27. Calyptra

This is conic-mitrate, naked and distinctly papillose at the apex (Figs 15.4–6) and the papillosity of the calyptra is one of the most important generic characters for *Codriophorus* and is unknown in any other segregate of *Racomitrium*. The calyptra is irregularly split at the base into 4-5 lobes and sometimes one slit is deeper, giving the calyptra a cucullate appearance. It covers only the beak and a small portion of the operculum. In cross-section, the calyptra is 3-5(-6)-stratose and composed of strongly incrassate and flattened cells.

FIGURE 13. SEM micrographs of peristomial details. — 1–2. Peristome teeth of *Codriophorus acicularis*. 3. Inner surface of the peristome tooth in *C. acicularis*. 4. Peristome teeth in *C. varius*. 5. Upper parts of the peristome teeth in *C. varius*. 6. Lower part of the outer surface of the peristome teeth in *C. varius*. 7. Lower part of the outer surface of the peristome teeth in *C. anomodontoides*. 8. Peristome teeth in *C. ryszardii*. 9. Ornamentation of the outer surface of the peristome teeth in *C. ryszardii*. — [1, 3 from *Allen* 27, COLO; 2 from *Sérgio et al.* 8296, LISU; 4–6 from *Schofield* 22633, KRAM; 7 from *Musci japonici* 1245, KRAM; 8–9 from *Schofield & Vaarama* 23970, DUKE].



FIGURE 15. SEM micrographs of the spores (1–3) and calyptrae (4–6) in *Codriophorus acicularis* (1), *C. varius* (2, 5–6) and *C. anomodontoides* (3–4). — [1 from *Sérgio et al.* 8296, LISU; 2 from *Schofield* 22633, KRAM; 3–4 from *Musci japonici* 1245, KRAM; 5–6 from *Lyford* 200, KRAM].

CYTOLOGY

The genus *Racomitrium s. lato* is poorly known cytologically and so far only 44 chromosomal records for 13 species and two varieties are available (Fritsch 1991). Five species currently positioned in *Codriophorus* have been studied chromosomally. These are: (1) *C. acicularis* for which in North America n = 12 was found (Ireland 1965, 1967) and in Europe n = 13 Smith & Newton 1967); (2) *C. aquaticus* for which n = 12 was found twice in material from the British Isles (Smith & Newton 1967; Ramsay 1969); (3) *C. depressus* with n = 14 in material from California (Steere 1954; Steere *et al.* 1954); (4) *C. fascicularis* has been studied three times chromosomally and the haploid chromosome number n = 13 was consistently obtained in material from Finland (Vaarama 1949) and the British Isles (Smith & Newton 1967; Newton 1971); (5) *C. varius* was studied three times cytologically and two different chromosome numbers have been found, n = 12 from Washington (Ireland 1965, 1967) and n = 13 from Canada (Ramsay & Schofield 1981).

In general, three chromosome numbers have hitherto been reported for *Codriophorus*: n = 12, n = 13 and n = 14, of which the first two evidently predominate. A similar cytological situation exists in other segregates of the genus *Racomitrium*. Astonishingly, species of *Codriophorus* and other segregates of *Racomitrium* show low levels of aneuploidy and polyploidy in comparison with, for instance, Pottiaceae species, which belong to a family generally considered to consist of mosses of a "harsh environment".
Chapter 5

PHYTOGEOGRAPHY AND ECOLOGY

DISTRIBUTION AND GEOGRAPHICAL ELEMENTS

GENERAL REMARKS

Codriophorus is essentially a Northern Hemisphere, or more precisely, a Holarctic genus (Figs 16-19). Of the fifteen species which are currently placed in it, only one (C. laevigatus) occurs in southern South America and on some islands of the South Atlantic. Moreover, of the fourteen Northern Hemisphere species, only one (C. dichelymoides) occurs beyond the Holarctic in northernmost South America. The remaining thirteen species are strictly Holarctic in distribution, although four of them occasionally penetrate beyond the Tropic of Cancer and are found at remote outposts at high elevations in tropical mountains, a situation typical of many Holarctic bryophyte species (Grolle 1969; Delgadillo 1971; Shaw 1982; Schuster 1983; Gradstein et al. 1983; Steere 1985; Menzel 1986; Gradstein & Váňa 1987; Menzel & Schultze-Motel 1987) and lichens (Hertel 1971). These four are C. mollis which has occasionally been recorded in the North Andes of Colombia (Fig. 40), C. carinatus which very slightly crosses the Tropic of Cancer on Taiwan (Fig. 63), C. fascicularis which has only once been found in the South Pacific in Oceania (Fig. 77) and C. anomodontoides which is known from a few records in the Philippines and the Hawaiian Islands (Fig. 89).

In the Northern Hemisphere *Codriophorus* species have greatest diversity in montane temperate areas which are affected by an oceanic climate, whereas in continental climate areas their occurrence is markedly reduced. Also, they only rarely extend into the Arctic and actually only *C. acicularis*, *C. fascicularis* and *C. corrugatus* have been found beyond the Arctic Circle, the first in Europe (Fig. 30), the second in Europe and Asia (Fig. 77) and the third in Asia (Fig. 95). Of these, *C. fascicularis* reaches its extreme northernmost occurrence at about 81° N on Spitsbergen, while *C. acicularis* extends as far south as roughly 28° N in the Canary Islands.

Only two species have a very wide, though strongly dissected and highly disjunct, pan-Holarctic distribution, namely *Codriophorus fascicularis* and *C. acicularis*. The latter is predominantly a Euro-North American species, with only a single known record in the Far East in Asia

and occasional stations in North Africa (Fig. 29). The remaining species have much narrower geographical ranges and their distributions are restricted to a single continent, except for *C. corrugatus* (Fig. 95) and *C. mollis* (Fig. 40) which occur in East Asia and western North America (the latter also in South America) and *C. laevigatus* (Fig. 101) which is known from the oceanic islands in the South Atlantic Ocean close to the western coast of South Africa.

North America has the highest diversity of Codriophorus species. Nine are known to occur there, two of which, C. acicularis (Fig. 31) and C. fascicularis (Fig. 79), are distributed bicentrically in its Atlantic and Pacific parts with no intermediate occurrences in the central part of North America. Of the remaining seven species, only one, C. aduncoides (Fig. 35), is endemic to eastern North America, whereas the other six are confined to the coastal areas of western North America. Four of these, C. norrisii (Fig. 44), C. ryszardii (Fig. 58), C. depressus (Fig. 67) and C. varius (Fig. 106) are endemics, while C. mollis (Fig. 40) and C. corrugatus (Fig. 95) are East Asian -North American disjuncts. In Greenland only one species is known to occur, C. fascicularis (Fig. 79), which extends to roughly latitude 70° N on Disko Island in West Greenland.

Asia is the second most *Codriophorus* rich continent and seven species are known to occur there, two of which, *Codriophorus carinatus* (Fig. 63) and *C. brevisetus* (Fig. 84), are strict endemics and *C. anomodontoides* (Fig. 89) occasionally extends to Oceania. *C. mollis* (Fig. 40) and *C. corrugatus* (Fig. 95) have East Asian – North American distributions, and the other two species, *C. acicularis* (Fig. 29) and *C. fascicularis* (Fig. 77) are pan-Holarctic disjuncts.

Europe has only three species, namely the most widespread species of the genus, *Codriophorus acicularis* (Fig. 30) and *C. fascicularis* (Fig. 78), and the subendemic *C. aquaticus* (Figs 53–54) which just extends to Macaronesia. In continental Africa only one species is known (*C. acicularis*) on its northernmost fringes, but on its offshore islands in the Atlantic Ocean three additional species have been recorded, namely *C. fascicularis* and *C. aquaticus* in Macaronesia and *C. laevigatus* (Fig. 101) on Tristan da Cunha and Gough Island.

South America contains three species, namely one narrow endemic of the Northern Andes of Colombia,



FIGURE 16. Global distribution of Codriophorus.

Codriophorus dichelymoides (Fig. 71), one Afro-South American disjunct, *C. laevigatus* (Fig. 101) and one Holarctic species, *C. mollis* (Fig. 40), occurring at an altimontane outpost in the Northern Andes of Colombia. Finally, two species occur very rarely in Oceania. These are the East Asian endemic *C. anomodontoides* (Fig. 89) extending to the Hawaiian Islands and the pan-Holarctic *C. fascicularis* (Fig. 77), once recorded on Tahiti in the Society Islands in the South Pacific.

Codriophorus species exhibit a very broad altitudinal range, extending from sea level to the subalpine or alpine zones in mountains, but for the most widespread species the altitudinal maxima vary markedly on different conti-



FIGURE 17. Regions of known occurrence of the species of *Codriophorus*. Divisions of the regions according to Wijk *et al.* (1959), modified by Düll (1984).

nents, depending on local conditions and distribution of the vegetational zones. In Europe *C. acicularis* occurs at sea level in the northernmost part of its range but in the south of the continent it is restricted to the mountains and reaches its highest elevation of 2870 m in the Swiss Alps. Likewise, in North America it occurs at sea level in the eastern and western coastal regions but ascends as high as 3292 m in the Rocky Mountains of Colorado. No distributional data are available for the only Asian record of the species in Japan, but certainly it is much lower than 1500 m, judging from the topography of this part of Kyushu.

Other species with a wide geographical range possess a similar altitudinal distribution pattern. The highest recorded stations of Codriophorus acicularis are 2663 m in the Tatras of Slovakia (Europe), 4100 m in the Rocky Mountains of Colorado (North America) and 3000 m on Mt Ontake in Honshu in Japan (Asia). The elevation on Tahiti is unknown but the highest mountain on this island has an elevation of 2237 m. C. corrugatus occurs at 300 m in Kamchatka, 2300 m in Southern Siberia, 350-2300 m in Japan and 3040-3400 m in China. C. carinatus is distributed at heights ranging from 100-1700 m in Japan and China and at 2100-2500 m in Taiwan beyond the Tropic of Cancer. C. laevigatus occurs from sea level to 215 m on Subantarctic South Georgia, then reaches 1200 m in Tierra del Fuego while on Tristan da Cunha it occurs only at high elevations from 600 to 2000 m. C. anomodontoides has a wide altitudinal range but this is not correlated with latitudes and in Japan it occurs from 0–3100 m, China 700-2700 m, Taiwan 500-3090, the Philippines 1160-2800 m, whereas in the Hawaiian Islands it is found at lower elevations of 245-1065 m.



FIGURE 18. Number of species of Codriophorus in the geographical areas proposed by Wijk et al, (1959) and modified by Düll (1984).

Species with narrower geographical ranges also have wide altitudinal ranges, usually extending usually from sea level to the subalpine or alpine zones. Thus, *Codriophorus aquaticus* reaches its highest elevation of 2600 m in Europe and *C. ryszardii* and *C. varius* have the highest recorded stations at 2130 m and 1700 m respectively. However, others are typically montane species, growing exclusively at higher elevations, although it is necessary to state that for many records no altitudinal data are available. Nonetheless, *C. brevisetus* has been found at 400–2600 m in Japan, *C. aduncoides* at 300–2013 m in eastern North America, and *C. norrisii* and *C. depressus* at



FIGURE 19. Number of species of *Codriophorus* in different continents (nominator) and number of endemic species in each region (denominator). Last number indicates percentage of endemic species.

505–1585 m and 1325–2760 m, respectively, in western North America.

The highest known records for *Codriophorus* species are those for *C. dichelymoides* which is a truly altimontane moss, occurring at elevations from 2800 to 4520 m in the Northern Andes of Colombia. *C. mollis* was discovered in the same region at 4100 m, whereas in the Northern Hemisphere it occurs at 450–1300 m in Japan and from sea level to 2000 m in North America.

GEOGRAPHICAL ELEMENTS

Codriophorus is a rather small genus which consists of only 15 species. They can be grouped so as to form several distinct distribution patterns which are in accord with well-established and precisely defined biogeographical elements. The distribution of each species of the genus was fairly accurately determined by dint of examination of a large number of specimens from every possible geographical region. Unlike Racomitrium and Niphotrichum, Codriophorus species are distributed in the temperate regions of both hemispheres, although in the austral region the genus is exceedingly rare and represented by just a single species, C. laevigatus. It only very slightly penetrates into the Arctic where only C. fascicularis is occasionally found in some areas, but it does not constitute a prominent component of the tundra vegetation. In this respect the genus concurs with Bucklandiella which exhibits a similar general distribution, although this genus is well-represented also in the temperate and polar regions of the Southern Hemisphere as well as montane areas in the tropics. Interestingly, Codriophorus does not contain of any bipolar species.

1. Pan-Holarctic Temperate

Two species: *Codriophorus acicularis* and *C. fascicularis*. Both are boreal-montane species which have strongly dissected and highly disjunct ranges in the Holarctic and exhibit a strong preference for an oceanic climate. They, especially *C. fascicularis*, penetrate into the Arctic only occasionally. The latter species is also found at a remote station in the tropics in the Society Islands in the South Pacific. The maximum occurrence of both species is in western and northern Europe and on the Atlantic and Pacific coasts of North America, whereas in East Asia they are exceedingly rare (*C. acicularis*) or infrequent and occasional (*C. fascicularis*). Additionally, *C. acicularis* extends to North Africa in the Mediterranean region.

2. Circum-North-Pacific

Two species: *Codriophorus mollis* and *C. corrugatus*. This element consists of species which have a more or less continuous range from East Asia across the Aleutian arc to north-western North America (Schofield 1965, 1969, 1972). *C. mollis* extends from Hokkaido and northern Honshu in Japan through to the southern tip of Kamchatka and the Aleutian Islands and from British Columbia to

California in western North America, with a highly isolated disjunct station in the Northern Andes of Colombia. *C. corrugatus* is widely distributed in Japan and in mainland Asia in China, Southern Siberia to Yakutia in the Arctic through the southernmost part of Kamchatka to southern Alaska.

3. East Asian-Pacific

One species: *Codriophorus anomodontoides*. It is essentially an East Asian temperate species which is widely distributed in Japan (except Hokkaido), Korea and southeast, south central and north central China and extends beyond the Tropic of Cancer in Taiwan, Hainan and the Philippines, appearing at highly disjunct stations in the Hawaiian Islands.

4. European-Macaronesian

One species: *Codriophorus aquaticus*. This element may be also designated a European (sub)endemic since *C. aquaticus* is mainly distributed in north-western, western and central Europe and only sporadically is it found in the Canary Islands and Madeira in Macaronesia. This type of distribution is exhibited by a number of moss species which are commonly designated European endemics, for example *Glyphomitrium daviesii* (Dicks.) Brid., *Neckera crispa* Hedw., *N. pumila* Hedw. and *Cirriphyllum crassinervium* (Taylor) Loeske & M.Fleisch.

5. Amphiatlantic South-Temperate

One species: Codriophorus laevigatus. This element comprises species which are distributed mainly in the temperate regions of southern South America and South Africa, including Tristan da Cunha and Gough Island in the South Atlantic, and extend to the Subantarctic islands in the South Indian Ocean (Engel 1978, 1990; Ochyra 1998; Ochyra et al. 1998; Bednarek-Ochyra et al. 2000). It is represented by a single Codriophorus species, C. laevigatus, which is admittedly quite widespread and locally common on Subantarctic South Georgia, but its northward occurrences are not restricted to higher elevations, especially in Tierra del Fuego and western Patagonia, where it occurs from sea level to 1200 m and 900 m respectively. However, on the Juan Fernandez Islands and Tristan da Cunha it is a truly montane species, occurring at 1100-1350 m and 600-2000 m respectively.

6. Endemics

Western North American — Four species: Codriophorus norrisii, C. ryszardii, C. depressus and C. varius. The occurrence of four endemic species in western North America makes this area the most prominent centre of diversity of the genus. It well corresponds with the high level of moss endemism of Pacific North America where approximately 90 endemic moss species are known to occur (Schofield 1980; Schuster 1983). Of the four Codriophorus endemics, C. depressus has the narrowest range, being restricted to California and the border area of adjacent Nevada. Likewise, C. norrisii has its main centre of occurrence in California with additional stations in Idaho. The other two species have broader ranges. C. ryszardii extends from southern Alaska to northern Oregon and C. varius ranges from the Queen Charlotte Islands in British Columbia to central California. The great number of endemic species of Codriophorus well corresponds with a similar high level of endemism in Bucklandiella (6 species) and Niphotrichum (2 species) in this region.

Eastern North American — One species: *Codriophorus aduncoides*. The Atlantic part of North America has a similar level of moss endemism to the Pacific part (Schofield 1980). According to Crum (1972) the greatest number of these endemics are most likely survivors of the Arctotertiary flora. Frisvoll (1988) detected one endemic species in *Bucklandiella* in eastern North America.

East Asian — Two species: *Codriophorus carinatus* and *C. brevisetus*. East Asia, especially Japan, is a remarkable centre of moss endemism, both at generic and specific levels (Schuster 1983). These two species, along with the subendemic *C. anomodontoides*, contribute to the general pool of moss endemics in this region. It is worth noting that a similar number of endemic species is known in the related genera *Bucklandiella* (3 species) and *Niphotrichum* (2 species).

North Andean — One species: Codriophorus dichelymoides. The Andean region is a remarkable centre of moss endemism and, for example, about 12% of the mosses recorded in Peru have not been found elsewhere (Menzel & Schultze-Motel 1987). Unfortunately, many of these are known only from the type specimen(s) which have never been taxonomically assessed and therefore this great number of "endemics" reflects a rather artificial taxonomy (Touw 1974; Greene 1976; Schultze-Motel 1982) which probably exaggerates the number of species which truly exist. Nonetheless, C. dichelymoides is a very distinct and quite taxonomically isolated species which has no close relatives, either in the Andean region or elsewhere. Bucklandiella cucullatifolia (Hampe) Bednarek-Ochyra & Ochyra, a North Andean endemic species from Colombia, has nothing to do with C. dichelymoides and it is closely related to or conspecific with the pantropical Bucklandiella subsecunda (Hook. & Grev.) Bednarek-Ochyra & Ochyra.

GENERAL ECOLOGY

The importance of habitat in defining any group of plant species is not to be underestimated and often it may be considered to have a value equivalent to many structural features. In general, *Codriophorus* species are almost always associated with aquatic, terrestrial-aquatic or otherwise wet sites where they form more or less loose tufts or extensive mats and patches but they can tolerate periodic desiccation. All species are saxicoles growing predominantly on acidic rocks, especially granite, gneiss, basalt, diorite, serpentine and sandstone, but some species, for example C. mollis, C. varius, C. corrugatus and C. acicularis, thrive occasionally on base-rich limestone rocks. C. aquaticus has been found in Sweden on quartziferous cliffs with calcareous intrusions, and in the Polish Carpathians it often grows on sandstone rocks which are generally enriched with lime (Stebel & Bednarek-Ochyra 2004). Most species grow also on soil and humus covering moist rock outcrops and ledges, on alluvial, gravelly, clayey or sandy soil on stream banks or in late snow patches in the mountains and on pockets of soil in temporarily dried up river beds. C. laevigatus is usually associated on South Georgia with Chorisodontium aciphyllum-Polytrichum strictum peat banks and also grows on scree and in seepage areas in Festuca erecta grassland and Rostkovia magellanica marshes.

The most usual habitats for the majority of *Codriophorus* species are dripping or periodically water-splashed cliffs and rocks, boulders, slabs and blocks in stream beds or close to brooks and rivers as well as in seasonal creeks and streamlets and on lake shores that are periodically wave swept or submerged. Quite often they grow attached to boulders that are subject to temporary inundation or entirely submerged in fast-moving water in rapids and in waterfalls as typical rheophytic mosses. They are usually found in shady, diffusely lit or, less often, open habitats, mostly in forest and woodland.

While all species of Codriophorus occur in wet habitats, there are differences in the niches occupied by individual species. For example, C. depressus is distributed along intermittent streamlets, rivulets, and slopes of otherwise bare rocks where the plants are wetted during snow melt, whereas C. acicularis and C. norrisii occur in perennial aquatic systems generally along streams and rivers where they are seasonally submerged on rocks and boulders. Consequently, plants of C. depressus have a prostrate growth-form across the substrate and can form mats that may extend for metres over rock slabs and rock terraces, whereas the last two species are mostly erect- or curved-ascending plants. C. aquaticus does not grow in permanently submerged or inundated sites and is usually associated with sheltered, steeply sloping or vertical rocks that are moistened or flushed, at least seasonally, on cliff faces in damp places, mostly in forest and woodland but also in open, treeless areas and on wet soil in areas of late snow lie.

Species of *Codriophorus* usually form pure stands and only occasionally grow associated with other moss or liverwort species. The great similarity in autecology of most species would suggest the existence of a great number of mixed stands, but actually these are uncommon and, for example, only occasionally has *C. acicularis* been found to grow mixed with *C. aduncoides* and *C. varius*.

Codriophorus acicularis is a frequent component of bryophyte-dominated communities that are classified into the class *Platyhypnidio-Fontinaletea antipyreticae* and the order *Brachythecietalia plumosi*, and *C. acicularis* itself is considered a characteristic species of the alliance *Racomitrion acicularis* to which belong several moss associations that develop in montane streams and brooks on non-calcareous rocks, such as *Brachythecietum plumosi*, *Scapanietum undulatae*, *Hygrohypnetum ochraceae* and *Fontinaletum squamosae* (Hübschmann 1986) belong.

In contrast, *Codriophorus aquaticus* and *C. fascicularis* are considered by phytosociologists to be characteristic species of the class *Grimmio-Racomitrietea* heterostichi, the order Racomitrietalia heterostichi and the alliance Grimmion hartmanii (Hübschmann 1986; Marstaller 1993). The former is a relatively frequent constituent of such associations as Diplophylletum albicantis, Racomitrio-Andreaetum rupestris, Andreaeetum nivalis and Diplophyllo-Scapanietum nemorosae, whereas the latter is a component of Hedwigietum ciliatae and Gymnomitrietum concinnati as well as Trifido-Distichetum salicetosum herbaceae and Cynodontio-Paraleucobryetum longifolii.

Chapter 6

TAXONOMY

SYSTEMATIC POSITION OF THE GENUS CODRIOPHORUS

Apart from the first twenty years of the 19th century, species which are currently placed in Codriophorus have been firmly associated with *Racomitrium*. This genus was established by Bridel (1819) to accommodate 17 species. Its diagnostic characters were calyptrae that frayed at the base into several lobes and peristome teeth that were deeply divided nearly to the base into two or three, or sometimes even four, filiform branches. The genus was divided into two informal groups, the first of which contained 14 species with leaves straight on drying and the second with the remaining three with leaves crisped when dry. From the point of view of modern moss taxonomy, Racomitrium in its original circumscription was a heterogeneous taxon which, apart from 12 species which have been residual in it until the present day, contained also three species currently positioned in Cinclidotus P.Beauv. and two within Ptychomitrium Fürnr.

This concept was adopted by Bridel (1826-1827), with only slight modification, in his main work, Bryologia universa, which crowned his many years' studies on mosses. He only added two new species to the first group, namely Racomitrium borbonicum Brid. from Réunion in the Indian Ocean and R. cataractarum Brid. from Germany. Additionally he excluded from the group R. fontinaloides which was transferred to Cinclidotus. The number of species in the second group remained unchanged, although one, R. falcifolium Brid., was reduced to varietal rank within R. polyphyllum (Sw.) Brid., but this loss was compensated for by the newly described R. lingulatum Brid. from France. It is worth noting that two other species, which later became firmly rooted in Racomitrium, R. ellipticum (Turner) Bruch. & Schimp. and R. sudeticum (Funck) Bruch & Schimp., were placed by Bridel (1826–1827) in the genus Dryptodon Brid.

As with many taxonomic novelties, the genus *Racomitrium* did not initially gain wide acceptance among bryologists, who followed the traditional concept of placing its species in *Trichostomum* and *Dicranum* (Hooker & Taylor 1827; Schultz 1828; Wallroth 1831; Hooker 1833). It received just a mention in the synopsis of genera in *Bryologia germanica* (Nees *et al.* 1823) but without description or list of species. Duby (1830) reduced *Racomitrium* to sec-

tional rank within Trichostomum and placed eight species in this section, all of which, except T. polyphyllum (Sw.) Turner, represented Racomitrium in its modern interpretation. Then, Racomitrium was accepted by Hübener (1833) in his Muscologia germanica but he changed somewhat the original concept of the genus and subdivided it into two groups. The group Rectiseti comprised ten species which all belonged within the group with straight leaves sensu Bridel (1819), while the second group Curviseti consisted of three species, R. patens (Hedw.) Hübener, R. incurvum (Hoppe & Hornsch.) Hübener and R. funale (Schwägr.) Hübener which had been considered members of the genus Dryptodon by Bridel (1826-1827). Racomitrium was subsequently accepted in its original species composition by the Italian bryologists Garovaglio (1837, 1840*a*, *b*) and De Notaris (1838).

The turning-point in Racomitrium history was its treatment in Bryologia europaea (Bruch et al. 1845) which was to be long considered the oracle as far as taxonomy and nomenclature of European mosses were concerned. The authors of this fundamental moss Flora introduced a refinement of the concept of *Racomitrium* which has survived until the present day. Nine species were placed in the genus which was divided into two subgenera: (a) subg. Dryptodon (Brid.) Bruch & Schimp. which contained four species, namely R. ellipticum, R. aciculare (Hedw.) Brid., R. protensum and R. sudeticum and (b) subg. Racomitrium with five species, R. fasciculare (Hedw.) Brid., R. heterostichum (Hedw.) Brid., R. microcarpon (Hedw.) Brid., R. lanuginosum (Hedw.) Brid. and R. canescens (Hedw.) Brid. This concept of Racomitrium was subsequently consolidated by Schimper (1856) in his Corollarium Bryologiae europeae and in both editions of Synopsis muscorum europaeorum (Schimper 1860, 1876). In the last work one more species was added to the genus, R. patens, which nevertheless was placed in the separate subgenus Campylodryptodon Schimp.

The concept of *Racomitrium* outlined in *Bryologia europaea* gained broad acceptance and was widely used in Floras, taxonomic treatments and floristic papers (e.g., Sullivant 1856; Zetterstedt 1861; Chałubiński 1882, 1886; Husnot 1884–1890; Limpricht 1890; Kindberg 1898; Brotherus 1902). Since the early 1850s, when intensive exploration yielded rich moss collections from exotic regions, many new species were added to the genus (e.g., Dozy & Molkenboer 1847; Zollinger 1855; De Notaris 1859; Hampe 1863; Lorentz 1864*a*; Bescherelle 1880, 1894). Interestingly, *Racomitrium* was largely ignored by two outstanding bryologists of the nineteenth century, namely Karl Müller of Halle (1818–1899) who described more than a dozen exotic species, but under *Grimmia*, and only once used the generic name *Racomitrium* in his work on species of the *R. lanuginosum* complex, describing three new species and proposing one new combination (Müller 1869). Likewise, William Mitten (1819–1906) only once used the name *Racomitrium* for the New Zealand *R. ptychophyllum* (Mitt.) Mitt. (Mitten 1867) which, however, was originally described by this author as *Grimmia ptychophylla* Mitt. (in Lindsay 1866).

Strong adherents of the genus *Racomitrium* were the compilers of the two most important bryological compendia of the 19th century, A. Jaeger and E. G. Paris, who in their major works, *Adumbratio florae muscorum to-tius orbis terrarum* (Jaeger 1874) and *Index bryologicus* (Paris 1894–1898), transferred to *Racomitrium* many species originally described in other genera, mostly *Grimmia*. Since the treatments of *Racomitrium* in the Musci in both editions of *Die Natürlichen Pflanzenfamilien* (Brotherus 1902, 1924*a*) the genus has been universally used and the aptness of its recognition has not been questioned.

When proposing a refined concept of *Racomitrium*, Bruch et al. (1845) placed this genus in the Grimmiaceae along with Grimmia and Schistidium but they could not show unequivocal features separating these genera. As basic characters distinguishing Racomitrium from Grimmia they indicated the irregular branching of the plants, strongly sinuose-walled laminal cells, more robust costa, elongate calyptra, long rostrate operculum and deeply cleft peristome teeth, usually nearly to the base. Of these, the peculiar leaf areolation and the deeply split peristome teeth are readily observable and have impressed themselves on the consciousness of bryologists as the fundamental generic characters of Racomitrium. However, the strongly sinuose-walled laminal cells are not exclusively restricted to this genus but occur throughout the Grimmiaceae and are especially frequent in Schistidium Bruch & Schimp., for example in S. urnulaceum (Müll. Hal.) B.G.Bell, S. praemorsum (Müll.Hal.) Herzog, S. cupulare (Müll.Hal.) Ochyra, S. amblyophyllum Ochyra & Hertel, S. frigidum H.H.Blom, and Dryptodon, in for instance D. trichophyllus (Grev.) Brid. D. leibergii (Paris) Ochyra & Żarnowiec and D. jacuticus (Ignatova, Bednarek-Ochyra, Afonina & J.Muñoz) Ochyra. Conversely, in many species of Racomitrium, for example R. macounii Kindb., R. sudeticum, R. aquaticum, R. aciculare and R. canescens, the upper cells are isodiametric with not or only slightly sinuose walls.

In a number of *Racomitrium* species, for example *R. sudeticum*, *R. heterostichum* and *R. macounii*, the peristome teeth are cleft into two or three prongs in the upper half only and sometimes they are only irregularly perforated. Moreover, deeply cleft peristome teeth are known also in other grimmialean genera and species, for instance in *Dryptodon patens* in which the teeth are divided in the upper two thirds into two branches. Nonetheless, the peristome of *Racomitrium* does differ from that in other grimmialean genera in some characters which have generally been overlooked but are otherwise important for its characterisation. The peristome teeth in *Grimmia, Schistidium* and other satellite genera are lanceolate, entire or perforate to variously split into two or three unequal, smooth or variously ornamented prongs, lack a basal membrane and have distinctly thicker and trabeculate dorsal side and thin ventral side (*Schistidium* type). In contrast, the peristome in *Racomitrium*, in its typical form, has linear teeth which are divided nearly to the base into two filiform, somewhat paired segments, usually arising from a low but distinct basal membrane. They are equally thickened and less prominently trabeculate on both dorsal and ventral sides. Moreover, the prostome is usually present (*Racomitrium* type).

Thus, *Racomitrium* really is a distinct genus which is diagnosed by the following set of characters: (*a*) thick- and sinuose-walled epidermal cells of the vaginula; (*b*) consistent lack of a central strand in the stem; (*c*) presence of a preperistome; (*d*) *Racomitrium*-type peristome. On the basis of this combination of characters *Racomitrium* has been placed in the separate subfamily Racomitrioideae within the Grimmiaceae (Ochyra *et al.* 2003).

Racomitrium has sometimes been associated with Ptychomitrium Fürnr. and Campylostelium Bruch & Schimp. and placed in the subfamily Ptychomitrioideae in the Grimmiaceae (Brotherus 1902; Churchill 1981). Despite their overall morphological similarity these genera seem to be only remotely related and most bryologists prefer to keep Racomitrium and its allied genera apart. Racomitrium species are characterised by their consistently sinuosenodulose leaf cell walls and smooth calyptrae, and the plants are cladocarpous. By contrast, in Ptychomitrium the leaf cells are straight or only weakly sinuose, the calyptrae deeply plicate and the plants acrocarpous. In addition, the preperistome is lacking, the peristome teeth lack trabeculae and have a characteristic air gap at the base of the teeth (Edwards 1979). Moreover, the plants are cryptoicous because the male branches are small and arise from the base of the vaginula within the ring of perichaetial leaves (Deguchi 1977).

It would seem appropriate here to explain the contradiction associated with the spelling of the generic name Racomitrium. Since the middle of the 19th century it has been a subject of major controversy and, to the present day, two versions may be found in the bryological literature. Many authors continually use the original spelling Racomitrium, proposed by Bridel (1819), but others use an orthographic variant of this name, *Rhacomitrium*, used for the first time by Lorentz (1864b). It is necessary to bear in mind that according to the current Code (Greuter et al. 2000) the original spelling of a generic name must be retained. However, at the same time, the Code suggests that the transliteration of names of Greek origin into Latin should follow the classic rules in which the spiritus asper is rendered by **h**, but this does not apply to names already in existence.

In such a situation, if the second variant of a spelling is to be used, the spelling *Rhacomitrium* should be presented for conservation against *Racomitrium*. Because this is a marginal question, it seems unwise to start a discussion on this spelling change, especially as there are other generic names which present the same problem, for instance *Racopilum* P.Beauv. versus *Rhacopilum* P.Beauv. *ex* Mitt. Moreover, it seems that nowadays the original spelling has gained wide acceptance and is almost exclusively used in the modern literature. It is worth noting, however, that there is a precedent in this matter and the orthographic variant of the generic name *Rhaphiolepis* Lindl. *ex* Poir. (Rosaceae) is conserved against the original spelling *Raphiolepis* Lindl. (Crundwell 1970).

In conclusion it is necessary to add that the generic name *Rhacomitrium* was proposed for conservation against *Trichostomum* and this proposal was discussed at the Fifth International Botanical Congress held in Cambridge in 1930 (Cardot 1930). The Committee for Nomenclature postponed its decision on this question and it proved in fact to be *ad Kalendas Grecas* because the matter has never been raised again. Some bryologists were unhappy about this decision and Dixon (1932) commented that "the matter should be settled at once, without waiting for the next International Congress".

In its traditional circumscription *Racomitrium* exhibits remarkable internal differences in the morphology of both gametophytes and sporophytes. This ostensible morphological diversification of the genus prompted several authors to propose an infrageneric classification. Hübener (1833) divided it into two groups ["Reihe"], *Rectiseti* and *Curviseti*. The former contained species which corresponded to the first unnamed group which had been recognised within the genus by Bridel (1826–1827) and which, with a few minor exceptions, was an equivalent of *Racomitrium* as presently conceived. The latter group comprised three species placed by Bridel (1826–1827) in his genus *Dryptodon*.

The next attempt at an infrageneric classification of *Racomitrium* was made by Bruch *et al.* (1845). As discussed above, these authors divided the genus into two subgenera on the basis of branching pattern and form of the peristome teeth. Subg. *Dryptodon* contained species with forked stems and peristome teeth divided merely to the middle into two or three segments, whereas subg. *Racomitrium* comprised species with subpinnately branched stems with short lateral branchlets and peristome teeth split to the base into two filiform prongs.

Kindberg (1898) presented an entirely different internal classification of *Racomitrium*, subdividing the genus into four groups, namely *Lanuginosa*, *Papillosa*, *Canescentia* and *Laevifolia*, but without assigning to them definite taxonomic rank. This classification was largely based upon the form of papillosity of the laminal cells and confirmed his exceptional intuition in matters concerning the natural relationships among mosses. At species level N. C. Kindberg was an unprecedented splitter and very many of his species have been "sunk". In contrast, a number of moss genera and families proposed by him are still accepted in modern moss taxonomy (Steere & Crum 1977). Unfortunately, his classification of *Racomitrium* was ignored

by Brotherus (1902, 1924*a*) in his fundamental treatments of the Musci in *Die Natürlichen Pflanzenfamilien* and consequently it fell into obscurity and became totally forgotten.

Vilhelm (1926) in his revision of the Czech and Slovak species of *Racomitrium* divided the genus into three subgenera: (*a*) subg. *Canescentia* with three species (*R. canescens*, *R. lanuginosum* and *R. fasciculare*); (*b*) subg. *Microcarpae* with four species (*R. sudeticum*, *R. heterostichum*, *R. alopecurum* Brid. and *R. microcarpon*); and (*c*) subg. *Cataractae* with two species (*R. protensum* and *R. aciculare*). This classification was largely based on growth-form, plant coloration, capsule shape and leaf apex and these characters carry no weight in any phylogenetic consideration of mosses.

Kindberg's (1898) forgotten classification of *Racomitrium* was resurrected by Noguchi (1974) who validated the unranked groups distinguished by him as sections: sect. *Racomitrium* (= *Canescentia* group), sect. *Lanuginosa* (Kindb.) Nog. (= *Lanuginosa* group), sect. *Papillosa* (Kindb.) Nog. (= *Papillosa* group) and sect. *Laevifolia* (Kindb.) Nog. (= *Laevifolia* group). Nomenclature of the infrageneric taxa of *Racomitrium* is heavily affected by typification of the generic name *Racomitrium*. Until the mid-1990s *R. canescens* was commonly accepted as lectotype and this lectotypification was made by Pfeiffer (1874). However, a much earlier and long overlooked lectotypification of *Racomitrium* had been made by Schimper (1860) who had designated *R. lanuginosum* as lectotype.

The internal classification of Racomitrium first suggested by Kindberg (1898) was further developed by Bednarek-Ochyra (1995). On the basis of peristome structure, form of the innermost perichaetial leaves and type of cell papillosity, the genus was subdivided into four subgenera: (a) subg. Racomitrium, (b) subg. Cataractarum Vilh., (c) subg. Niphotrichum Bednarek-Ochyra and (d) subg. Ellipticodryptodon (Vilh.) Bednarek-Ochyra & Ochyra. They corresponded well to the four unranked groups recognised within the genus by Kindberg (1898), namely Lanuginosa, Papillosa, Canescentia and Laevifolia respectively, which had subsequently been given the status of sections by Noguchi (1974). In addition, within each subgenus except for subg. Racomitrium, a number of sections and subsections were distinguished to accommodate almost all the known species then positioned in Racomitrium.

Subsequent revisionary studies of *Racomitrium* led to the conclusion that the genus in its generally accepted circumscription was a heterogeneous taxon and a convenient repository of many distantly related species groups which was given a cohesion by the characteristic areolation of the laminal cells and epidermal cells of the vaginula, the *Racomitrium* type of peristome and the consistent lack of a stem central strand. Accordingly, Bednarek-Ochyra & Ochyra (in Ochyra *et al.* 2003) split it into four genera, namely *Racomitrium s. str.*, *Codriophorus* P.Beauv., *Niphotrichum* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra and *Bucklandiella* Roiv. These were considered to be distinctive taxa through various combinations of unique or otherwise presumably advanced characteristics for the Grimmiaceae such as the presence of pellucid alar cells, variously papillose laminal cells, papillosity of seta and calyptra, torsion of seta, shape of peristome teeth, anatomy of costa, and shape of hair-point. These segregates of the former large and artificial genus *Racomitrium* are natural and well-established taxa which are easily distinguished from one another.

Splitting Racomitrium into four segregates may not be popular, especially amongst conservative bryologists who are firmly accustomed to the traditional concept of genera, but such division is a widely accepted practice and trend in modern bryology. Many large and artificial moss genera have been split into a number of segregates in recent decades, although initially these new concepts were heavily criticised, for example Koponen's (1968) division of Mnium Hedw. (Crum & Anderson 1981) and Zander's (1989, 1993) segregates of Tortula Hedw. (Blockeel 1994). However, these new or resurrected concepts gained wide acceptance with time because smaller genera were truly more natural and better defined taxa. These changes have also been imposed to some extent by the rule of comparability of higher taxa which is still small between the taxa at one rank in some families. Much has been written on the "generic concept" in various families and it has undergone remarkable evolution in muscology since the early days of this science (Steere 1947a). In fact it amounts to little more than personal judgement aimed at producing a workable classification. Most taxonomists look for discontinuities in variation which can be used to delimit orders, families or genera. Others make a more conscious attempt to use the criterion of equivalence or comparability, which, although highly subjective, is frequently useful within a group of relatively closely related taxa.

Nonetheless it is necessary to retain a "generic balance" in families and genera should be defined by characters of more or less equivalent weight. This balance seems to be highly disturbed in some moss families, especially the Grimmiaceae. The genus Coscinodon Spreng. is actually only a weak segregate of the broadly conceived Grimmia and is recognised only by its strongly plicate calyptra which usually covers the whole capsule or only up to the middle. Other character states which are considered to be diagnostic for this genus are widely variable elsewhere, in Grimmia and its segregates including Orthogrimmia (Schimp.) Ochyra & Żarnowiec, Dryptodon, Guembelia Hampe and Schistidium Bruch & Schimp. For example, strongly biplicate leaves are typical of Orthogrimmia caespiticia (Brid.) Ochyra & Żarnowiec; the immersed capsules in enlarged perichaetial leaves occur in all species of Grimmia, in Guembelia involucrata (Cardot) Ochyra & Zarnowiec and G. kidderi (James) Ochyra & Zarnowiec as well as in Dryptodon pseudoanodon (Deguchi) Ochyra & Żarnowiec; and cribrose peristome teeth are found in some species of Schistidium, for example in S. cribrodontium (Herzog) Ochyra from East Africa.

Schistidium is closely related to Grimmia and gametophytically the two genera are difficult to distinguish, but the scarcely differentiated costa which lacks a central band of small stereids or hydroids, as clearly seen in transverse section, may be considered a reliable character separating *Schistidium* from *Grimmia* and its segregates. Nonetheless, these genera basically differ in only two sporophyte characters. *Schistidium* has consistently systylious capsules, i.e. with the operculum remaining permanently attached to the tip of columella after dehiscence (an exception being *S. trichodon* (Brid.) Poelt), and small, mitrate to cucullate calyptrae which do not reach the capsule mouth.

In the Dicranaceae some genera are recognieed on a single character alone, for instance Orthodicranum Loeske is separated from the large genus *Dicranum* Hedw. on the basis of unistratose alar cells. The monotypic genus Arctoa Bruch & Schimp. is demarcated from Kiaeria I.Hagen primarily on the basis of shorter and stout setae and wide-mouthed capsules and the monotypic genus Cnestrum I.Hagen differs from the medium-sized genus Cynodontium Schimp. in its short-stalked androecium which is sessile in the latter. In the Mniaceae the genus Mnium differs from the closely related Plagiomnium T.J.Kop. in having the leaf margins with single teeth (versus leaf margin with double teeth). In the Seligeriaceae the geners Seligeria Bruch & Schimp. and Blindia Bruch & Schimp. are scarcely distinct and actually differ only in the plant size (Seligeria is a very small Blindia and, conversely, Blindia is a large Seligeria).

Such examples can be added to and clearly show that in each case the classification is largely one of convenience, perhaps having arisen by historical accident. Despite this there was an understandable reluctance to suggest radical changes because of the upheaval and confusion that this would cause. However, in the context of the above examples the segregates of Racomitrium are in no way weaker than those of Mnium, Tortula or Dicranum. The genus *Codriophorus* is primarily recognised by the presence of large, flat papillae distributed over the longitudinal cell walls and covering a major part of the lumina which, apart from the genus Racomitrium s. str., does not occur in any moss genus. In addition, the calyptra in Codriophorus is densely papillose, the costa falls well short of the leaf apex, the innermost perichaetial leaves are epilose and the seta is dextrorse, with the exception of C. fascicularis in which the seta is only once twisted to the right immediately below the capsule and further down is twisted to the left. Also, in the majority of species, hair-points are lacking and, if present, they are weakly denticulate and non-decurrent.

In the papillosity of the laminal cells *Codriophorus* resembles *Racomitrium* but this genus is made distinct by additional characters, including strongly papillose setae twisted to the left; long hyaline, strongly papillose leaf hair-points which are long decurrent down the leaf margins, eroso-dentate and often distinctly wavy and ruffled; long piliferous innermost perichaetial leaves; slightly ventricose capsules; and very long peristome teeth divided to the base into 2(-3) filiform branches. Of these, papillosity of the setae is a character unique throughout acrocarpous mosses.

The other two segregates are very distinct and are rather distantly related to both Codriophorus and Racomitrium. Niphotrichum is primarily diagnosed by having strongly papillose laminal cells with tall conical papillae situated over the lumina, such papillae being unknown in any other taxon of the Grimmiaceae. Moreover, its angular cells are hyaline or yellowish-hyaline, thin-walled and form large convex and most often decurrent auricles; the leaf hairpoints are massive, papillose and denticulate and often decurrent down the leaf margins; the costae are spurred or branched at the tip, ending at mid-leaf or well below the leaf apex and are situated at the bottom of a shallow and wide-angled furrow; the innermost perichaetial leaves are hyaline, sheathing the seta and pilose; the setae are smooth, twisted to the left on drying; the capsules are long cylindrical and plicate when dry and have a long operculum with a beak as long as or longer than the urn; and finally the peristome teeth are long and split into two or rarely three filamentous branches.

Finally, Bucklandiella is the largest and taxonomically most difficult segregate of the former genus Racomitrium although it is a clearly outlined and easily recognised taxon. In contrast to the other three segregates Bucklandiella comprises taxa with smooth laminal cells. They may eventually be pseudopapillose due to many longitudinal cuticular thickenings which give the leaf cells a papillose appearance in transverse section. The smooth laminal cells are coupled with relatively short, lanceolate or triangular peristome teeth which are irregularly divided in the upper half into 2–3 or occasionally 4 branches sometimes being only variously irregularly perforate along the median line or even remaining undivided. Additionally, the following combination of characters is characteristic of this genus: narrowly lanceolate to ovate-triangular and mostly carinate leaves; unbranched, percurrent costa, hair-point, if present, smooth, denticulate or spinulose but never papillose; seta always smooth, dextrorse when dry; and smooth calyptra.

Codriophorus, Racomitrium and *Niphotrichum* are certainly derived genera of the Racomitrioideae and the character states of papillose laminal cells and elongate peristome teeth split at least to the middle are the most important synapomorphy in these genera. In contrast, smooth laminal cells and short peristome teeth, irregularly divided at the middle or only rarely lower, are evidently ancestral features in *Bucklandiella*.

INFRAGENERIC CLASSIFICATION

The first attempt to classify species which are currently placed in the genus *Codriophorus* was undertaken by Bednarek-Ochyra (1995) within *Racomitrium* subg. *Cataractarum*. Twelve species then placed in this subgenus were subdivided into four sections: sect. *Fascicularia* Bednarek-Ochyra (*Racomitrium fasciculare*, *R. papeetense*), sect. *Chrysea* Bednarek-Ochyra (*R. laevigatum*), sect. *Pilifera* Bednarek-Ochyra (*R. carinatum*, *R. varium*, *R. lepervanchei* Besch.) and sect. *Stenotrichum* (Chevall.) 45

Bednarek-Ochyra. The last section was subsequently subdivided into five subsections: subsect. *Papillosa* (Kindb.) Bednarek-Ochyra (*R. aciculare*, *R. hespericum*), subsect. *Hydrophilus* (*R. aquaticum*), subsect. *Cucullaria* Bednarek-Ochyra (*R. cucullatifolium* Hampe), subsect. *Andicola* Bednarek-Ochyra (*R. dichelymoides*) and subsect. *Grimmiiformia* Bednarek-Ochyra (*R. grimmioides*). This was a tentative classification based on a global overview of species which in some cases required a detailed taxonomic assessment in order to establish their true interrelationships.

As a result of the present monographic study of Codriophorus, three species (Racomitrium lepervanchei, R. cucullatifolium and R. grimmioides) have been excluded from the genus and two considered conspecific with others (R. papeetense and R. hespericum). They have been replaced by four species recently newly described (Codriophorus aduncoides, C. norrisii, C. ryszardii and C. corrugatus), three reinstated (C. mollis, C. brevisetus and C. anomodontoides) and one transferred to Codriophorus from Bucklandiella (C. depressus). Thus, in total, Codriophorus contains fifteen species which fall into two sections, sect. Codriophorus and sect. Fascicularia (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra. These are subsequently subdivided into four and three subsections respectively. The taxa are based on morphological similarities and not on phylogenetic analysis. Many of the characters used are associated with adaptation to moist or aquatic habitats with subsequent structural reduction and they are subject to parallel evolution.

1. Sect. Codriophorus

The character states of isodiametric upper laminal cells and a broad and robust costa lying at the bottom of a shallow and wide-angled groove are synapomorphies in this section. It is further characterised by the multistratosity and strong dorsal convexity of the costa in the median and lower parts which, additionally, has a strongly developed stereid band on the dorsal side in the lower part and a single row of enlarged ventral epidermal cells; the irregular branching pattern of the stems, always without short lateral tuft-like branchlets; the leaf margins variously recurved on one or both sides in the lower half (rarely three quarters); the lingulate to broadly ovate or ovate-lanceolate, concave to broadly canaliculate-concave leaves; and the setae twisted to the right. The states of stem branching, recurvature of leaf margins, leaf shape and seta torsion are more or less restricted to the type section, but are not shared by all species. For example, the only species of subsect. Andicola, Codriophorus dichelymoides, has the seta twisted to the right but with only a single torsion to the left immediately below the capsule.

The section consists of nine species and is divided into four distinct subsections.

Subsect. Codriophorus — This subsection consists of four species, *Codriophorus acicularis*, *C. aduncoides*, *C. mollis* and *C. norrisii*. Lingulate, elliptical to broadly

ovate-lanceolate leaves, a broadly rounded-obtuse or subacute to acute, entire to irregularly toothed leaf apex, distinct alar cells and the lack of a basal marginal border characterise this subsection. The most widespread C. acicularis is the most generalised species, whereas C. aduncoides (costa shorter, usually spurred and extending three quarters of the way up the leaf but often ceasing only in mid-leaf, flat to tubular or subcucullate leaf apex), C. mollis (very broadly rounded and entire or subentire leaf apex, spurred costa vanishing in the middle to three quarters of the leaf) and C. norrisii (bistratose laminal cells in the distal portion with or without indistinct papillae over the cell walls, mostly bistratose limbidia of the leaves extending from near the base to the apex) possess apotypic states and are more derived. They have mostly restricted geographical ranges, being narrow endemics of western (C. norrisii) and eastern (C. aduncoides) North America and only C. mollis has a wider northern trans-Pacific range.

Subsect. Hydrophilus - The ovate-lanceolate or lanceolate leaves which are concave below and canaliculateconcave to obtusely keeled, narrowly rounded-obtuse, muticous to shortly hyaline tipped and entire to erosodentate or cristate at the apex are characteristic of this section. The leaf apices are either consistently entire and muticous (Codriophorus aquaticus), entire and muticous to shortly hyaline tipped (C. carinatus) or eroso-dentate and muticous (C. ryszardii). The robust costa which is distinctly convex on the dorsal side gives a cohesion to the subsection. C. carinatus is a somewhat isolated species in the subsection in having opaque laminal cells which is a unique character within the whole genus, all other species having a distinctly translucent leaf areolation. The three species comprising this subsection are highly isolated endemics of three continents of the Northern Hemisphere, namely western North America (C. ryszardii), Europe and Macaronesia (C. aquaticus) and the Far East of Asia (C. carinatus).

Subsect. Depressi — The entirely smooth laminal cells (sometimes weakly papillose on young leaves) may be a synapomorphy in this subsection. Other character states are the very broad and strongly flattened costa and the acute to obtuse, entire to bluntly irregularly dentate leaf apex. The obloid or cylindrical capsules are straight or often somewhat curved and gibbous and this is the unique character state in the genus *Codriophorus*, all other species having straight capsules. These character states indicate that *C. depressus*, the only species of this monotypic subsection which is a Californian endemic, is one of the most derived species of the genus.

Subsect. Andicola — The strongly falcato-secund to circinate, concave to subtubular leaves, smooth to slightly papillose laminal cells, entirely chlorophyllous innermost perichaetial leaves, the strongly flattened costa not lying in a furrow and the fairly stout and dextrorse seta but with a single torsion to the left immediately below the capsule

are the most distinctive synapotypic states in this subsection. Subsect. *Andicola* is a monotypic taxon containg a single and highly isolated species, *Codriophorus dichelymoides*, which is endemic to the Northern Andes of Colombia.

2. Sect. Fascicularia

Cells elongate throughout the lamina, a narrow costa lying at the bottom of a deep and narrow-angled furrow, bistratose throughout, not or weakly convex dorsally or seldom tristratose and prominent on the dorsal side in the lower half, and not differentiated anatomically throughout most of its length as well as the frequent presence of many short, lateral, tuft-like branchlets are the most important diagnostic characters. Other shared character states include leaves that are narrowly lanceolate to lanceolate and muticous to hyaline hair-pointed, setae that are basically sinistrorse but with a single torsion to the right immediately below the urn.

Sect. *Fascicularia* consists of six species that are placed in three subsections.

Subsect. Fasciformes — The lack of a hyaline hair-point, entire to dentate or eroso-dentate and cristate leaf apex, unfolded or scarcely plicate leaf base, weakly developed, flat or somewhat swollen and not or slightly decurrent auricles composed of cells with thin to moderately thickened walls and weakly plicate to unfolded innermost perichaetial leaves are the most important characters of this subsection. It contains four species of which *Codriophorus fascicularis* appears to be the most generalised taxon, having the widest geographical range in the Holarctic. Of the remaining three species, *C. brevisetus* appears to be an isolated taxon in its short and partly bistratose upper laminal cells.

Subsect. Chrysei — The hyaline or yellowish-hyaline and denticulate hair-points, the plicate leaves with distinct and coloured auricles composed of cells with strongly incrassate walls and the convolute, chlorophyllous and plicate innermost perichaetial leaves that are truncate and notched or cuspidate at the apex are the most characteristic feature of this subsection. Sporophyte characters in the subsection are largely unknown since in its only species, *Codriophorus laevigatus*, merely immature sporophytes have been found. The species appears to be isolated taxonomically as well as geographically. It is the only one widely distributed in the Southern Hemisphere, in southern South America with some extensions to the Subantarctic (South Georgia) and Tristan da Cunha in the southern cool-temperate zone.

Subsect. Piliferi — Codriophorus varius stands out from the other species of the genus in its piliferous leaves with distinctly plicate bases, its 3–4-stratose costa, strongly convex dorsally in the lower half of the leaf and its long cylindrical capsules and very long peristome teeth divided to the base into two filiform prongs. It is a highly isolated species which exhibits some intermediate characters between the type section and sect. *Fascicularia*. Linking it with the former is the costa, strongly convex on the dorsal side and tristratose or occasionally 4-stratose in the lower part. However, it shares elongate, short-rectangular to

linear laminal cells, a fairly narrow costa lying in a deep and narrow-angled channel, and frequent lateral tuft-like branchlets with sect. *Fascicularia*. The species is a narrow endemic of western North America.

SYNOPSIS OF CODRIOPHORUS SPECIES

CODRIOPHORUS sect. CODRIOPHORUS — Lectotype: C. acicularis (Hedw.) P.Beauv.

CODRIOPHORUS subsect. CODRIOPHORUS

C. acicularis (Hedw.) P.Beauv.

C. aduncoides (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

C. mollis (Cardot) Bednarek-Ochyra & Ochyra

C. norrisii (Bednarek-Ochyra & Ochyra) Bednarek-Ochyra & Ochyra

CODRIOPHORUS subsect. HYDROPHILUS (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra — Type: C. aquaticus (Schrad.) Bednarek-Ochyra & Ochyra

C. aquaticus (Schrad.) Bednarek-Ochyra & Ochyra

C. carinatus (Cardot) Bednarek-Ochyra & Ochyra

C. ryszardii (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

CODRIOPHORUS subsect. DEPRESSI Bednarek-Ochyra, subsect. nov.

C. depressus (Lesq.) Bednarek-Ochyra & Ochyra

CODRIOPHORUS subsect. ANDICOLA (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra — Type: C. dichelymoides (Herzog) Bednarek-Ochyra & Ochyra

C. dichelymoides (Herzog) Bednarek-Ochyra & Ochyra

CODRIOPHORUS sect. FASCICULARIA (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra — Type: C. fascicularis (Hedw.) Bednarek-Ochyra & Ochyra

CODRIOPHORUS subsect. FASCIFORMES Bednarek-Ochyra, subsect. nov.

C. fascicularis (Hedw.) Bednarek-Ochyra & Ochyra

C. brevisetus (Lindb.) Bednarek-Ochyra & Ochyra

C. anomodontoides (Cardot) Bednarek-Ochyra & Ochyra

C. corrugatus Bednarek-Ochyra

CODRIOPHORUS subsect. CHRYSEI (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra — Type: C. laevigatus (A.Jaeger) Bednarek-Ochyra & Ochyra

C. laevigatus (A.Jaeger) Bednarek-Ochyra & Ochyra

CODRIOPHORUS subsect. PILIFERI (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra — Type: C. varius (Mitt.) Bednarek-Ochyra & Ochyra

C. varius (Mitt.) Bednarek-Ochyra & Ochyra

KEY TO THE SECTIONS, SUBSECTIONS AND SPECIES OF CODRIOPHORUS

- Laminal cells rectangular to linear throughout (except *Codriophorus brevisetus*); costa fairly weak and narrow, usually less than 70 μm wide below, bistratose and strongly flattened and weakly convex dorsally throughout or rarely 3(–4)-layered and convex on the dorsal side in the lower part (*C. varius*), situated at the bottom of a deep, narrow-angled furrow; leaves narrowly lanceolate to lanceolate (sect. *Fascicularia*)...... 10

3. Costa subpercurrent, entire and only shortly forked at the tip 4

	4. Laminal cells strongly papillose, uni- or rarely bistratose; leaves unbordered
	1. <i>C. acicularis</i>
	4. Laminal cells indistinctly papillose over the cell walls, always variously bistratose in
	the distal part; leaves distinctly bordered with fleshy limbidia 4. C. norrisu
5.	Leaf apex broadly rounded-obtuse to subacute, often tubular, strongly dentate to sub-
	entire
5.	Leaf apex broadly rounded, flat to subcucullate, entire to subentire 3. <i>C. mollis</i>
	 6. Laminal cells distinctly papillose (subsect. <i>Hydrophilus</i>)
7.	Leaf apex irregularly bluntly eroso-dentate, muticous; basal marginal border absent
7	Leaf apex entire muticous or shortly hyaline tipped: basal marginal border present 8
<i>,</i> .	2 Costa robust 100 120 um wide below in transverse section with 4.7 wantral ani
	dermal cells equal in size to the median and dorsal cells; laminal cells transparent;
	leaf apex always muticous
	8. Costa slender, 80–105 µm wide below, in transverse section with 2 large ventral epi-
	tipped 7. <i>C. carinatus</i>
9.	Leaves broadly ovate to ovate-lanceolate, straight; costa robust and broad, 100–200 μ m
	wide below, lying in a shallow channel (subsect. Depressi) 8. C. depressus
9.	Leaves lanceolate to oblong-lanceolate, strongly falcato-secund to circinate; costa slender
	and narrower, 80–100 µm wide, not grooved (subsect. Andicola) 9. C. dichelymoides
	10. Leaves without a hair-point (subsect. <i>Fasciformes</i>)
	10. Leaves with a hyaline hair-point, if muticous than the costa 3(–4)-layered and strongly
	convex dorsally in the lower half14
11.	. Costa vanishing in mid-leaf or slightly above; leaf acumen usually serpentine and wavy
11.	. Costa extending $\frac{3}{4}$ of the way up the leaf
	12. Upper laminal cells isodiametric, mostly quadrate, most often bistratose at the
	margins 11. C. brevisetus
	12. Upper laminal cells elongate, unistratose
13	. Costa convex on the ventral side; leaf apex eroso-dentate 12. C. anomodontoides
13	. Costa flattened on the ventral side; leaf of the apex entire 10. C. fascicularis
	14. Costa bistratose throughout, flattened dorsally, $50-75 \mu\text{m}$ wide near the base, extending
	$\frac{1}{2}-\frac{3}{4}$ way up the leaf (subsect. <i>Chrysei</i>)
	14. Costa 3(-4)-stratose, lunate and strongly convex dorsally in the lower half, $75-100 \mu m$
	wide below, percurrent to subpercurrent (subsect. Piliferi) 15. C. varius

REGIONAL KEYS TO THE SPECIES

ASIA AND OCEANIA

1.	Upper laminal cells isodiametric	2
1.	Upper laminal cells elongate	5
	 Leaves lanceolate; leaf margins and upper laminal cells usually bistratose Leaves lingulate to elliptical; laminal cells always unistratose throughout 	3 4
3.	Laminal cells opaque; leaf apex narrowly rounded-obtuse and entire or with a short hyalin tip; costa with 2 much enlarged ventral epidermal cells in the median part in transvers	e e
_	section	S
3.	Laminal cells transparent; leaf apex acute and eroso-dentate, always lacking a hair-point	t;
	ventral epidermal cells of the costa not differentiated in the median part in transvers	e
	section C. brevisetu	S
	 Leaf apex irregularly dentate; costa subpercurrent, entire <i>C. aciculari</i> Leaf apex entire to subentire; costa extending ¹/₂-³/₄ of the way up the leaf, distinctl spurred <i>C. molli</i> 	s y is

5.	Costa ceasing in mid-leaf or only slightly above C. corrug	atus
5.	Costa extending ³ / ₄ - ⁵ / ₆ of the way up the leaf	. 6
	6. Costa convex on the ventral side; leaf apex eroso-dentate C. anomodonto	oides
	6. Costa flattened on the ventral side; leaf apex entire C. fascicu	laris

EUROPE, MACARONESIA AND NORTH AFRICA

1.	Leaves lingulate, elliptical, broadly ovate to broadly ovate- or oblong-lanceolate; leaf
	apex broadly rounded-obtuse to subacute, irregularly toothed C. acicularis
1.	Leaves lanceolate to narrowly ovate-lanceolate; leaf apex narrowly rounded-obtuse to
	acute, entire
	2. Upper laminal cells mostly rounded-quadrate; costa multistratose, reniform to lunate
	and strongly convex dorsally in the lower half C. aquaticus
	2. Laminal cells elongate throughout; costa bistratose throughout, except for the extreme
	base, flattened and weakly convex dorsally C. fascicularis

NORTH AMERICA

1.	Upper laminal cells mostly short and isodiametric; costa robust and broad, usually more than 80 µm wide below, 2–3-stratose above, 3–6-layered below, lying at the bottom of a shallow, wide-angled groove and strongly covex dorsally; leaves lingulate to broadly ovate-lanceolate or lanceolate
1.	Laminal cells short-rectangular to linear throughout; costa fairly weak and narrow, usullay less than 70 μ m wide below, bistratose and strongly flattened and weakly convex dorsally throughout or 3(-4)-layered and convex on the dorsal side in the lower part (<i>C. varius</i>), situated at the bottom of a deep, narrow-angled furrow; leaves narrowly lanceolate to lanceolate
	 Leaves lingulate, elliptical to broadly ovate or ovate-lanceolate; leaf apex broadly rounded-obtuse to acute, irregularly dentate to entire, always muticous; basal marginal borders absent
3. 3.	Costa subpercurrent, entire and only shortly forked at the tip $\dots \dots \dots \dots \dots 4$ Costa extending $\frac{1}{2}-\frac{3}{4}$ of the way up the leaf, distinctly spurred $\dots \dots \dots$
	4. Laminal cells strongly papillose, uni- or very rarely bistratose; leaves unbordered <i>C. acicularis</i>
	4. Laminal cells indistinctly papillose over the cell walls, always variously bistratose in the distal part; leaves distinctly bordered with fleshy limbidia <i>C. norrisii</i>
5.	Leaf apex broadly rounded-obtuse to subacute, often tubular, strongly dentate to sub- entire
5.	C. aduncoides Leaf apex broadly rounded, flat to subcucullate, entire to faintly bluntly denticulate or sinuate. C. mollis
	 Laminal cells smooth or nearly so; leaves broadly ovate to ovate- or oblong-lanceolate; costa robust and broad, 100–200 μm wide below, lying in a shallow channel
	 6. Laminal cells disistinctly papillose; leaves lanceolate; costa weak, to 100 μm wide near the base, lying at the bottom of a deep groove
7.	Costa 3(-4)-stratose, lunate and distinctly convex on the dorsal side, 75–135 µm wide below
7.	Costa bistratose throughout except the extreme base, flattened and weakly convex on the dorsal side, less than 70 µm wide near the base
	8. Leaf apex eroso-dentate, muticous; leaf base non-plicate; peristome teeth 0.5–0.65 mm long

	8. Leaf apex usually piliferous, if muticous then entire; leaf base distinctly plicate; peristome teeth 1.0–1.8 mm long <i>C. varius</i>
9.	Costa extending ³ / ₄ of the way up the leaf to subpercurrent; leaf apex entire; leaf acumen straight <i>C. fascicularis</i>
9.	Costa ceasing in mid-leaf or only slightly above; leaf apex eroso-dentate; leaf acumen serpentine, strongly wavy <i>C. corrugatus</i>

SOUTH AMERICA AND SOUTH AFRICA

1.	Le	aves elliptical to lingulate; leaf apex broadly rounded C. mollis
1.	Le	aves lanceolate to oblong lanceolate; leaf apex narrowly obtuse to acute 2
	2.	Leaves falcato-secund to circinate, muticous; costa 80–100 μ m wide, not grooved
	2.	Leaves straight, piliferous; costa 50–75 μ m wide near the base, lying at the bottom
		of a deep and narrow-angled furrow C. laevigatus

Chapter 7

SYSTEMATIC ACCOUNT OF THE TAXA

CODRIOPHORUS P.BEAUV.

Codriophorus P.Beauv., Mém. Soc. Linn. Paris 1: 445. 1822 (before 20 Oct.). — Lectotype (*vide* Bednarek-Ochyra *et al.* 2001: p. 109): *Codriophorus acicularis* (Hedw.) P.Beauv. (*Dicranum aciculare* Hedw.).

Codriophorum P.Beauv., Mém. Soc. Linn. Paris 1 (fasc. planch.): pl. 3, f. 2-3. 1822, orthogr. pro Codriophorus P. Beauv.

Codonophorus P.Beauv. ex Desv., Mém. Soc. Linn. Paris 3: 219. 1824, nom. illeg. incl. gen. prior. [Codrio-phorus P.Beauv., 1822].

Racomitrium Brid. subg. Cataractarum Vilh., Věstn. Král. Česke Společn. Nauk Tř. Mat.-Přir. 1925(5): 31. 1926 ['Cataractae']. — Lectotype (vide Bednarek-Ochyra 1995: p. 127): Racomitrium protensum (Duby) Bruch & Schimp. (Trichostomum protensum Duby) [= Codriophorus aquaticus (Schrad.) Bednarek-Ochyra & Ochyra (Trichostomum aquaticum Schrad.)]. First synonymised by Ochyra et al. (2003: 140).

Plants moderately sized to large, rarely small, relatively slender to robust and coarse, stiff and rigid, somewhat wiry in texture or fairly pliable, loosely to relatively densely caespitose or forming extensive patches or mats, sometimes submerged at high water and floating and having a fruticose habit, dull or sometimes slightly lustrous, usually olivaceous, green, yellow, yellow-brown, yellow-green to golden-, rusty- or blackish-brown above, brown, reddish- or blackish-brown below, sometimes brown, black to blackish- or dirty brown throughout. Stems erect, erect- to curved-ascending or creeping and trailing, tough, often denuded in the lower part because of erosion of the leaf laminae leaving just the costae in swiftly flowing water, repeatedly sparingly or copiously dichotomously or fasciculately branched, often with numerous short, tuft-like, horizontal branchlets giving the shoots a nodose appearance, occasionally almost unbranched, in transverse section circular, oval to obscurely angular, lacking a central strand and with a thick, multilayered cortex of small stereid cells with brown to reddish-brown incrassate walls and small lumina surrounding a central medulla of large, hyaline, thick-walled cells; rhizoids smooth, branched, brown, reddish- or blackishbrown, sparse or numerous at the base or in the lower part of the stem, sometimes scattered in clusters along the stem, occasionally copiously so, making the stem tomentose; axillary hairs filiform, hyaline throughout or with 1-2 basal cells brownish pigmented, composed of relatively short, barrel-shaped cells below and elongate cells in the distal portion. Leaves crowded or sometimes distant, evenly set, loosely or tightly appressed to imbricate, erect to erecto-patent, often secund and homomallous, occasionally with flexuose or rarely crisped points when dry, loosely erect or erect-spreading to occasionally wide spreading-recurved when moist, straight to somewhat curved, rarely strongly falcate, variously lingulate, elliptical, broadly ovate, ovate-, oblong- or linear-lanceolate to broadly or narrowly lanceolate from an ovate, oblong- or ovate-lanceolate, not or distinctly plicate base, gradually shortly or long acuminate, often with a long, subulate, canaliculate, canaliculate-concave to broadly carinate, straight or sometimes wavy to serpentine acumen, concave to broadly canaliculate-concave below, usually distinctly auriculate and shortly decurrent at the base; leaf apex subacute, acute or narrowly or broadly rounded-obtuse, muticous, shortly hyaline-tipped or terminated with a hyaline or yellowish-hyaline, flat, smooth or denticulate, straight or flexuose, erect or recurved hair-point, papillose-crenulate owing to projecting cell papillae, entire or sharply to bluntly, remotely irregularly toothed, erosodentate, denticulate-cristate, cristate to sinuate; margins variously recurved to revolute on one or both sides to varying extents, usually from near the base to mid-leaf or to the apex or only somewhat below, seldom plane and erect, entire throughout or variously denticulate to denticulate-cristate at the apex, unistratose throughout to variously 2(-4)-stratose in 1 to as many as 10-13 rows of cells; costa single, strong and broad, well-demarcated from the laminal cells, ceasing in mid-leaf to subpercurrent or percurrent, entire throughout or spurred in the

distal portion and forked at the tip, in the proximal portion situated at the bottom of a deep or shallow, wide- or narrow-angled groove, open or partly enclosed by the strongly infolded leaf base, in cross-section bistratose throughout with only occasional tristratose spots near the base or 2-4-stratose in the upper and median parts and 3-7-layered in the lower half, flat or convex on the ventral side, weakly to strongly convex, reniform, crescent-shaped to semi-terete or rectangular and distinctly flattened, very rarely canaliculate on the dorsal side, composed of anatomically undifferentiated cells or with a weak or strong, (1-)2-6-layered dorsal stereid band of small sclerenchymatous cells in the lower half or only near the base and a single row of (3-)5-11(-15) enlarged ventral epidermal cells; laminal cells unistratose throughout to variously bistratose in the distal portion, long rectangular to linear throughout or isodiametric, irregularly rounded-quadrate, subquadrate, oval, rounded-hexagonal to bluntly angular or shortly rectangular, thick- and mostly straight-walled in the upper part and long rectangular in the median part with thick and distinctly sinuose longitudinal walls, pellucid or rarely opaque, strongly papillose on both surfaces with large flat papillae covering the longitudinal walls and major part of the lumina leaving only a narrow slit in the centre, very rarely smooth or nearly so throughout; basal cells rectangular to linear-rectangular, with strongly incrassate, nodulose and porose longitudinal walls, often with distinct spiral thickenings, forming an intensely bright yellow or yellow-brown, 1-2(-3)-seriate strip along the leaf insertion; *alar cells* scarcely to strongly differentiated, quadrate to short-rectangular, with moderately thick to strongly incrassate walls, forming mostly distinct, vellow, brown to orange-brown, flat or somewhat swollen, not or shortly decurrent auricles; supra-alar cells not or scarcely differentiated and similar to the adjacent laminal cells or subquadrate to rectangular, hyaline to yellowishhyaline, with thin to thick, straight walls, forming a transparent, 1(-2)-seriate marginal border consisting of 5-25 cells. Dioicous. Perigonia gemmiform, with the outer perigonial bracts generally similar to the vegetative leaves but somewhat smaller and the inner broadly ovate, strongly concave, gradually or abruptly narrowed to a short narrowly obtuse, entire apex, brown to orange-brown, with a single, subpercurrent costa, the innermost ones bearing up to about 25 club-shaped, short-stalked, brownish antheridia intermingled with a few to several filiform, hyaline to brownish-hyaline paraphyses scarcely exceeding half the antheridia length. Outer perichaetial leaves similar to the cauline leaves; innermost perichaetial leaves elliptical or lingulate, oblong, oblong-lanceolate to oblong-ovate, acute, subacute to rounded-obtuse, entire to sinuate, occasionally truncate or shortly apiculate at the apex, concave and sheathing the seta, not or scarcely to strongly longitudinally plicate, hyaline or yellowishbrown or chlorophyllous, thin-walled throughout or thickand sinuose-walled in the upper third or at the extreme apex only, unistratose or very rarely bistratose at the apex. Setae 1-3 per perichaetium, erect, straight, very short to moderately long, smooth, brown, dextrorse throughout or with a single torsion to the right immediately below the capsule and twisted counter-clockwise below; vaginula cylindrical, dark or light brown to brown-reddish, with rectangular, thick- and sinuose-walled epidermal cells. *Capsules* exserted, erect, straight and symmetric or rarely slightly curved and gibbous, ovoid, obloid, ellipsoid to cylindrical, smooth or slightly ribbed when dry pachydermous; operculum conical-rostrate, with a long or short, straight or slanted, acicular or stout beak; annulus tardily or readily deciduous, composed of 2-4 rows of large, vesiculose cells with strongly incrassate walls; exothecial cells variable in shape from isodiametric through to elongate or rectangular, thick- to thin-walled, often with distinct corner thickenings, sometimes arranged in regular longitudinal rows, distinctly or scarcely differentiated at the mouth; stomata at the base of the urn, about 20 or more, disposed in 2-4 rows, circular, phaneroporous, bicellular, with rounded pori; peristome teeth 16, lanceolate, 0.3-1.8 mm long, with a low to fairly tall basal membrane, reddish, orange-reddish, brown to orange-, yellowor reddish-brown, densely spiculate- or low-papillose, rarely almost smooth throughout or only above, finely papillose to nearly smooth below, bifid or irregularly tripartite down to the middle or for two thirds of their length or deeply cleft nearly to the base into 2-3 filamentous branches. Spores globose, pale yellowish-brownish to brownish, finely papillose, 10-20 µm in diameter. Calyptra conical-mitrate, 4–5-lobed at the base, slightly scabrous to strongly verrucose at the apex.

Etymology — The name of the genus derives from the distorted Greek κώδων (*codon*) referring to the opening of a bell or trumpet and φορέω (*phoreo*) meaning to carry or bear, referring, somewhat fancifully, to "a moss bearing capsules with bell-shaped calyptrae".

A. Section Codriophorus

Trichostomum Hedw. sect. *Stenotrichum* Chevall., Fl. Gen. Env. Paris 2: 44. 1827. ≡ *Racomitrium* Brid. sect. *Stenotrichum* (Chevall.) Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 143. 1995, *nom. illeg. incl. lectotyp. gen.* — Lectotype (*vide* Bednarek-Ochyra 1995: p. 143): *Trichostomum aciculare* (Hedw.) P.Beauv. (*Dicranum aciculare* Hedw.).

Racomitrium [unranked] 3. Papillosa Kindb., Eur. N. Am. Bryin. 2: 236. 1898. ≡ Racomitrium sect. Papillosa (Kindb.) Nog., J. Hattori Bot. Lab. 38: 349. 1974. ≡ Racomitrium subsect. Papillosa (Kindb.) Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 144. 1995, nom. illeg. incl. lectotyp. gen. — Lectotype (vide Noguchi 1974: p. 349): Racomitrium aciculare (Hedw.) Brid. (Dicranum aciculare Hedw.).

Plants moderately sized to large, rarely small, slender to robust and coarse, wiry in texture to rather soft, forming dull, loose or rather dense, dark green, yellowor olive-green to yellow-, olive- or blackish-brown tufts or extensive mats. Stems erect, prostrate to curved-ascending, sparsely or copiously irregularly, dichotomously or fasciculately branched, sometimes filiform and almost unbranched, lacking short, lateral tuft-like branchlets, sparsely to densely radiculose near the base with dark, reddish- or blackish-brown, smooth, lustrous rhizoids or with sparse or dense clusters of rhizoids scattered along the creeping stems. Leaves crowded or distant, evenly set, straight or curved to falcate, loosely or tightly appressedimbricate, erect to secund and homomallous when dry, erect-spreading when moist, lingulate, elliptical, broadly ovate, ovate- or oblong-lanceolate to broadly or narrowly lanceolate, long acuminate to acute or narrowly or broadly rounded-obtuse, muticous or rarely shortly hyaline-tipped at the apex, non-plicate, usually distinctly auriculate and shortly decurrent at the base, concave to broadly canaliculate-concave; margins variously recurved on one or both sides in the lower half or sometimes three quarters, occasionally plane and erect throughout, unistratose to variously 2(-4)-stratose in (1-)2-10(-13) rows of cells, entire throughout or sharply to bluntly, remotely irregularly toothed, eroso-dentate, sinuate to cristate in the upper $\frac{1}{5}$ to $\frac{1}{4}$, including the apex; *costa* single, strong and broad, subpercurrent to percurrent, entire to variously spurred distally, forked not or at the apex, in cross-section 2-4-stratose in the upper and median parts, weakly to strongly convex, reniform, crescent-shaped to semiterete dorsally, flat or convex on the ventral side, in the basal part situated at the bottom of a shallow or deeper, usually wide-angled groove, lunate, reniform or rectangular and distinctly flattened, strongly convex on the dorsal side, 3-6(-7)-layered, consisting of a single row of (3-)5-11(-15) enlarged ventral cells and a 2-6-layered dorsal stereid band of small sclerenchymatous cells; laminal cells unistratose throughout to variously bistratose in the distal portion, pellucid to opaque, strongly papillose to smooth, isodiametric, irregularly rounded-quadrate, subquadrate, oval, rounded-hexagonal to bluntly angular or shortly rectangular, thick- and mostly straight-walled in the upper part, becoming long rectangular in the median part with thick and distinctly sinuose longitudinal walls; basal cells long to linear-rectangular mostly with strongly incrassate, nodulose and porose longitudinal walls, often with distinct spiral thickenings, forming an intensely bright yellow or yellow-brown, 1-2(-3)-seriate strip along the leaf insertion; alar cells usually strongly differentiated, quadrate to short-rectangular, with moderately to strongly thickened walls, forming distinct, colourful, convex or fairly flat, shortly decurrent auricles; supra-alar cells not differentiated and similar to the adjacent laminal cells or forming a pellucid, hyaline or yellowish-hyaline basal marginal border, composed of 5-14(-24) thickand straight-walled cells. Dioicous. Innermost perichaetial leaves oblong-lanceolate, oblong-ovate or lingulate, acute, subacute to rounded-obtuse, entire to sinuate at the apex, hyaline or yellowish-brown, thin-walled throughout or chlorophyllous and thick-walled in the upper third or at the extreme apex only. Setae 1-3 per perichaetium, erect, straight, very short to moderately long, smooth, dextrorse or rarely with a single torsion to the left immediately below the capsule. Capsules exserted, erect, straight or slightly curved and gibbous, ovoid, ellipsoid, obloid to cylindrical, smooth, pachydermous; operculum conical-rostrate, with a long or short, straight or slanted, needle-like or stout beak; peristome teeth 16, lanceolate, 0.3-0.5(-0.65) mm long, with a low to fairly tall basal membrane, reddish, orange-reddish, brown to orange-, yellow- or reddish-brown, densely spiculate- to low-papillose throughout or only above, finely papillose to nearly smooth below, bifid or irregularly tripartite down to the middle or for two thirds of their length, rarely to the base, into regular or irregular prongs. Spores spherical, pale yellowish-brownish to brownish, finely papillose, 10-20 µm in diameter. Calyptra conical-mitrate, 4-5-lobed at the base, scabrous at the apex.

The type section of Codriophorus is primarily diagnosed by its costal anatomy. The costa is generally stout and broad and vanishes a few cells below the leaf apex, and only occasionally does it cease in mid-leaf or extend ³/₄ of the way up the leaf. It is situated at the bottom of a shallow and wide-angled channel, but occasionally the leaf is not furrowed or the costa lies in a deeper and narrower-angled groove. In transverse section it is bistratose only in the upper part and becomes mostly 3-4-layered in the median part and is composed of undifferentiated cells, whereas in the lower half it is 3-6(-7)-stratose with a single row of enlarged ventral epidermal cells and a 2-5(-6)-stratose dorsal stereid band composed of small, sclerenchymatous cells with strongly incrassate walls and minute lumina. The costa is variously exposed on the dorsal side, from only slightly convex and almost of the same thickness as the lamina to prominently convex dorsally. The outline of the costa in cross-section is very variable and ranges from strongly flattened to reniform, lunate or semi-terete on the dorsal side and plane on the ventral side, although sometimes in Codriophorus acicularis the costa is distinctly biconvex.

Leaf areolation is another characteristic feature of *Codriophorus* sect. *Codriophorus*. The upper laminal cells lack a typical 'racomitrioid' shape, especially the sinuose cell walls. They are generally short and isodiametric, rounded-quadrate, subquadrate, oval, transversely rectangular, rounded-hexagonal to irregularly angular and are intermixed with shortly rectangular cells with weakly sinuose walls. All species of this section have sparsely or copiously irregularly, dichotomously or fasciculately branched stems and always lack short, lateral, tuft-like branchlets. Moreover, the seta is always dextrorse and only incidentally is it once twisted to the left immediately below the capsule.

Codriophorus sect. *Codriophorus* has twice been recognised as a separate section within the genus *Racomitrium*. Chevallier (1827) distinguished it as a separate taxon

within *Trichostomum* and although Wijk *et al.* (1969) claimed that its rank was unclear, Chevallier explicitly and unequivocally designated it as a section ["... surtout ceux de la première section, aux quels nous donnons, pour la distinguer, le nom de *Stenotrichum*"]. Because the section originally comprised three species, namely *Trichostomum aciculare* (Hedw.) P.Beauv., *T. patens* (Hedw.) D.Mohr and *T. funale* Schwägr., Bednarek-Ochyra (1995) lectotypified this name with *T. aciculare* and made the appropriate transfer to the genus *Racomitrium* resulting in a new combination, *Racomitrium* sect. *Stenotrichum*. However, in the genus *Codriophorus* this name has to be considered illegitimate because it includes the lectotype species of this generic name and under the rules it has to be replaced by sect. *Codriophorus*.

The same is also true for another sectional name, namely *Racomitrium* sect. *Papillosa*. This name was introduced by Kindberg (1898) for an unranked taxon within *Racomitrium* which was subsequently given a sectional recognition within *Racomitrium* by Noguchi (1974). Because this section was lectotypified with *R. aciculare*, it is automatically illegitimate in *Codriophorus* because the species name serves also as a lectotype of the generic name.

Codriophorus sect. *Codriophorus* consists of nine species which are subdivided into four subsections, namely subsect. *Codriophorus*, subsect. *Hydrophilus*, subsect. *Depressi* and subsect. *Andicola*. The first of these accommodates four species of the Northern Hemisphere belonging within the *C. acicularis* complex, the second comprises three species, endemic to Europe and Macaronesia (*C. aquaticus*), East Asia (*C. carinatus*) and western North America (*C. ryszardii*), whereas the last two are monotypic taxa consisting of, respectively, *C. depressus*, a Californian endemic, and *C. dichelymoides* which is endemic to the Colombian Andes in South America.

A1. Subsection Codriophorus

Racomitrium [unranked] 3. Papillosa Kindb., Eur. N. Am. Bryin. 2: 236. 1898. ≡ Racomitrium subsect. Papillosa (Kindb.) Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 144. 1995, nom. illeg. incl. lectotyp. gen. — Lectotype (vide Noguchi 1974: p. 349): Racomitrium aciculare (Hedw.) Brid. (Dicranum aciculare Hedw.).

Plants small, medium-sized to large, fairly slender to robust and coarse, mostly rigid and stiff, rarely quite pliable, loosely or densely caespitose, dull, mostly olivaceous, olive-, yellow- to dirty green or yellow- to blackish-brown above, brown to blackish-brown below, sometimes black to blackish-green throughout. Stems erect-ascending, erect or prostrate, sparingly or copiously irregularly dichotomously or fasciculately branched, sparsely or densely radiculose at the base, seldom with clusters of rhizoids scattered along the stem. Leaves crowded, loosely or closely appressed to imbricate, erect or rarely erectspreading, straight or somewhat curved, often secund and homomallous when dry, erecto-patent when moist, varying greatly in shape being lingulate, elliptical, broadly ovate, ovate- or oblong-lanceolate, broadly lanceolate to oblong-elliptical, rounded, broadly rounded-obtuse, subacute or acute, muticous at the apex, concave to broadly canaliculate-concave, sometimes obtusely carinate below, not plicate, usually distinctly auriculate and shortly decurrent at the base; margins variously recurved on one or both sides in the lower half, entire throughout or, most often, sharply or bluntly irregularly dentate, eroso-dentate or sinuate at the apex and in the uppermost $\frac{1}{4}-\frac{1}{5}$ of the leaf, unistratose or 2(-4)-layered in (1-)2-10(-13) rows of cells; costa single, robust and wide, ending a few cells below the apex or ceasing $\frac{1}{2}-\frac{3}{4}$ of the way up the leaf, entire or spurred above, mostly forked at the tip, situated at the bottom of a shallow and wide-angled furrow in the proximal half, in transverse section 2–4-stratose, weakly to strongly convex, reniform, crescent-shaped or rectangular and flattened in the distal half, 3-6(-7)-layered, strongly convex dorsally, lunate, reniform to rectangular and strongly flattened in the proximal half with a row of (3-)5-11(-14) enlarged ventral epidermal cells and 2-6 layers of small stereid cells forming a prominent dorsal band; laminal cells unistratose to variously bistratose in the upper and median parts, mostly isodiametric above, becoming rectangular and sinuose-walled in mid-leaf and below, long to linear-rectangular, with nodulose and porose walls at the base; alar cells mostly differentiated, forming swollen, colourful, shortly decurrent auricles; supra-alar cells not differentiated. Dioicous. Innermost perichaetial leaves oblong-ovate, oblong-lanceolate to lingulate, rounded-obtuse or subacute to acute at the apex, strongly concave and sheathing the seta, hyaline to yellowishbrown and thin-walled throughout or chlorophyllous and thick-walled in the upper third or at the extreme apex. Setae 1-3 in the perichaetium, erect, twisted clockwise. Capsules exserted, erect, symmetric, straight, ovoid, obloid to shortly cylindrical, smooth, lustrous, brown, pachydermous; operculum conical-rostrate, with a long, straight beak; peristome teeth 16, lanceolate, mostly 300-500 µm long, divided into 2-3 mostly irregular prongs down to $\frac{1}{2}-\frac{2}{3}$ of their length, sometimes to the base, spiculate- or low-papillose throughout, sometimes finely papillose to nearly smooth below, with a low basal membrane. Spores spherical, yellowish-brownish to brownish, minutely papillose. Calyptra conical-mitrate, 4-5-lobed at the base, verrucose at the apex.

The type subsection of *Codriophorus* consists of four species which constitute the *C. acicularis* complex, namely *C. acicularis*, *C. aduncoides*, *C. mollis* and *C. norrisii*. They are distributed exclusively in the Northern Hemi-

sphere, except for C. mollis which occasionally penetrates into the tropics in the Northern Andes of Colombia. The subsection is recognised by the following set of characters: (1) leaves varying greatly in shape, being lingulate, elliptical, broadly ovate, ovate- or oblong-lanceolate, oblong-elliptical to broadly lanceolate; (2) leaf apex muticous, rounded, broadly rounded-obtuse or subacute to acute, entire or most often sharply or bluntly irregularly toothed, eroso-dentate or sinuate extending down as far as the upper $\frac{1}{4}-\frac{1}{5}$ of the leaf margin; (3) alar cells with moderately thin to strongly thickened walls, forming swollen, shortly decurrent auricles; (4) supra-alar cells not differentiated and similar to the adjacent laminal cells. The essential difference between the type subsection of Codriophorus and the remaining three subsections of Codriophorus sect. Codriophorus lies in the completely different vegetative leaf shape and the form of the leaf apex. These two features that are unique within the genus and clearly define this distinct species complex.

1. Codriophorus acicularis (Hedw.) P.Beauv.

(Figs 20-28)

Codriophorus acicularis (Hedw.) P.Beauv., Mém. Soc. Linn. Paris 1 (fasc. Planch.): pl. 3, f, 2. 1822 ['aciculare']. = Dicranum aciculare Hedw., Sp. Musc. Frond.: 135. 1801 ['Bryum aciculare L.', Spec. Plant. 2: 1118. 1753, non rite publ.; 'Mnium aciculare Gmel.', Syst. Nat. Ed. 13, 2(2): 1328. 1791, non rite publ.; 'Hypnum aciculare Scop.', Fl. Carn. Ed. 2, 2: 335. 1772, non rite publ.; 'Dicranum aciculare Hedw.', Descr. Adumbr. Musc. Frond. 3: 79, pl. 33. 1792, non rite publ.]. = Trichostomum aciculare (Hedw.) P.Beauv., Prodr. Aethéog.: 90. 1801. = Racomitrium aciculare (Hedw.) Brid., Mant. Musc.: 80. 1819. = Codriophorum aciculare (Hedw.) P.Beauv., Mém. Soc. Linn. Paris 1 (fasc. planch.): pl. 3, f. 2. 1822. = Campylopus acicularis (Hedw.) Wahlenb., Fl. Suec. 2: 749. 1826. = Grimmia acicularis (Hedw.) Müll.Hal., Syn. Musc. Frond. 1: 801. 1849. -TYPE CITATION: In Helvetia, Gallia, Carniolia, Saxonia, Thuringia, Anglia, Scotia ad saxa fluviorum montanorum et ad rupes bumidas; additionally, references to Dillenius (1741), Linnaeus (1763), Haller (1768), Hedwig (1792) and Bridel (1798) are given. [Lectotype (selected here): the third shoot from the left in the upper row on the sheet bearing the following label data "Dicranum aciculare St. Crypt. III. p. 79. tab 33. Bryum aciculare Linn. tenus Poenig ad Muldae lect" - Hedwig/Schwägrichen!].

Orthotrichum submarginatum Brid., Bryol. Univ. 1: 792. 1827. — TYPE CITATION: In insula Terre Neuve. La Pylaie. [Holotype: "Orthotrichum obtusifolium var. majus In insula <u>Terra-Neuva</u> La Pylaie Parn. 1825" – B-Bridel!]. First synonymised with *Racomitrium aciculare* by Vitt (1973: p. 200).

Racomitrium aciculare var. denticulatum Bruch & Schimp. in Bruch, Schimp. & W.Gümbel, Bryol. Eur. 3: 140, pl. 262, f. 1, 1b. 1845 (Fasc. 25–28 Mon. 6. Dryptodon, 1 f. 1, 1b). – TYPE CITA-TION: Europe [no locality given]. [Lectotype (selected here): (icon in) Bruch et al. (1845): pl. 262, f. 1b. 1845], syn. nov.

Grimmia nevii Müll.Hal., Flora 56: 483. 1873 ["Neevii"]. \equiv *G. nevii* Müll.Hal. *in* C.Mohr, Bull. Torrey Bot. Cl. 5: 6. 1874 *orthogr. pro* G. neevii Müll.Hal. \equiv *Racomitrium nevii* (Müll.Hal.) S.Watson, Bot. Calif. 2: 381. 1880. \equiv *R. aciculare* var. *nevii* (Müll.Hal.) Frye, Bryologist 20: 95. 1917. — TYPE CITATION: Portland Oregon, vere 1873: Rever. Dr. Neevius legit, C. Mohr ex Mobile Alabamae misit [Lectotype (*selected here*): "Grimmia (Dryptodon) Nevii C.M. n.s. Portland Oregon Dr Nevius leg" – BM!; isotype: "Flora: Oregon. Racomitrium (Dryptodon) Nevii Wats. Grimmia Nevii C.M. Ad saxis rivulis. Dr R. D. Nevious Portland Herbarium. Chas. Mohr,

Mobile"; handwritten label: "Prof. C. Mohr from this lot collected by Nevius in the spring 1873 and sent by me to Prof. Mueller the description of this new species was taken" – US!]. First synonymised with *Racomitrium aciculare* by Jones (1933: p. 53).

Racomitrium aciculare fo. *falcatum* Jaap *in* Loeske, Moosfl. Harz: 194. 1903. $\equiv R.$ *aciculare* var. *falcatum* (Jaap) Podp., Consp. Musc. Eur.: 293. 1954, *hom. illeg.* — TYPE CITATION: Auf einem Block im Abbegraben bei Torfhaus, 800 m (!) fand Jaap [...]. [Holotype: "<u>Fl.</u> <u>V. Harz</u>. Racomitrium aciculare f. falcatum m. Torfhaus, in der Abbe auf einem Felsblock. 18.7.1902 leg. O. Jaap" – HBG!], *syn. nov.*

R. aciculare var. *falcatum* Grav. *in* Warnst., Krypt. Fl. Mark Brandenburg 2: 309. 1904. — TYPE CITATION: [...] in Juni 1885 in Belgien bei Louette–Saint–Pierre [...]. [Holotype: "Herbarium Haussknecht, Jena Rhacomitrium aciculare Brid. var. falcatum Grav. Sur les pierres. Louette–Saint–Pierre (Belgique) 3 Juin 1885. F. Gravet" – JE-Schliephacke!; isotype: BR!], *syn. nov.*

R. aciculare var. *radiculosum* Guim., Rev. Liceus 1: 29. 1916. — TYPE CITATION: [Portugal] Serra d'Arga. Setembro 1915. [Holotype: PO (not seen); isotype: "Rhacomitrium aciculare (Linn.) Brid. var. radiculosum A. Mach. Familia Grimmiaceae N° 989B. Localidade Serra de Arga, nas peches dos regados Colector A. Machado Data IX-1915" – LISU!]. First synonymised with *Racomitrium aciculare* by Sérgio *et al.* (1995: p. 116).

R. aciculare fo. *humile* Vilh., Věstn. Král. Česke Společn. Nauk Tř. Mat.-Přir. 1925: 33. 1926 ["humilis"]. — TYPE CITATION: Habitat in montibus Corconticis (Krkonoše – Seifenbach, 1919 Vilh.) et apud flumen Sázava in Bohemia centrali prope Senohraby [SE of Prague] (1919, Vilh.). [Lectotype (*selected here*): "Herbarium J. Vilhelm. Racomitrium aciculare f. humilis Vilh. č. 91/919. <u>Krkonoše</u>. Seifenbach. 2/8 1919. Vilhelm" – PRC!; syntype: "Herbarium J. Vilhelm. Racomitrium aciculare n.f. humilis Vilh. č. 9/5/919. Senohraby. 19/6 1919 Vilhelm" – PRC! = *Niphotrichum canescens*!], *syn. nov.*

R. aciculare fo. *fluviatile* Vilh., Věstn. Král. Česke Společn. Nauk Tř. Mat.-Přir., 1925: 33. 1926 ["fluviatilis"]. — TYPE CITATION: Habitat in rivulis supra dejectum magnum aquae prope Kolbach in Tatris (Vilh.). [Holotype: "Herbarium J. Vilhelm. Racomitrium aciculare f.n. fluviatilis Vilh. č. 198/919. Vys. Tatry – nad obvod. vodopádem (až k vodopádu) smrkový les začíná kosodř. do Malé Studené doliny (Malý Kolbach) 27/8 919. Vilhelm" – PRC!], *syn. nov.*

R. hespericum Sérgio, J.Muñoz & Ochyra, Bryologist 98: 112, *f.* 1-25. 1995. ≡ *Codriophorus hespericus* (Sérgio, J.Muñoz & Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. — TYPE CITATION: Portugal. 29T PE26, Beira Baixa, Serra da Estrela, a l km das Penhas da Saúde, 1,400 m, 1992.01.21, *Sérgio* 7785. [Holotype: "Herbário do Museu, Laboratório e Jardim Botânico de Lisboa (LISU) Racomitrium hespericum Sérgio, Muñoz & Ochyra Det. C. Sérgio Stat. Beira Baixa: Serra da Estrela, a l km das Penhas Saúde. Ecol. Linha de água, nos blocos graníticos e na base de *Erica*. Alt. 1400 m UTM PE26 Data 92.01.21 Leg. C. Sérgio N[®] 7785" – LISU!; isotypes:, KRAM!, MA!], *syn. nov.*

Plants mostly medium-sized, occasionally small or very large, stiff and rigid, mostly coarse and robust, less often rather slender, forming loose tufts or mats, often submerged at high water and floating and having a fruticose habit, dull, mostly divaceous, dark or yellow- to olive-green or yellow-, olive-, golden-, rusty- to blackish-brown above, brown, reddish- or blackish-brown below, sometimes black, blackish- or dirty brown or brown throughout. *Stems* curved-ascending to erect, less often creeping and trailing, often attached to rocks by a discoid radiculose foot, (0.5-)3.0-11.0(-20.5) cm long, tough, reddish-brown to brown, lustrous, often leafless below be-

cause of erosion of the laminae except for the costae in rapidly flowing water and having a bristly appearance, repeatedly forked or sparsely to copiously dichotomously or fasciculately branched, sometimes almost unbranched, in cross-section circular to obscurely angular, lacking a central strand, consisting of a 3-4(-5)-stratose cortex of small stereid cells with reddish-brown to brown, strongly incrassate walls and small lumina and a 6-8-layered medulla of large, yellowish-hyaline, reddish-yellowish to pale orange-brownish, thin- to thick-walled cells with distinct corner thickenings; rhizoids smooth, glistening, sparingly branched, brown, reddish-brown to reddish, sparse or copious, sometimes almost lacking near the base or scattered in clusters along the shoots, sometimes very copious and giving the stems and branches a tomentose appearance; axillary hairs numerous, filiform, hyaline throughout, 6-20-celled, usually with short basal cells and elongate upper cells. Leaves crowded, rigid and stiff, straight to somewhat curved, loosely erect-appressed to imbricate, occasionally erecto-patent, often secund and homomallous, not or rarely slightly crisped on drying, erect-spreading on wetting, (1.5-)2.2-2.9(-3.2) mm long, (0.8-)1.0-1.2 mm wide, variously lingulate, elliptical, broadly ovate, ovate- or oblong-lanceolate to broadly lanceolate, acute, subacute, rounded to broadly rounded-obtuse and muticous at the apex, concave to broadly canaliculate-concave, often auriculate and shortly decurrent at the base; margins recurved on both sides in the lower half, usually more broadly so on one side than the other, plane, erect or somewhat inflexed in the distal part, unistratose throughout or sometimes with 2-3(-4) layered, 2-4-seriate swollen marginal thickenings, entire for about $\frac{3}{4}-\frac{4}{5}$ of the distance to the apex, rarely throughout, irregularly remotely, coarsely, bluntly or sharply toothed, eroso-dentate to sinuate at the apex down the margins to about $\frac{1}{5}-\frac{1}{4}$ of the way below the leaf apex; *costa* single, subpercurrent, ending a few cells from the tip, distinct, vellow, yellow- or reddish-brown to brown, sharply delimited from the laminal cells, sometimes imperceptibly merging with the bistratose laminal cells near the leaf apex, entire or infrequently weakly spurred above, mostly shortly and equally forked at the tip, $(60-)70-160(-180) \, \mu m$ wide near the base, somewhat thinner only in the median and distal parts, in cross-section 2-3-stratose in the distal and median parts, flat ventrally and reniform or lunate, not distinctly convex on the dorsal side or distinctly biconvex and lenticular in outline, anatomically not differentiated, with 3-7 ventral epidermal cells, plano-convex and strongly flattened or crescent-shaped dorsally, 3-6(-7)layered in the basal part, situated in a shallow and wideangled, seldom deeper and narrower-angled furrow, with (3-)5-10(-14) enlarged ventral epidermal cells in a single layer and 2-5(-6) layers of small, thick-walled sclerenchymatous cells forming a distinctly convex stereid band on the dorsal side; laminal cells unistratose throughout to variously bistratose in the distal and median parts, strongly papillose throughout, sometimes weakly so, with large flat papillae situated over the longitudinal walls and covering o major part of the lumina leaving only a narrow slit in

the centre, occasionally smooth or nearly so throughout; upper cells mostly isodiametric, from irregularly roundedquadrate, subquadrate, oval, rounded-hexagonal to bluntly angular or shortly rectangular, thick- and mostly straightwalled, $5-15(-20) \mu m \log$, $(4-)6-10 \mu m$ wide, becoming short-rectangular in mid-leaf, 10-20(-25) µm long, 8–10 µm wide, and long rectangular above the base, (15-)30-55 µm long, 5-8 µm wide; basal cells long rectangular to linear, with strongly thickened, nodulose and porose longitudinal walls, 25-55(-70) µm long, 8-10 µm wide, forming dark yellow, yellow-brown or orangeyellow 2-3-seriate strip along the insertion; alar cells subquadrate to short-rectangular, with rather thin to strongly incrassate, straight or sinuose walls, 20-50 µm long, (10-)15-20(-25) µm wide, forming distinct, inflated or flat, orange-brown, brownish-yellow, brown, yellow to hyaline somewhat decurrent auricles, sometimes only slightly differentiated from the adjacent laminal cells; supra-alar cells shortly rectangular, chlorophyllous, thickand sinuose-walled, usually with distinct spiral thickenings, not differentiated from the adjacent laminal cells. Dioicous. Perigonia gemmiform, 1.2-1.8 mm long; outer perigonial bracts lingulate to ovate-lanceolate, similar to vegetative leaves but somewhat the smaller. 1.2-1.8 mm long, 0.6-0.9 mm wide; inner perigonial bracts broadly ovate, 0.9-1.2 mm long, 0.9-1.0 mm wide, gradually or abruptly narrowed to a short narrowly obtuse, entire apex, brown to orange-brown, with a single, subpercurrent costa, strongly concave, the innermost one bearing about 20 claviform, short-stalked, brownish antheridia intermingled with a few, filiform, hyaline to brownish-hyaline paraphyses scarcely exceeding half the length of the antheridia. Outer perichaetial leaves oblongto ovate-lanceolate, 2.3-3.2 mm long, 0.8-1.0 mm wide, gradually long to short-acuminate, narrowly rounded-obtuse, muticous and entire at the apex; inner perichaetial leaves sheathing the seta, oblong-lanceolate to oblongovate, 1.8-2.5 mm long, 0.8-1.0 mm wide, gradually acuminate, acute to subacute, entire at the apex, with a fairly weak costa vanishing well below the apex, hyaline, yellowish- or brownish-hyaline with an areolation of thinwalled cells throughout the lamina, sometimes with chlorophyllous, thick-walled cells in the distal half or, more often with a small group of chlorophyllous cells at the extreme apex. Setae solitary or sometimes geminate, very rarely triple in the perichaetium, straight or flexuose when dry, erect, (1.8-)4.0-15.0(-17.0) mm long, dextrorse when dry, smooth, lustrous, blackish-brown below, reddish-brown above or brown, brownish-black to dark red throughout; vaginula cylindrical, 1.0-2.0 mm long, dark or rarely light brown to reddish-brown, with rectangular, thick- and sinuose-walled epidermal cells. Capsules exserted, erect, ovoid, ellipsoid, obloid to shortly cylindrical, (1.0-)1.5-2.8(-3.1) mm long, 0.8-1.1(-1.3) mm wide, slightly constricted below the orifice, gradually or suddenly narrowed into the seta, dark or light brown, smooth, dull to slightly lustrous, pachydermous; operculum erect, straight, subulate-beaked, 1.0-2.0 mm long; annulus tardily deciduous, yellow-brown, 60-75 µm high,



FIGURE 20. *Codriophorus acicularis.* — 1. Plant with mature sporophyte. 2. Portion of branch, wet. 3. Portion of branch, dry. 4–9. Leaves. 10–15. Axillary hairs. 16. Transverse section of stem. 17. Leaf apex. 18. Mid-leaf cells. 19. Basal juxtacostal cells. 20–21. Alar cells. 22–27. Transverse sections of leaves, sequentially from apex to base. — [1 from *Ochyra s.n.*, 23 Jun 1973; 2–3, 11–15, 17, 22–24 from *Ochyra 629*; 4–9, 16, 18–21, 25–27 from *Lisowski 93776*; 10 from *Lisowski 91102*; all in KRAM]. — Scale bars: a – 1 mm (2–9); b – 100 μ m (10–27); c – 1 cm (1). (Reproduced from *Fragmenta Floristica et Geobotanica Series Polonica*, 2: 147, 1995, with permission).

2-3-seriate, composed of large vesiculose cells with strongly incrassate walls; exothecial cells predominantly rectangular, mixed with irregularly-shaped cells, (15-)20-50(-65) µm long, 10-20(-25) µm wide, thickwalled, becoming shorter, subquadrate to rounded-quadrate, reddish-brown in 2-4 tiers at the mouth; stomata phaneroporous, numerous at the base of the urn, 15-40 disposed in 2-4 rows, brown to dark reddish-brown, rounded, 25-38 µm wide, bicellular with rounded pori; *peristome* single, consisting of 16 teeth, erect when dry, (300-)350-450(-500) µm long, lanceolate, yellowishbrown to dark reddish-brown, densely low- or spiculatepapillose throughout, bifid or tripartite down to the middle or two thirds of their length, with unequal, terete, articulate, free or cohering branches, often with irregular gaps below, arising from a fairly low, brownish- or orange-yellow basal membrane 25-60 µm tall; preperistome present, hyaline, as high as the basal membrane. Spores spherical to ellipsoid, greenish- or yellowishbrownish, frequently anisomorphic, finely papillose, (10-)15-20(-32) µm in longest dimension. Calvptra conic-mitrate, dark brown and verrucose at the apex, often stramineous when young, naked, not plicate, 4-5lobed at base.

Etymology — The species name derives from the Latin *acicularis* meaning narrow, stiff and pointed like a needle and it was coined by Linnaeus (1753) in reference to the subulate and long-rostrate lids, often reaching two thirds of the urn length.

Diagnostic characters and differentiation — Codriophorus acicularis is one of the most distinctive and easily recognisable moss species which has only rarely been misidentified and misinterpreted. It owes this quite unusual situation amongst mosses to a set of both gametophyte and sporophyte characters which, tout ensemble, warrant its distinctiveness and quite isolated position within the broadly conceived genus Racomitrium. It can obviously be mistaken for the three other species of the type subsection of Codriophorus but two of these have only recently been given taxonomic recognition as new species (C. aduncoides and C. norrisii) and the other (C. mollis) is only here reinstated as a species in its own right. Because these segregates are otherwise closely related and morphologically similar to C. acicularis, the precise definition and characterisation of this core species of the type subsection should obviate any possibility of confusion. Thus, C. acicularis is best circumscribed by the following set of characters: (1) plants variable in size and robustness, predominantly moderately sized to fairly large and robust, rather coarse, stiff and rigid, forming loose tufts or patches, dull, basically dark green or yellowish to blackish-green but quite often in various combinations of these colours or brown, orange, reddish and their hues; (2) stems mostly curved-ascending to erect, sometimes floating in water, attached to rocks and having a fruticose habit, sparingly or copiously dichotomously or fasciculate-branched, occasionally almost unbranched; (3)

leaves straight to weakly falcate, erect, appressed to imbricate when dry, erect-spreading when moist, rigid and stiff, varying greatly in shape from lingulate, elliptical, ovate, ovate- or oblong-lanceolate to broadly lanceolate, acute, subacute, rounded to broadly rounded-obtuse at the apex, concave to broadly canaliculate-concave; (4) margins recurved on both sides in the lower half, unistratose or sometimes limbate with 2-3(-4)-stratose thickenings, entire below or very rarely throughout, irregularly bluntly or sharply and coarsely dentate, eroso-dentate or only sinuate in the upper $\frac{1}{4}-\frac{1}{5}$; (5) costa percurrent, entire or weakly spurred distally, usually shortly and equally forked at the tip, plano-convex or biconvex, 2-3-stratose, anatomically not differentiated, with 3-7 ventral epidermal cells, reniform to crescent-shaped or elliptical to lenticular in outline and not distinctly convex dorsally in the upper ane median parts, 3-6(-7)-stratose in the proximal portion, situated at the bottom of a shallow or moderately deep, wide- or, rarely, narrow-angled groove, with a row of (3-)5-10(-12) enlarged ventral cells and 2-5(-6) layers of small sclerenchymatous cells, forming a distinctly convex, strongly flattened to lunate dorsal stereid band; (6) laminal cells unistratose to variously bistratose in the upper half, distinctly papillose to rarely nearly smooth, thick- and mostly straight-walled, irregularly roundedquadrate, oval to shortly rectangular in the upper part, short-rectangular and distinctly sinuose-walled in midleaf to long rectangular below, linear, with incrassate, nodulose and porose walls at the base; (7) alar cells subquadrate to short-rectangular, moderately thin- to strongly thick-walled, forming convex to flat, colourful, somewhat decurrent auricles; (8) supra-alar cells not differentiated; (9) setae mostly single in the perichaetium, erect, straight or somewhat flexuose, (1.8-)4.0-15.0(-17.0) mm long, twisted clockwise when dry, brown, blackish- or reddish-brown to dark red; (10) capsules erect, ellipsoid, obloid to short-cylindrical, (1.0-)1.5-2.8(-3.1) mm long, 0.8-1.1(-1.3) mm wide, dark or light brown, dull to slightly lustrous, pachydermous; (11) peristome teeth erect, lanceolate, (300-)350-450(-500) µm long, densely covered with low or spiculate papillae throughout, irregularly divided into 2 or 3 branches to the middle or for two thirds of their length, with a fairly low basal membrane.

As stated above, Codriophorus acicularis is most closely related to the other three species of subsect. Codriophorus, two of which are only recently recognised segregates of this species which has been known from the beginnings of bryology. The characters distinguishing these species are discussed in detail under the species concerned and here are only briefly summarised. The principal character which accurately and unmistakably distinguishes C. acicularis from C. mollis and C. aduncoides is the shape of the costa. In C. acicularis it is invariably long and percurrent, ending only a few cells below the leaf apex and, additionally, it is entire or only slightly spurred in the distal portion and is only shortly and equally forked at the apex. In contrast, in C. mollis and C. aduncoides the costa is much shorter and typically extends for $\frac{1}{2}-\frac{3}{4}$ of the leaf length. Furthermore, it is dis-



FIGURE 21. Codriophorus acicularis. — 1. Perigonium. 2–4. Outer perigonial bracts. 5–9. Inner perigonial bracts. 10. Inner perigonial bract with antheridia. 11–14. Outer perichaetial leaves. 15–18. Inner perichaetial leaves. 19. Apex of inner perichaetial leaf. 20. Basal cells of inner perichaetial leaf. 21–22. Capsules with operculum. 23–32. Deoperculate capsules. 33. Operculum. 34. Calyptra. 35–37. Transverse section of calyptra. 38. Transverse section of seta. 39. Epidermal cells of seta. 40. Epidermal cells of vaginula. 41. Exothecial cells in middle of urn. 42. Lower exothecial cells and stomata. 43. Peristome teeth, spores aned exothecial cells at orifice. — [1–10 from *Lisowski 389*; 11–19, 23, 27–29 from *Ochyra s.n.*, 23 Jun 1973; 20, 24–26, 33–34, 41–42 from *Lisowski 93776*; 22–22 from *Limpricht 220*; 30 from *Bornmüller s.n.*, 13 Aug 1927; 31–32 from *Schoepke s.n.*, 20 Jul 1879; 35–40 from *Ochyra 629*; all in KRAM]. — Scale bars: a – 1 mm (21–32); b – 1 mm (11–18, 33–34); c – 100 µm (19–20, 35–43); d – 1 mm (1–10). (Reproduced from *Fragmenta Floristica et Geobotanica Series Polonica*, 2: 149, 1995, with permission).

tinctly spurred and forked at the apex but the branches of the fork are slender and unequal and usually one of them is much longer and may extend much higher up than the other, sometimes for 5% of the way up the leaf.

A supplementary character which is a great help in separating *Codriophorus mollis* from *C. acicularis* is the very broadly rounded-obtuse and often cucullate leaf apex that is perfectly entire or only sometimes sinuate or with a few low, indistinct, distant and blunt teeth. In contrast, *C. aduncoides* often has narrowly subacute to acute leaf apices with incurved, sharply dentate margins giving them a tubular to subcucullate appearance.

Codriophorus acicularis shares costa shape with C. norrisii from the Pacific coast of North America. The latter species is primarily diagnosed by having salient bistratose limbidia at the leaf margins that extend from base to apex and are usually 2-10-seriate. Conversely, C. acicularis has predominantly unistratose laminal cells including those at the margins, although in many European populations the leaf cells are variously polystratose. These forms are especially frequent in the Iberian Peninsula and reach the culmination in populations described as Racomitrium hespericum (Sérgio et al. 1995) in which the leaf cells in the distal half are mostly bistratose and the margins are distinctly bordered with fleshy, 2-4-layered thickenings. They are truly likely to be mistaken for C. norrisii. However, North American plants of C. acicularis are very uniform with regard to the stratosity of the laminal cells which are always unistratose and only in a single population from California (Shevock & York 18322, CAS KRAM) are the leaf cells bistratose. The populations of C. acicularis with multistratose laminal cells may safely be distinguished from C. norrisii by essential differences in the papillosity of the leaf cells. C. acicularis has strongly papillose laminal cells with very large, flat papillae covering the cell walls and major part of the lumina, leaving only a narrow central slit, whereas C. norrisii has almost glabrous older leaves and in younger leaves the papillae cover only the cell walls, leaving the lumina without cuticular thickenings.

Codriophorus acicularis is such a distinctive and unmistakable species that misnamings are only very occasional and are the result of careless examination of solitary leaves rather than by any wide-ranging variation in the essential structural characters of the plants themselves. Very rarely, some specimens of C. aquaticus and C. depressus have been misdetermined as C. acicularis, probably owing to the external similarity of the plants growing in identical aquatic habitats. This is particularly likely in the case of plants of C. acicularis having ovate to ovatelanceolate leaves with narrowly acute or subacute apices which are more or less distinctly dentate or sinuate, at least on some leaves, in contrast to the perfectly entire leaf apices in C. aquaticus. In C. depressus the leaf apex may occasionally be indistinctly and bluntly dentate, but the smooth laminal cells, especially on the older leaves, definitely preclude the possibility of confusion.

Codriophorus acicularis has sometimes been mistaken for species belonging within other, mostly unrelated,

genera having lingulate leaves with broadly roundedobtuse apices. Bridel (1827) described *Orthotrichum submarginatum* from Newfoundland which he initially intended to recognise as a variety of *O. obtusifolium* as is clear from the label on the type material. Additionally both species possess papillose laminal cells and subpercurrent costae. However, putting aside the essential differences in the sporophyte characters between *Codriophorus* and *Orthotrichum*, these genera definitely differ in leaf areolation. The latter has irregularly rounded upper and median leaf laminal cells with a large, single, central conical papilla.

Palisot de Beauvois (1805) described from North America *Trichostomum obtusifolium* which was subsequently transferred by Bridel (1819) to *Racomitrium* as *R. obtusifolium* (P.Beauv.) Brid. and Arnott (1825) reduced this species to an unranked infraspecific taxon within *Trichostomum aciculare*. Lindberg (1875) formally reduced this species name to synonymy with *Racomitrium aciculare*, a concept accepted by Jones (1933). The taxonomic status of this species was clarified by Bednarek-Ochyra (2001) who showed its conspecificity with *Anomodon minor* (Hedw.) Lindb. The pleurocarpous moss genus *Anomodon* Hook. & Taylor indeed shares with *Codriophorus acicularis* lingulate leaves with broadly rounded apices but its small, hexagonal and pluripapillose laminal cells are immediately distinctive.

Occasionally, *Codriophorus acicularis* has also been mistaken for some environmental modifications of certain species of *Niphotrichum* characterised by ovate to elliptical, concave leaves with rounded-obtuse and muticous apices. Such plants have been confused with *C. acicularis* in China (Cao 2000; Cao *et al.* 2003) but they actually represent *Niphotrichum japonicum* (Dozy & Molk.) Bednarek-Ochyra & Ochyra and the presence of tall conical papillae over the lumina as well as large, hyaline, swollen auricles exclude any alliance of these plants with *C. acicularis* (Bednarek-Ochyra 2004*a*). Likewise, one of the syntypes of *Racomitrium aciculare* fo. *humile* from Slovakia (Vilhelm 1926) actually represents an epilose ecad of *Niphotrichum canescens*.

Variability — As is the case with with all geographically widely distributed moss species associated with aquatic habitats Codriophorus acicularis exhibits a remarkable phenotypic plasticity. This is evidently induced environmentally and is manifested in to a number of quantitative characteristics including the size, stature, branching pattern and colour of the plants, the size and shape of both leaves and capsule as well as seta length. Despite this variation, C. acicularis has been quite correctly interpreted by bryologists and actually only three heterotypic synonyms of this name at species level are known. There are quite a number of infraspecific names which have been proposed for various phenotypes of this species or for indicating a concrete ecological status of the plants, although the identity of some of these taxa cannot be precisely established due to the lack of the relevant type collections. At least some of these taxa



FIGURE 22. Codriophorus acicularis. — 1. Portion of branch, wet. 2. Portion of branch, dry. 3–13. Leaves. 14–28. Transverse sections of three leaves, sequences from base to apex. — [1 from Sérgio, Séneca & Jansen 8296; 2, 11–12 from Muñoz 2042; 3 from Sérgio et al. 8293; 4, 14–18 from Sérgio 5806; 5–6 from Melo s.n., 28.3.1990, LISU; 7–8 from Sérgio 8662; 9–10, 21–24, 26–27 from Sérgio 7785, isotype of Racomitrium hespericum; 13, 19–20, 25, 28 from Luisier 7548, LISU; all in KRAM unless otherwise stated.]. — Scale bars: a – 0.5 cm (1–2); b – 100 μ m (14–28); c – 1 mm (3–13).



FIGURE 23. *Codriophorus acicularis.* — 1. Leaf apex. 2. Upper laminal cells at margin. 3. Mid-leaf cells. 4. Basal juxtacostal cells. 5. Angular cells. 6. Transverse section of stem. 7–9. Axillary hairs. — [1–3, 6 from *Sérgio 7785*, isotype of *Racomitrium hespericum*; 4–5 from *Muñoz 2042*; 7–9 from *Sérgio, Séneca & Jansen 8296*; all in KRAM]. — Scale bars: a – 100 µm (7–9); b – 100 µm (1–5); c – 100 µm (6).



FIGURE 24. *Codriophorus acicularis.* 1. Plant with mature capsule, wet. 2. Perigonium. 3–5. Perigonial bracts, sequence from outermost to innermost. 6. Innermost perigonial bract and antheridia. 7–9. Perichaetial leaves, sequence from outermost to innermost. 10. Apex of innermost perichaetial leaf. 11. Epidermal cells of vaginula. 12. Transverse section of seta. 13. Calyptra. 14. Transverse section of calyptra. 15–16. Deoperculate capsules, wet. 17. Operculate capsule. 18. Operculum. 19. Exothecial cells in mid-urn. 20. Exothecial cells at base of urn and stomata. 21. Exothecial cells at capsule mouth, annulus, peristome and spores. — $[1-6, 13-15 \text{ from Sérgio, Seneca & Jansen 8296; 7–9, 11–12, 16–21 from Melo s.n., 28.3.1990, LISU; 10 from Sérgio 5806; all in KRAM unless otherwise stated]. — Scale bars: a – 1 cm (1); b – 1 mm (6); c – 100 µm (10–12, 14, 19–20); d – 1 mm (2–5, 7–9); e – 100 µm (21); f – 1 mm (13, 15–18).$

actually refer to other species, not to *C. acicularis*, for instance *Racomitrium aciculare* var. *brachypodium* described by Bescherelle (1893) from China is identical to *Codriophorus carinatus*. Likewise, Turner (1804) recognised three varieties within his *Dicranum aciculare* but only one of these, var. *fluitans*, probably refers to aquatic plants of *C. acicularis*. The other two varieties, var. *gracile* and var. *pumilum*, are respectivedly identical to *C. aquaticus* and *Bucklandiella obtusa* (Brid.) Bednarek-Ochyra & Ochyra (Frisvoll 1988).

Codriophorus acicularis plants are typically mediumsized and their stems are on average 3-11 cm long. The largest and most robust specimens have been collected in Spain (Franco 1090, BCB) with stems reaching to 20.5 cm, whereas the smallest known plants, reaching only 5 mm, were described by Vilhelm (1926) as Racomitrium aciculare fo. humile from the Czech part of the Giant Mountains in the Sudetes. There is a broad spectrum of variation in the type of branching which ranges from shoots which are filiform and almost unbranched (e.g., Florin s.n., 17 Sep 1927, s) to others which are copiously and repeatedly branched, giving the plants an attractive bushy appearance (e.g., Eyerdam s.n., 15 Oct 1940, WTU). C. acicularis plants are normally sparsely or copiously radiculose near the base or in the lower parts of the shoots, but exceptionally stems are densely tomentose with long rhizoids throughout their length. Such phenotypes were given taxonomic recognition as Racomitrium aciculare var. radiculosum but this variety does not otherwise deviate from typical expressions of the species in the structural characters of the leaves. The colour of the plants varies markedly and is usually correlated with inundation and insolation, with most being dark green or yellow- to olivegreen, but submerged plants are often blackish-brown to entirely black (e.g., Florin s.n., 29 Jun 1942, s).

The leaves are subject to remarkable variability in Codriophorus acicularis and their shape ranges from lingulate through oblong- or ovate-lanceolate to broadly ovate or elliptical (Fig. 26). The size of the leaves is correlated with the robustness of the plants and on average the length ranges from 2.2 to 2.9 mm, with the extremes extending to 1.5 and 3.2 mm. The width of the leaves is also variable, though within narrower limits, from 1.0 to 1.2 mm, and only rarely are they as narrow as 0.8 mm. Two varieties have been described within C. acicularis and designated as Racomitrium aciculare var. angustifolium, one from the Sierra Nevada in Spain (Höhnel 1895) and the other from the Ore Mountains (Erzgebirge) in Central Europe (Röll 1907). The varietal epithet suggests narrow-leaved expressions of the species but because the type collections have not been located, these taxa could not be taxonomically evaluated. The leaves are usually straight but sometimes weakly falcate and such plants were recognised as separate taxa, R. aciculare fo. falcatum (Loeske 1903) and var. falcatum (Warnstorf 1906). The leaf apex varies from broadly rounded-obtuse to narrowly acute and in general it is nearly always distinctly toothed, especially on the younger leaves (Figs 25.1-5). The dentation of the leaf apex is irregular and rather remote and varies from sharp

and coarse to blunt and indistinct. Only seldom is it considerably reduced and the leaves are subentire to occasionally entire at the apex. Bruch *et al.* (1845) established a status for the plants with sharply dentate leaf apices by the recognition of *Racomitrium aciculare* var. *denticulatum*, but no original material bearing this name has been located. However, a good illustration of this taxon is here selected as lectotype and it clearly indicates that this variety does not deserve the separate status.

The costa is fairly stable with regard to its length and it invariably ceases several cells below the apex. More variable is its width and anatomical structure. The costa width is correlated with the robustness of the plants and varies within the limits typical of all aquatic mosses, generally ranging from 70 to 160 µm at the base, only occasionally falling slightly outside these values. The costa is either flat throughout its whole length on the ventral side or distinctly convex ventrally in the upper and median parts. Plants with a biconvex costa are especially frequent in western North America (Fig. 27.1-3) and initially this character was assumed to have good diagnostic value for an intended new taxon segregated from Codriophorus acicularis. However, detailed examination of the costal anatomy throughout the whole range of this species has revealed that the ventral convexity of the costa is observed with varying frequency in many populations in North America and Europe and recognition of western North American plants with a distinctly lenticular or elliptical costa in the upper and median parts is unjustified as it would create an artificial taxon which could hardly be distinguished from C. acicularis.

Leaf areolation is rather uniform in Codriophorus aci*cularis* with regard to cell shape. Most cells are strongly papillose but sometimes the papillosity is weak to entirely absent, especially on older leaves (e.g., Norris 12258, UC; Ireland 5914, ALTA, CANM, MICH, NY, US) (Fig. 27.5-6). In all Floras, handbooks and taxonomic treatments this species is described as having perfectly unistratose laminal cells. However, careful study of the leaf anatomy of the populations from the Iberian Peninsula revealed the frequent occurrence of bistratose laminal cells which are even 2-3(-4)-layered at the margins (Fig. 22.20, 23-27; 28.1–4). These plants were described as a new species, Racomitrium hespericum, which appeared to be a sound taxon (Sérgio et al. 1995). Closer examination of the leaf anatomy showed fairly frequent bistratosity of laminal cells, especially at the margins, in Europe, including Scotland (Walton s.n., 1 Mar 1939, KRAM), France (Dismier 96, BCB, BR, KRAM, NY, WTU), Bulgaria (Petrov 3865-B, SOM), Iceland (Jóhannsson 4905, ICEL), Sweden (Hasslow s.n., 4 May 1914, KRAM), and Germany (Schemann s.n., 1 Jan 1892, KRAM). Interestingly, so far only a single population of C. acicularis with entirely bistratose laminal cells has been discovered in North America (Shevock & York 18322, CAS, KRAM) with just two others containing some bistratose strands in the upper part (McGrew 156, UC; Norris 76740, KRAM, UC). Additionally, examination of the type collections of Racomitrium hespericum showed that the tendency for multiplication of layers of



FIGURE 25. Codriophorus acicularis. — 1–5. Leaf apices. 6. Upper cells at margin. 7. Mid-leaf cells. 8. Alar cells. — [1, 4 from Macoun 17B, BM; 2, 5–8 from Landals & Scotter 810, ALTA; 3 from McCleary 520, COLO]. — Scale bar: 100 µm.

laminal cells is random in this species and even on the same shoot there are leaves with perfectly unistratose laminal cells sitting next to ones whose laminal cells are entirely bistratose. Sometimes on one leaf the lamina is variously bistratose on one side of the costa and wholly unistratose on the other (Figs 28.1,3). Because all possible intergradations and combinations may be observed in this character, its diagnostic value must be considered doubtful. The stratosity of the laminal cells is evidently an adaptation and reaction of the species against the destructive action of rapidly flowing water and presumably the genetic determination of this character can be easily modified. A similar situation is observed in other aquatic mosses, including the genus *Codriophorus* itself



FIGURE 26. *Codriophorus acicularis.* — 1–53. Spectrum of vegetative leaves showing geographical variation of plants from Japan, Asia (1–2), North America including California (3–13), Washington (14–16), Colorado (17–20), Arizona (21–23), British Columbia (24–35) and Arkansas (36–38), Europe including Portugal (39–44), the Faeroe Islands (45–46) and the Kola Peninsula (47–49), Madeira, Macaronesia (50–51) and Algeria, North Africa (52–54). — [1–2 from *Iwasaki s.n.*, Aug 1916, NICH; 3–5 from *Norris 12258*, UC; 6–9 from *Norris 23272*, UC; 10–13 from *McGrew 550*, UC; 14–16 from *Schofield & Boas 22276*, CANN; 17–20 from *Rolston 82185*, COLO; 21–23 from *McCleary 520*, COLO; 24–26 from *Macoun 17B*, BM; 27–32 from *Landals & Scotter 810*, ALTA; 33–35 from *Vitt 34393*, ALTA; 36–38 from *Redfearn & Shimizu 33201A*, ALTA; 39–40 from *Sérgio 8877*, LISU, paratype of *Racomitrium hespericum*; 41–42 from *Sérgio & Séneca 8769*, LISU, paratype of *Racomitrium hespericum*; 43–44 from *Sérgio 285*, LISU; 45–46 from *Lewinsky 4638*, ALTA; 47–49 from *Shlyakov s.n.*, 27 Jul 1957, KRAM; 50–51 from *Persson s.n.*, 6 Jun 1952, ALTA; 52–53 from *Trabut s.n.* (Djudjura), PC]. — Scale bar: 1 mm.



FIGURE 27. *Codriophorus acicularis.* — 1–9. Transverse sections of leaves showing variation in plants from North America including Colorado (1), California (2, 5), British Columbia (3–4), Washington (6), Madeira, Macaronesia (7), the Kola Peninsula (8) and Japan, Asia (9). — [1 from *Rolston 82185*, COLO; 2 from McGrew 550, UC; *Landals & Scotter 810*, ALTA; 4 from *Shaw 2762*, ALTA; 5 from *Norris 12258*, UC; 6 from *Ireland 5914*, ALTA; 7 from *Persson s.n.*, 6 Jun 1952, ALTA; 8 from *Shlyakov s.n.*, 27 Jul 1957, KRAM; 9 from *Iwasaki s.n.*, Aug 1916, NICH]. — Scale bar: 100 µm.

(*C. aquaticus*, *C. depressus*), but also in *Vittia pachyloma* (Mont.) Ochyra (Ochyra 1987*a*), *Platylomella lescurii* (Sull.) A.L.Andrews (Ochyra 1987*b*) and *Gradsteinia andicola* Ochyra (Ochyra 1990). Therefore recognition of *Codriophorus hespericus* as a separate species has weak foundations and its name is here considered synonymous with *C. acicularis*.

The sporophyte of Codriophorus acicularis varies much with regard to seta length and capsule shape and length. The setae are generally solitary in the perichaetium, and only occasionally are they geminate or triple (e.g., Hintze & Kohlhof 337, POZG). The length of the seta varies from very short, 1.8-2.0 mm (e.g. Muñoz 592, herb. Frahm) to 17 mm (e.g., Frye s.n., 15 Aug 1922, WTU), but on average they are 4-15 mm long. Likewise the capsules vary in shape from ovoid to short-cylindrical and are typically 1.5-2.8 mm long, although sometimes they can be only 1.0-1.1 mm (e.g., Loof E51, MICH) or 3.1 mm long (e.g., Schofield & Krajina 39669, DUKE). There is no correlation between the lengths of capsules and setae, nor do they show any geographical affiliation. The specimens from western North America having fairly short capsules (1.4-1.6 mm) sitting on relatively short setae (1.5-1.8 mm) were described as Racomitrium nevii (Müller 1873; Mohr 1874) but similar sporophytes are not infrequent in other parts of the geographical range of C. acicularis and it is impossible to consider them as a peculiar character state.

Reproduction — Codriophorus acicularis is a prolific species which frequently produces mature sporophytes throughout its wide geographical range. In practice sporophytes were observed in roughly half the specimens examined, but they rather infrequently occured in great abundance.

Taxonomic and nomenclatural notes - In contrast to other Codriophorus species described early on, C. acicularis has a fairly simple and straightforward taxonomic and nomenclatural history. It is one of eight species recognised by Dillenius (1741) in Historia muscorum within the broadly understood genus Racomitrium which was designated by the polynomial phrase-name Bryum montanum hemiheterophyllum, operculis acutis. This author cited as a synonym another polynomial name of this species, Bryum hypnoides erectum montanum, erectis capitulis acutis proposed by Ray (1724) and this is the earliest recognition of C. acicularis as a species in its own right. The Dillenian species was subsequently accepted by Linnaeus (1753) who proposed for it the binomial name 'Bryum aciculare L.' and under this name it exists in many Floras and taxonomic treatments of the second half of the 18th century (e.g., Hudson 1762; Linnaeus 1763, 1767; Lightfoot 1777; Murray 1784; Lamarck 1785). However, it was also given a name in other genera, including Mnium (Gmelin 1791; Laicharding 1794), Hypnum (Scopoli 1772) and Dicranum (Hedwig 1782, 1792; Hoffmann 1796; Swartz 1799; Röhling 1800; Roth 1800). It is worth noting that Haller (1768) proposed another phrase-name for Codriophorus acicularis, Bryum foliis imbricatis, lanceolatis, setis alaribus, capsulis aristatis.

Hedwig (1801) accepted Dicranum aciculare in his Species muscorum frondosorum and gave direct references to pre-1801 descriptions of this species, thus validating this name. The generic placement of the species was accepted only by Turner (1804) and Smith (1804) and most authors approved Trichostomum as its home (Palisot de Beauvois 1805; Weber & Mohr 1807; Schkuhr 1811; Schwägrichen 1811; Hooker & Taylor 1818; Funck 1820). Subsequently, Bridel (1819) positioned Dicranum aciculare in his newly recognised genus Racomitrium and since then the species has been firmly established as a member of this genus as R. aciculare. In the first half of the 19th century some authors placed the species in other genera, including Campylopus (Wahlenberg 1826) and the then all-encompassing Grimmia (Müller 1849), but these taxonomic concepts have not gained approval. Palisot de Beauvois (1822a, b) described a new genus Codriophorus to accommodate two species, C. acicularis and C. pulvinatus, but this generic name fell into total oblivion. Bednarek-Ochyra et al (2001) lectotypified this generic name with C. acicularis and reinstated Codriophorus as a proper name for the second largest segregate of the catch-all genus Racomitrium.

In the validating description of Dicranum aciculare Hedwig (1801) failed to quote any specimen(s) and only listed many places in Europe whence this species had been collected. He gave only direct and indirect references to the many pre-1801 publications in which this species was described, including his own work of 1792 in which he provided an excellent analytical plate with illustrations of various details of D. aciculare (Hedwig 1792). In that publication is mentioned one locality of this species, namely "Saxa alveorum fluviorumque montosorum. Mihi copiose obviam fuit in saxis Muldae, ubi Arcem Rochsburg oppidumque Poenig in Saxonia praeterfuit". A specimen corresponding to this locality is present in Hedwig's personal herbarium at G (Price 2005) and was selected as lectotype of Dicranum aciculare (Bednarek-Ochyra & Ochyra 1994a). It contains six shoots permanently attached to the herbarium sheet which evidently originate from the same population. Nonetheless, in order to fulfil the requirements of orthodox nomenclaturalists, the third specimen from the left in the upper row was selected as lectotype and its details were illustrated by Bednarek-Ochyra & Ochyra (1994a).

Codriophorus acicularis has been unequivocally interpreted by bryologists and consequently it has only twice been recognised as a different species in North America and once in Europe. Bridel (1827) described it as *Orthotrichum submarginatum* from Newfoundland and Müller (1873) as *Grimmia nevii* from Oregon. The latter species was redescribed by Mohr (1874) and subsequently transferred to *Racomitrium* by Watson (1880). Frye (1917) considered this species as a variety of *Racomitrium aciculare* and Jones (1933) placed *R. nevii* in synonymy with *R. aciculare*. The only European heterotypic synonym of *C. acicularis* is proposed here and it is *Racomitrium hes-*



FIGURE 28. Codriophorus acicularis. — 1–5. Transverse sections of leaves showing variation in plants from the Iberian Peninsula. — [1 from Sérgio & Schumacker 5403, LISU (cross-sections of leaves from two branches of the same plant); 2 from Sérgio & Séneca 8769, LISU, paratype of Racomitrium hespericum; 3 from Sérgio 8877, LISU, paratype of Racomitrium hespericum (cross-sections of leaves from tip of a single branch); 4 from Muñoz 2042, ALTA; 5 from Fuertes s.n., 11 Jul 1984, MA].). — Scale bar: 100 μm.

pericum which refers to a species described from the Iberian Peninsula for plants with variously bistratose laminal cells (Sérgio *et al.* 1995).

Chromosome number — So far, *Codriophorus acicularis* has been studied chromosomally three times. In three populations originating from Washington on the Pacific coast of North America the haploid chromosome number of n = 12 was found (Ireland 1965, 1967), whereas in 13 populations examined from the British Isles the constant number n = 13 was recorded (Smith & Newton 1967).

Habitat — Codriophorus acicularis is a hydrophilous moss that tolerates periodic desiccation. It grows on bare rock faces or thin soil over rock outcrops. The most usual habitat for it is on dripping cliffs and on rocks, boulders, slabs and blocks in stream beds or close to brooks and rivers, as well as in seasonal creeks and on lake shores that are periodically washed by wave action or submerged. It occurs in open or shady places, at a level that makes the moss liable to periodic submersion. Sometimes the species is found permanently submerged in swiftly flowing streams, waterfalls and among rapids and then the stems of such plants may attain a remarkable length. The moss decidedly prefers acidic rocks including granite and sandstone, although occasionally it has been found on calciferous rocks. Very rarely the moss the moss has been found on tree bark. The species usually forms pure stands and only occasionally does it grow mixed with *C. aduncoides*, *C. norrisii*, *C. aquaticus* and *C. varius*. Admixtures in herbarium specimens of *C. acicularis* are rather scarce and include such bryophyte species as *Brachythecium plumosum* (Hedw.) Schimp., *Dichodontium pellucidum* (Hedw.) Schimp., *Hygrohypnum ochraceum* (Turner) Loeske, *Platyhypnidium riparioides* (Hedw.) M.Fleisch., *Schistidium rivulare* (Brid.) Podp., *Scapania undulata* (L.) Dumort. and *Chiloscyphus polyanthos* (L.) Corda var. *rivularis* (Schrad.) Nees.

The bryophyte communities dominated by the aforementioned moss and liverwort species are assigned to the class *Platyhypnidio-Fontinaletea antipyreticae* and the order *Brachythecietalia plumose*. *Codriophorus acicularis* itself is considered as a characteristic species of the alliance *Racomitrion acicularis* to which belong several moss associations that develop in montane streams and brooks on non-calcareous rocks (Krusenstjerna 1945; Philippi 1956; Hübschmann 1957, 1986; Sjögren 1964; Hertel 1974; Marstaller 1993). One of the commonest of them is *Brachythecietum plumose*, an association widely distributed in the mountains of central and northern Europe for which *C. acicularis* is considered to be a characteristic species (Philippi 1956; Neumayr 1971; Hertel 1974; Hübschmann 1986). In addition, it is a frequent component of such associations as *Scapanietum undulatae*, *Hygrohypnetum ochraceae* and *Fontinaletum squamosae* (Hübschmann 1986).

Geographical distribution — Codriophorus acicularis is a boreal-montane species, slightly penetrating into the Arctic in Europe, with a marked oceanic affiliation (Ochyra *et al.* 1990*a*; Bednarek-Ochyra 1995). It has a strongly fragmented pan-Holarctic distribution with its maximum occurrence in Europe and North America, whereas in Asia it is known only from a single locality on the island of Kyushu in Japan (Fig. 29). Other records of this species from China in mainland Asia proved to be misdeterminations of the specimens correctly referred to *Niphotrichum japonicum* (Dozy & Molk.) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra 2004*a*).

In Europe (Fig. 30) Codriophorus acicularis is widespread and locally abundant in the north-western part of the continent, especially in Iceland (Jóhannsson 1993), the British Isles (Proctor 1992a) and western and southern Fennoscandia including Norway where it is especially common in the lowlands in the south-western part of the country, becoming infrequent and scattered northwards, reaching its northernmost known station in Måsöy in Finmark at lat. $ca 71^{\circ}$ N. It also occurs in southern Sweden and in eastern Fennoscandia the species is fairly rare and localised in southern and central Finland, extending east-



FIGURE 29. Global distribution map for Codriophorus acicularis.


FIGURE 30. Distribution map for Codriophorus acicularis in Europe and North Africa.

wards to Karelia, with a fairly frequent occurrence in the western part of the Kola Peninsula (Shlyakov & Konstantinova 1982) and a single, inexactly localised station in Nenetzkij Autonomous Okrug in the north-eastern part of Arkhangelsk Province in the Arctic. In mainland Europe C. acicularis is widely distributed and locally common and abundant, becoming less frequent in southern Europe. It is especially frequent in the mountains, ranging from the Iberian Peninsula where it is widespread in the northern and central parts of the area, through to the Alps and lower mountain ranges of Central Europe, eastwards to the Eastern Carpathians of Poland (Stebel & Bednarek-Ochyra 2004) and the Ukraine and the Southern Carpathians of Romania and the mountains of Bulgaria. In addition, it is scattered in relictual stations on erratic blocks in the Central European Plain of northern Germany and Western Pomerania of northern Poland. In the Mediterranean region the species is infrequent and localised, ranging from southern Spain through to Corsica, Sardinia and Sicily and the Apennines Peninsula where it extends to Calabria (Cortini Pedrotti 2001), eastwards to Montenegro and Serbia, northern Greece on the Balkan Peninsula and western Turkey in Asia Minor. Additionally, some highly isolated and disjunct localities are known from the Pontic Mountains of north-eastern Turkey, the Caucasus and the Ural Mountains. Moreover, C. acicularis is known from some localities in North Africa (Fig. 30) including the coastal mountains of Algeria and Tunisia and once it was recorded on the Sinai Peninsula (Decaisne 1834; Hart 1891; El-Saadawi et al. 1999) but no voucher specimen confirming this record has been located during the present revision. Outside continental Europe C. acicularis is known from some Macaronesian islands in the Atlantic Ocean including the Azores, Canaries and Madeira. The



FIGURE 31. Distribution map for Codriophorus acicularis in North America.

altitudinal range of *C. acicularis* in Europe extends from sea level to 2870 m in the Swiss Alps (Limpricht 1890).

In North America *Codriophorus acicularis* is bicentric in distribution and very common both in the Pacific and Atlantic parts of the continent (Fig. 31). In western North America it occurs in the Aleutian Islands, extending from Attu Island to the Kenai Peninsula in southern Alaska, then ranging along the Coastal Mountains from south-eastern Alaska and northern British Columbia through the Queen Charlotte Islands to Vancouver Island and continung southwards along the Coastal Ranges and the Cascades from Washington through to Oregon to the Sierra Nevada in central California, then recurring in the Rocky Mountains of southern British Columbia, Idaho and Montana, with a highly isolated and disjunct station in the Rockies of northern Colorado where it reaches its highest altitude of 3292 m. Another isolated, southernmost North American locality is situated at the high elevation of 2240 m in southern Arizona. In eastern North America *C. acicularis* has a continuous range from south-eastern Labrador, Newfoundland and the maritime provinces of Canada along the Appalachians from Maine to northern Georgia and Alabama and in the Great Lakes basin in Québec, Ontario, New York, Pennyslvania, Ohio, Michigan, west to Minnesota and Wisconsin, with two isolated stations on the Ozark Plateau of Arkansas and Oklahoma. In this part of the continent it reaches its highest elevation of 1525 m in the Great Smoky Mountains of Tennessee.

The bryological literature often indicates the occurrence of Codriophorus acicularis in South Africa. It was reported from the Cape region by Sim (1926) who interpreted Grimmia pseudoacicularis Müll.Hal. [= Racomitrium pseudoaciculare (Müll.Hal.) Paris] as a synonym of Racomitrium aciculare. Apart from the superficial similarity of the names and identical ecological requirements of these species, the South African taxon has nothing in common with the Holarctic Codriophorus acicularis. Magill (1981) found this species to be conspecific with Racomitrium nigroviride (Müll.Hal.) Paris and Ochyra et al. (1988) suggested its definite identity with R. lamprocarpum (Müll.Hal.) A.Jaeger [= Bucklandiella lamprocarpa (Müll.Hal.) Bednarek-Ochyra & Ochyra]. Although this issue was discussed in detail by Ochyra et al. (1990a) who presented global distribution maps for *C. acicularis*, even in some recent treatments (e.g., Dierßen 2001) the misleading information on the occurrence of this species in South Africa is repeated. This prompted Bednarek-Ochyra (2004a) to reiterate that C. acicularis has never been correctly reported south of the equator.

EXSICCATI

- Allen *Mosses of the Cascade Mountains, Washington* No. **30** (CANM, COLO, DUKE, F, FH, M, MICH, MO, NY, TENN, UC, US).
- Allen & Pursell Maine Mosses No. 33 (MO).
- ANDRES Dr. Phil. Wirtgen: Herbarium Plantae Criticae, Selectae, Hybridae Florae Rhenanae No. 16 (BR, M); No. 17 (BR); No. 220 & 627 (BR, M, W); No. 935 (BR, M).
- ARDISSONE Erbario Crittogamico Italiano Ser. II No 1312 (G, M, UC, W).
- AUSTIN Musci Appallachiani No. 147 (CANM, CAS, MICH, MO, NY, O, US).
- BAUER *Musci Europaei Exsiccati* No. **831** (BR, BRNM, COLO, herb. Frahm, JE, KRAM, M, POZG, PRC, UC, W).
- BERDOWSKI Flora Silesiaca Exsiccata No. 1265 (CANM, herb. Frahm, KRAM, W).
- BILLOT Flora Exsiccata De C. Billot (cont. par Bavoux, Guichard, Guichard & Paillot) No. **3964** (US).
- BLANDOW Musci Frondosi Exsiccati No. 115 (UC, W).
- BRASSARD Bryophyta Exsiccata Terrae-Novae et Labradoricae No. 105 (ALTA, BM, BR, COLO, CANM, H, MICH, MO, O, TENN).
- BREUTEL Flora Germanica Exsiccata No 43 (BR, GJO, M, UC); No 64 (UC, W).
- BROTHERUS Bryotheca Fennica No. 31 (M, S).
- BROTHERUS Musci Fenniae Exsiccatae No. 379 (G, S, W).
- CRUM & ANDERSON *Mosses of North America* No. **220** & **227** (BM, BR, COLO, CANM, FLAS, H, KRAM, MICH, MO, O, POZG, TENN, UC).
- DE SLOOVER Herbier Bryologique No. 640 (ALTA, BR, H, KRAM)
- DELOGNE & GRAVET Les Mousses de L'Ardenne No. 66 (BR).
- DISMIER Bryotheca Gallica No. 96 (BCB, BR, KRAM, NY, WTU);
- DRUMMOND *Musci Americani* No. **133** (BM, CANM, E, MICH, NY). DRUMMOND – *Musci Scotici* No. **46** (W).
- DURIEU Plantae Selectae Hispano-Lusitanicae No. 101 (BR, G).

- FAMILLER Flora Exsiccata Bavarica: Bryophyta No. 183 (GZU, M).
- FUNCK Cryptogamische Gewächse des Fichtelgebirg's No. 8 (M, UC, W); No. 36 (M, W); No. 64 (BR, GZU, M, O, UC, POZG, W).
- GRAVET Bryotheca Belgica No. 124 (BR, G).
- GROUT *North American Musci Perfecti* No. **90** (BM, COLO, CANM, CAS, MICH, MO, NY, TENN, UC, US).
- HARTMAN Bryaceae Scandinaviae Exsiccatae No.196 (COLO, W).
- HELLBOM Unio itneraria. Cryptogamica No. 98 (G, JE, M, S).
- HOLMEN Bryophyta Danica Exsiccata No. 190 (ALTA, BR, CANM, CAS, COLO, DUKE, KRAM, O, POZG, S, UC, W); NO. 191 (ALTA, BR, CANM, CAS, COLO, KRAM, O, POZG, S, UC, W).
- Holzinger *Musci Acrocarpi Boreali-Americani* No. 238 (BM, COLO, CANM, DUKE, F, FH, H, M, MICH, MO, NY, UC, WTU, WVA); No. 620 (CANM, H, NY).
- HUSNOT Musci Galliae No. 28 (BR, G, M, S).
- JACK, LEINER & STIZENBERGER *Kryptogamen Badens* No. **746a** & **746b** (JE, M, POZG, W).
- JĘDRZEJKO, KLAMA & ŻARNOWIEC Musci Macroregioni Meridionali Poloniae Exsiccati No. 267 (Alta, Br, Colo, JE, KRAM, M, POZG, SOSN, W).
- JĘDRZEJKO & ŻARNOWIEC Musci Macroregioni Meridionali Poloniae Exsiccati No. 25 (ALTA, BR, JE, KRAM, M, POZG, SOSN).
- KAVINA & HILITZER Cryptogamae Čechoslovenicae Exsiccatae No. 290 (BRNM).
- Konstantinova, Belkina, Likhachev & Shlyakov Bryophyta Murmanica Exsiccata No. 89 (kram, mo).
- KOPSCH Bryotheca Saxonica No. 131 (JE, KRAM).
- LIMPRICHT *Bryotheca Silesiaca* No. **220** (Br, GJO, JE, KRAM, M, PRC, W, WRSL); No. **314** (JE).
- LINDGREN Musci Sueciae Exsiccati No. 19 (KRAM).
- LISOWSKI Bryotheca Polonica No. 112 (BR, CANM, KRAM, M); No. 389 (BR, CANM, KRAM, M, O); No. 540 (BR, CANM, KRAM, M).
- MACOUN *Canadian Mosses* No. 97 (BM, CANM, DUKE, NY, UC); No. 98 (CANM, DUKE, H); No. 279 (DUKE).
- MACOUN *Canadian Musci* No. **280** (CANM, FH, DUKE, WTU); No. **296** (CANM); No. **485** (BM, COLO, CANM, H, MO, NY, UC, US).
- MIGULA Kryptogamae Germania, e Austriae et Helvetiae Exsiccatae No. 14 (GJO, GZU, JE, W).
- MOUGEOT & NESTLER *Stirpes Cryptogamae Vogeso-Rhenanae* No. 22 (COLO, CANM, JE, M, W).
- MÜLLER *Westfalens Laubmoose* No. **194** (CANM, JE, KRAM, M, POZG, WW).
- Ochyra *Musci Poloniae Exsiccati* No. **629** (Alta, Br, Canm, Je, Kram, Tenn, UC).
- PILOUS Musci Čechoslovenici Exsiccati No. 218 (BRNM, W); No. 494 (BRNM); No. 1148 (ALTA, CANM, DUKE, JE, POZG, W); No. 1161 (POZG, W).
- PILOUS Bryotheca Čechoslovenica No. 2 (BRNM, KRAM, M, PRC).
- PODPĚRA Bryophyta Exsiccata Reipublicae Čechoslovenicae No. 66 (BRNM, KRAM, POZG, UC).
- POECH Musci Bohemici No. 35 (PRC, W).
- RABENHORST *Bryotheca Europaea* No. **194** (CANM, KRAM); No. **220** (BR, CANM, G, JE, KRAM, M, UC); No. **1177** (JE, KRAM); No. **1178** (BR, G, JE, KRAM, M, UC).
- REDFEARN, ALLEN & MAGILL *Mosses of the Interior Highlands* No. 75 (herb. Frahm, KRAM).
- RENAULD & CARDOT Musci Americae Septentrionalis Exsiccati No. 28 (BM).
- SCHOFIELD Bryophyta Canadensis No. 61 (COLO, CANM, E, KRAM, MO).
- SCHRADER Systematische Sammlung Cryptogamischer Gewächse No. 45 (w).
- SCHULTZ Herbarium Normale No. 57 (JE, M, PRC, W).
- SILLÉN Musci Frondosi Scandinaviae Exsiccati No. 227 (W).
- STEBEL Musci Macroregioni Meridionali Poloniae Exsiccati No. 1356 (KRAM, SOSN).
- SULLIVANT & LESQUEREUX *Musci Boreali-Americani* No. 143 (COLO, FH, MICH, MO); NO. 217 (FH, M, MICH, MO, NY, UC, W).

Verdoorn – *Musci Selecti et Critici* No. **90** (BM, BR, COLO, FH, H, JE, M, MICH, NY, O, TENN, UC, US, W, WTU).

VERDOORN – Bryophyta Arduennae Exsiccatae No 5 (BR, DUKE, G, O, UC, W).

WILSON - Musci Britannici No. 163 (BR, CANM, G, W).

WOJTERSKI – Bryotheca Polonica No. 1257 (BR, KRAM).

ZETTERSTEDT – Grimmiae et Andreaeae Exsiccatae No. 26a & 26b (M, S).

SELECTED SPECIMENS EXAMINED

AFRICA. ALGERIA. Tamsguida massif des Babor, *sine dato*, *Trabut s.n.* (PC); Algeria Constantina, Ref Meridj el Aicha, *sine dato*, *Trabut s.n.* (PC); Djurdjura, *sine dato*, *Trabut s.n.* (PC).

TUNISIA. Ain-Draham, 900 m, Pitard 36 (G, PC).

ASIA. JAPAN. KYUSHU. *Oita Pref*.: Mt Hikosan (old name Prov. Buzen, Mt Hikosan), 27 Aug 1916, *Iwasaki s.n.* (NY).

EUROPE. ANDORRA. Llorts (Bixessarri), 1260 m, 16 Jul 1978, *Casas s.n.* (BCB).

AUSTRIA. Carinthia: Hochahnfall im Maltatale, 31 Sep 1902, Glowacki s.n. (GJO); Kalter Winkel an der Koralpe bei St. Paul, 21 Oct 1906, Glowacki s.n. (GJO); Gössfalle im Gössgraben near Gmünd, 8 Sep 1903, Glowacki s.n. (GJO); Rubenthaler Alm im Radlgraben bei Gmünd, 5 Aug 1903, Glowacki s.n. (GJO); Nasse Felsen unter der Maesenlingwand am W. Matreier Tauern, 1675 m, 11 Aug 1871, Breidler s.n. (GJO). Niederösterreich: Kremstal over Wartenstein, 10 Apr 1891, Baumgartner s.n. (w); above Wartenstein, Schiefer, ca 550 m, 10 Apr 1891, Baumgartner s.n. (GJO). Oberösterreich: Mühlviertel, Durchbruch des Naarn-Flusses above Perg, ca 350 m, 23 May 1922, Baumgartner s.n. (W); Mühlviertel, Waldbach east of Sandl. towards Gugu, ca 950 m, 24 May 1922, Baumgartner s.n. (W); valley of Gr. Mühl below Neufelden, ca 400 m, 28 May 1922, Baumgartner s.n. (W); Linz, Gandaf 266 (GZU, W). Steiermark: by Schwanberg, 500 m, 8 May 1888, Breidler s.n. (GZU); Weisse Sulm auf dem Abhang der Koralpe Schwanberg, 1400 m, 12 May 1888, Breidler s.n. (GJO); Klause by Deutschlansberg, Salzmann 3051a (GZU); Finster-Liesing by Wald, 1700-1800 m, 22 Jul 1888, Breidler s.n. (GJO, M); Kranz near Schladming, 1675 m, 23 Aug 1870, Breidler s.n. (w); by Schladming, 1220 m, 1 Aug 1870, Breidler s.n. (GZU, W); below Steiwender Alm near Schladming, 4 Aug 1869, Breidler s.n. (GJO); Rissachfall by Schladming, 2 Sep 1891, Glowacki s.n. (GJO); Steinriesthal by Schladming, ca 1100 m, 30 Jul 1876, Breidler s.n. (GJO); Seewigthal by Schladming, 24 Aug 1869, Breidler s.n. (GJO); Sonntagsee by Schladming, 1830 m, 7 Sep 1870, Breidler s.n. (GJO); Gössgraben by Trofabach, 8 Sept 1903, Glowacki s.n. (GZU): Bärenthal bei St. Johann. 1500 m, 3 Aug 1887, Breidler s.n. (GJO, PRC); Ingerringgraben in Gral, 1200 m, 28 Jul 1889, Breidler s.n. (GJO); Kleingradengraben by Schwanberg, 500 m, 8 May 1888, Breidler s.n. (GJO); Strochengraben by Rottenmann, 900-1000 m, 16 Jul 1887, Breidler s.n. (GJO); Kaltenbachalm in der Sölk, 1900-2000 m, 17 Jul 1884, Breidler s.n. (GJO); Reiherbach bei Vorau, 750 m, 8 Aug 1890, Breidler s.n. (GJO); Greimberg by Schöder, 1100-1200 m, 11 Aug 1888, Breidler s.n. (GJO); Kohlsingraben by St. Michael, 26 May 1892, Glowacki s.n. (GJO); Bärenthal by St. Johann, 2000 m, 31 Jul 1887, Breidler s.n. (GJO); Aschauer Bach in Gasengarten by Birkfeld, 540 m, 10 May 1893, Breidler s.n. (GJO); Hexstein towards Mittergger Grabe by Jadning, ca 1800 m, 18 Jul 1876, Breidler s.n. (GJO); Turracher Graben, 1050 m, 20 Aug 1889, Breidler s.n. (GJO); Prebengraben towards Putzenthaler Thörl in Krakau, 17 Aug 1874, Breidler s.n. (GJO); Wölzer Tauern, Planneralpe above Donnersbach, Liezen, ca 1700 m, 17 Jul 1972, Poelt s.n. (GZU); Sölk above Wasserspiegel near Hochwasser, Kann 749 (GZU); Koralpe, 11 Jun 1932, Baumgartner s.n. (GZU); "Hemelfeldeck" in the Krakauer Alpen, 2100 m, 13 Aug 1874, Breidler s.n. (GJO, W); Dürnmoosthal by St. Nikolai in Sölk, ca 1200 m, 5 Aug 1877, Breidler s.n. (GJO); between Alt König and Feldberg, 610 m, 9 Sep 1874, Zickendrath s.n. (GJO); Hohenwarth by Oberwölz, 1900 m, Breidler s.n. (GJO). Tirol: W of St. Leonhard, 1900 m, 27 Aug 1961, Poelt s.n. (GZU); Kleines Walsertal, Baad, Starzeltal, Karmulde by Starzelhütte, 1700 m, Lüth 2612 (M). Vorarlberg: Arlberg, 21 Sep 1876, Glowacki s.n. (GZU).

BELGIUM. Hainaut Prov.: Alysse, Oignies near Charleroi, De Sloover 2276 (BR). Liege Prov.: Malmedy, pont du Diable, 340 m, Ochyra 471/85 & 467/85 (KRAM); Weimes, Robertville, along the Warche river, 440 m, Ochyra 487/85 (KRAM); Robertville, Warche, Slembrouck 91/1641 & 98/3645 (BR); Forêt de l'Hertogenwald, 1877, Roemer s.n. (BR); Stavelot, 1902, Hadden (POZG); Laroche, Ourthe, Bailly 872 (BR); Marteau (Spa), de la vallée du Wayai, April 1904, Cornet s.n. (BR); Bévercé, Trôs Marets, entre le Pouhon des Cuves et la route, De Sloover 4482 & 4492 (BR); Hoegne, Hockai, 27 Jun 1937, Castagne s.n. (BR); Hockai, Louette-Vriton 82 (BR); Barraque Michel, Demaret 1662 (BR); between Theux and Polleur, Hoegne, Mar 1912, Cornet s.n. (BR); Châbrehé, Martin Moulin, 540 m, Raeymaekers 1047 & 1024, 1028, 1033 (BR); Found de Châbrehé, Slembrouck 901486 (BR); Gileppe, De Sloover 5052 (BR); Lierneux, De Sloover 3841 (BR); Commune d'Elsenborn, Schwalm valley, Galgenberg, De Sloover 11048 & 11049 (BR); confines Francorchamps and Bévercé, Eau-Rouge valley, De Sloover 5132 (BR). Luxembourg Prov.: St. Hubert, Masblette, Demaret 3043A (BR); St. Hubert, Bilaude, De Sloover 3658 (BR); Lomme, Poix St. Hubert, 20 Apr 1946, Vanden Berghen s.n. (BR); Bouillon, 18 Apr 1888, Lochenies s.n. (BR); Grand Hez (Bouillon), Rouge Ruisseau, De Sloover 9691 (BR); Semois near Bouillon, Lochenies 374 (BR); Chiny, De Zuttere 64/919 (BR); Mirwart (Parfoundry), De Sloover 3598 (BR); dans l'Ourthe orientale, Bistrain, commune de Chérain, De Sloover 3787 (BR); Tintange (near Fauvillers), De Zuttere 66/3175 (BR); Les Epioux, De Zuttere 69/6035 (BR); Mierchamp, Louette-Virton 82B (BR); Neffe-lez-Wardin, De Zuttere 66/3241 (BR); Vallé du Raffi Wardin, De Zuttere 66/3225 (BR); Corbion, Pendu, Semois, De Sloover 5715 (BR); Vallée de la Vierre, Suxy, Delvosalle 73 (BR); Semois, Frahan, 20 Sep 1867, Delogne s.n. (BR); Chassepierre, Froid-Vent, De Sloover 24624 (BR); Fays-les-Veneurs, La Cornette, De Sloover 11132 (BR); Vallée de l'Eau d'Our, entre Our, De Sloover 2399 (BR). Namur Prov.: Oignies, 200 m, Ochyra 499/85 (KRAM); between Orchimont and Nafraiture, 31 Jul 1872, Gravet s.n. (BR); Orchimont, De Zuttere 66/2789 (BR); between Marche and Marloré, Baude, Port du Prince de la Wamme, Demaret 3121A (BR); Nassogue, 12 Aug 1912, Vanden Berghen s.n. (BR); between Willerzie and Bourseigne-Neuve, vallée de la Hulle, De Sloover 5659 (BR); aux confins de Presgaux et de Gonrieux prés du pont de l'Eau-Noire, De Sloover 8659 (BR).

BULGARIA. *Belasica Mountains*: Kljuc stream, 1250 m, *Petrov* 3871B (SOM). *Pirin Mountains*: Kremenski ezera, 2300 m, *Petrov* 3896B (SOM). *Rila Mountains*: Nature Reserve Parangalitsa, Bystrica stream, *Ganeva* 7667B (SOM); Beli Iskur, 1500 m, 9 Sep 1995, *Papp s.n.* (BP). *Stara Planina (Balkan Range)*: near Kalofer, 4 Aug 1984, *Rettig s.n.* (JE); Vit stream above Ribarica, *Petrov* 3890B (SOM); Karandila, 800 m, *Petrov* 3865-B (SOM).

CROATIA. *Primorje/Lika*: Velebit, Poljana kod Sv. Ivana kod Metka, *ca* 650 m, 21 Jun 1912, *Baumgartner s.n.* (KRAM, W). *Split-Dal-matia*: Velebit over Raduč, 650 m, 18 Jun 1912, *Baumgartner s.n.* (KRAM, W); dolina Jažine kod Brušana prema Crnom vrhu, 650–750 m, 27 Jun 1912, *Baumgartner s.n.* (KRAM, W). *Istria*: Dletro-Wald by Zabice, 4 Aug 1906, *Glowacki s.n.* (GJO).

CZECH REPUBLIC. BOHEMIA. Brdy Mountains: Třítrubečný potok near Strašice, 520 m, Jun 1947, Pilous s.n. (ALTA, CANM, DUKE, JE, POZG, W) [Musci Čechosl. No. 148]; Strašice, 1932, Pilous s.n. (BRNM); Obecnice near Příbram, 30 Sep 1867, Juratzka s.n. (GJO). Chotěboř: Ždárské vrchy, ca 3 km east of Chotěboř, Doubravka river, ca 530 m, 13 Jul 1990, Soldán s.n. (PRC); Žďár, Doubravka valley near Hluboké, 5 Jun 1943, Šmarda s.n. (BRNM). Děčínské stěny: Divoká soutěska, 24 Jul 1973, Kůrková s.n. (BRNM); Labská stráň, Suchá Kamenná vallley, ca 160 m, Pospíšil 71333 (BRNM). Jizerské hory: Bílá Smědá near Smědava, 550 m, 21 Jul 1911, Blumrich s.n. (BR, BRNM, COLO, herb. Frahm, JE, KRAM, M, POZG, PRC, UC, W) [Musci Europaei Exs No 831]; Velký Štolpich, 520 m, 7 Oct 1995, Skalická s.n. (PRC); Hejnice, Poech s.n. (PRC, W) [Musc. Boh. No. 35]. Krkonoše: Kotel, Pilous 130 (CANM, DUKE, TENN); Labe river below Špindlerův Mlýn, ca 730 m, Jun 1946, Pilous s.n. (BRNM, W) [Musci Čechosl. No. 218]; Labský důl – Strmá stráň, 850 m, 28 Aug 1983, Šašková s.n. (PRC); okres Trutnov, Studniční hora, Čertova zahrádka, ca 1250 m, Stuchlý 344 (PRC); okres Vrchlabí, Bílé Labe, Čertův důl, ca 900 m, Stuchlý 345 (PRC); Dolní Malá Úpa, ca 610 m, May 1948, Pilous s.n. (BRNM) [Musci Čechosl. No. 494]; na Pančici, ca 1400 m, Aug 1945, Šmarda s.n. (BRNM); Bílá louka, ca 1400 m, 23 Aug 1945, Šmarda s.n. (BRNM); Sejfský stream near Harrachov, 950 m, 26 Jul 1954, Winkler s.n. (BRNM) and 2 Aug 1919, Vilhelm s.n. (PRC, isolectotype of Racomitrium aciculare fo. humile); Špindlerův Mlýn, Labe stream, ca 700 m, Pospíšilová 75862 (BRNM); Modrý důl, 1000 m, 1 Sep 1928, Wihan s.n. (PRC);

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Studničná, Studniční hora, 1500 m, 1 Sep 1928, Wihan s.n. (PRC); Pláň pod Sněžkou, 1450 m, 1 Sep 1928, Wihan s.n. (PRC); Obří důl, 900 m, Traxler 127 & 881 (PRC); Obří důl, pod Sněžkou, Vilhelm 10(919) (PRC). Krušné hory: okres Chomutov, Nová Ves, ca 750 m, Váňa 343 (PRC). Lužické hory: Česká Lípa, Nový Bor, Meinunger 16678 (M), 300 m, Strotzer 44 (PRC) and 400 m, Anders 95 (PRC); Hamr near Cvikov, 31 Jul 1891, Schiffner s.n. (GJO); Klíč, ca 500 m, 21 Oct 1982, Soldán s.n. (PRC). Orlické hory: Bartošovice, ca 580 m, 14 Apr 1985, Soldán s.n. (PRC). Šluknov: Mikulášovice, sine dato, Fischer s.n. (PRC). Šumava: Teplá Vltava at Františkov near Kvilda, ca 960 m, 12 June ?, Soldán s.n. (PRC); Nat. Res. Povydří, riverbank of Vydra between Turnerova and Hálkova chata, 800-830 m, Kučera 127/3 (PRC); Švarcenberský kanál at "Rosenauerova klausa" below Mt Třístoličník, 925 m, Kučera 172/8 (PRC); Vydra river before confluence with Křemelná by Čenkova Pila, 630 m, Kučera 118/10 (PRC); Modravský potok, 1.5 km N of Březník ("Na ztraceném"), 1100 m, Kučera 103/3 (PRC); Malá Vltava (Vltavský potok) W of Polední vrch by Borová Lada, 940-950 m, Kučera 102A/4 (PRC); Nová Pec, Jezerní potok, Pospíšilová 75768 (BRNM); Debrník near Železná Ruda, 25 Aug 1896, Bauer s.n. (PRC). Praha: Štěchovice, Vltavské valley over Štěchovice, 200 m, 1 Mar 1936, Vaněk s.n. (BRNM); Vltava by Štěchovice, 200 m, 1 Mar 1936, Vaněk s.n. (BRNM) [Crypt. čech. exs. No. 290]. MORAVIA. Beskydy: Čeladná, above Podolánky, 800 m, 23 May 1956, Duda s.n. (BCB, POZG, TENN); Čeladnice valley, 18 Jul 1941, Šmarda s.n. (BRNM); Šance" near Staré Hamry, ca 450 m, Podpěra 1377 (BRNM); Čeladnice between Smrk and Kněhyně, Podpěra 359 (BRNM). Bystřice n. Pernštejnem: u Víru, 25 Mar 1941, Šmarda s.n. (BRNM). Hrubý Jeseník: 1.6 km SW of Barborka, Bílá Opava, ca 1210 m, 22 Sep 1945, Doležal s.n. (BRNM); Bělá (Domašov), Vysoký vodopád, ca 1000 m, 2 Jul 1967, Pokluda s.n. (BRNM); Domašov, Zaječí potok at Lysý vrch, 650 m, Aug 1949, Duda s.n. (BRNM); Karlova Studánka, Bílá Opava, ca 900 m, 29 Jul 1949, Šmarda s.n. (BRNM); Kouty, Praděd (1492), Divoký důl, ca 1100 m, 26 Sep 1964, Pokluda s.n. (BRNM); Rýmařov, Malá Kotlina, Velký Máj, 1180 m, 26 Jul 1985, Novotný s.n. (BRNM); Velká Kotlina, ca 1350 m, 12 Jul 1946, Šmarda s.n. (BRNM); Kolštýn, Branné valley, ca 900 m, 2 Aug 1947, Šmarda s.n. (BRNM). Jihlava: Jihlava, near Dolomitz, Mar 1852, Pokorny s.n. (W). Králický Sněžník: Staré Město near Král. Sněžník, Stříbrnice, 850 m, 26 Oct 1947, Jedlička s.n. (Bryoph. Exs. Reipubl. Čechosl. No 66) (BRNM, KRAM, POZG, O, UC); Králický Sněžník, Tvarožné díry, Morava river, ca 780 m, Sep 1983, Soldán s.n. (PRC). Kunštát: Křetinka river near Svojanov, ca 460 m, 5 Jun 1938, Šmarda s.n. (BRNM, PRC). Nízký Jeseník: Rešovský vodopád at Uničov, 400 m, Jun 1908, Podpěra s.n. (BRNM); Nové Valteřice near Moravský Beroun, 500 m, 1 Oct 1984, Novotný s.n. (BRNM); Smilov, Bystřice valley, Hrubá Voda-Smilov, 400 m, 23 Aug 1986, Novotný s.n. (BRNM). Šumperk: Václavov, ca 500 m, 1911, Schenk s.n. (W). Tišnov: Chlébský potok, ca 600 m, 12 May 1947, Šmarda s.n. (BRNM). Žďárské vrchy: Velké Dářsko, 615 m, 12 Jul 1969, Slámová s.n. (PRC); Velké Dářsko na Ždársku, 6 June 1950, Vlach s.n. (BRNM); Nové Město na Moravě, Tisůvka, ca 650 m, Aug 1939, Šmarda s.n. (BRNM).

DENMARK. BORNHOLM. Bornholms Amt.: Gudhjem, 6 Jul 1908, Hesselbo s.n. (ALTA, BR, CANM, CAS, COLO, DUKE, KRAM, POZG, O, S, UC, W) [Bryoph. Dan. Exs. No 190]. JYLLAND. Nordjyllands Amt.: Store Arden Skov, 15 Aug 1901, Jensen s.n. (CANM, O, S). ZEALAND. Frederiksborg Amt.: Teglstrup Hegn, W of Elsinore, 8 Jul 1906, Hesselbo s.n. (ALTA, BR, CANM, CAS, COLO, KRAM, O, POZG, S, UC, W) [Bryoph. Dan. Exs. No 191].

FAEROE ISLANDS. BORDOY. Krossdalsá, 100 m, Lewinsky 3263
(DUKE). EYSTUROY. Elduvik, Stórá, Lewinsky 4509 (KRAM); Gjáarskard, road between Gjógv and Funningur, Lewinsky 4850, 5391 (DUKE); Skáli, Gjógvará, Lewinsky 5399 (DUKE). STREYMOY. Signaböur, Ravnafossur, Lewinsky 4638 (ALTA); Kaldbak, Högadalsá, Lewinsky 4038 (DUKE); Heljardalsá, Gásavatn and Reyná, at Gásavatn, Lewinsky 4173 (BR); Saksendalen, 8 Jun 1896, Jensen s.n. (WTU). SVINOY. Storá, between Kjóadalur and Mannaskard, Lewinsky 4592 (KRAM). SYDERØ. Ørdevig, 8 May 1896, Jensen s.n. (CANM); Trangisvaag, 22 Jun 1896, Jensen s.n. (DUKE, S). VAGÁR. Marknará, Lewinsky 3911 (ALTA, KRAM) & 4968 (ALTA). VIĐOY. Viđareidi, Northernmost Faeroes township, in valley between Malinsfjall (751 m) and Villingadalsfjall (844 m), Slack 5142 (ALTA) and 200 m, Lewinsky 4922 (BR).

FINLAND. ALANDIA. Geta, Getabergen, 10 Jul 1928, *Möller s.n.* (DUKE, POZG, S); Sund, Bomarsund, 18 Jul 1928, *Möller s.n.* (S); Saltvik, Fagervik, Tjärnbergen hills, *Alava 16194* (M); Kuggböle, 6 Jun 1886, *Bomansson s.n.* [*Musci Fenn. Exs.* No 379] (G, S, W). KARELIA BORE-

ALIS. Tuupovaara, Kovero, Törisevä, 10 Jun 1940, Tuomikoski s.n. (H). NYLANDIA. Ekenäs, Trollböle, 9 Jun 1909, Häyrén s.n. (M, S) [Bryoth. Fenn. No. 31]; Helsinki, Vestersundom, 24 May 1960, L. & H. Roivainen s.n. (POZG, W); Pusula, Arimaa, 21 May 1964, Roivainen s.n. (S); Uusimaa, Espoo, Långviksträsk, 25 Sep 1909, Brotherus s.n. (CANM); Backby, Myllyjärvi lake, 10 Jul 1961, Ulvinen s.n. (US). OSTROBOT-TNIA BOREALIS. Pohjois-Pohjanmaa, Ylikiiminki, Kiiminkijoki river, Juopulinkoski rapids, E of Oulu, 17 Jul 1975, Ulvinen s.n. (BR). REGIO ABOËNSIS. Lohja/Karjalohia Parish, Maila, Tamsaari, Vitt, Horton & Kopponen 25127 (ALTA); Nousiainen, Killainen-Palonkylä district, at Falkinkoski rapids of River Hirvijoki, 7 Aug 1974, Laine s.n. (COLO); Paimio, Huso, 9 Nov 1972, Hinneri & Laine s.n. (CANM, COLO, M, W); Sauvo, Leisku, E of Leiskunlahti bay, 8 Sept 1971, Hinner & Laine s.n. (CANM, W). SAVONIA BOREALIS. Kuopio, Humalajoki, W of the bridge of Hwy 5, Fagerstén 5155 (DUKE, H, KRAM). TAVASTIA AUSTRALIS. Jaala, Ilvesvuori, 18 May 1967, Roivainen s.n. (COLO); Etelä-Häme, Ruovesi, Mustajärvi, Pohtio, Saukko-oja brook, 28 Jul 1978, Söyrinki s.n. (CANM, GZU, S). TAVASTIA BOREALIS. Rautalampi, Kuorekoski, Fagerstén 5137 (DUKE, KRAM); Pohjois-Häme: Virrat, Jäähdyspohja, Munkkivuori, 5 Aug 1951, Sövrinki s.n. (W).

FRANCE. ALSACE. Bas-Rhin: Vosges, route Seevern, Seebach (next to Wissembourg), De Sloover 429 (BR). Haut-Rhin: Masevaux Seewen Lac d'Alsfeld, 620 m, Geissler 9844 (G); Les Vosges, Hohneck, Onraedt 62.F.7767 (BR). AQUITAINE. Pyrénées-Atlantiquesi: La Rhune, 28 Jul 1954, Excursion Congrès Intern. de Botanique s.n. (PC). AUVERGNE. Cantal: im Baths des Alagnon, 980 m, 17 Jul 1921, Culman s.n. (W); Puy Mary, rochers humide au col d'Eylac, ca 1700 m, July 1956, d'Alleizette s.n. (TENN). Puy-de Dôme: Monts du Forez, Chalmazel, Vallon do Gouffre du Faux, 19 Jun 1952, Gaume s.n. (PC); Monts du Forez, Vallee du Lignon, paroi de la riviere à l'entre du Bois de Chorsin, 1200 m, 26 May 1960, Bonnot s.n. (PC); Mons du Forez, dans de Lignon, au sud de Chalmazel, 800 m, 18 Jul 1951, Cuynet (PC-Bizot); Chalmazel, gouffre du Faux, rochers au-dessus de la Cascade, 900 m, 18 Jul 1952, Cuynet s.n. (PC); Gorges de la Loire près de Saint Victor, 380 m, 21 Feb 1953, Cuvnet s.n. (PC): au lac Guéry non loin du Mt Dore, 16 Aug 1902, Douin s.n. (BR); pentes du Puy de Sancy, 15 Aug 1899, Douin s.n. (BR); près du Lac Servières, 1000 m, d'Alleizette 417 (PC). BASSE NORMANDIE. Manche: Cherbourg, 1885, Le Jolis s.n. (M) Corbière 280 (BR). Orne: Ségrie-Fontaine, Avril, Husnot s.n. (BR, G, M, S) [Musc. Gall. No. 28]. BRETAGNE. Finistère: Chaos de St. Herbot SV for Huelgoat, 21 Jun 1954, Størmer s.n. (0); Chaos de Saint-Herbot, De Sloover 1508 & 1578 (BR); Huelgoat, Pierrot 154 (PC); Saint-Rivoal, Brèche de Toul-an-Dioul, Pierrot 54055 (PC); Le Cloître-Saint-Thégonnec, dans le Briou, près du Moulin Queuneut, 16 Jun 1947, Cuynet s.n. (PC). BOURGOGNE. Yonne, La Pierre-Qui-Vire, dans le Trinquelin, 23 Jul 1947, Cuynet s.n. (PCt). CHAMPAGNE-ARDENNE. Ardennes: Thilay, ruisseau de l'Ours, 19 Mar 1983, d'Hose (BR); Naux, Bois du Chaufour, cours inférieur du Ruisseau "Nanturu", De Sloover 14146 (BR). CORSE. Corse-du-Sud: L'Ospedale, 850 m, Hegewald 4639 (ALTA); Scala da St. Regina, 600 m, 30 Apr 1905, Schiffner s.n. (w); Evisa - Col de Vergio, 1200-1300 m, 29 Apr 1905, Schiffner s.n. (w); Von Evisa auf den Col de Vergio, 1000-1300 m, 29 Apr 1905, Schiffner s.n. (W); Ajaccio, 15 April 1905, Fürbringer s.n. (M); Les Calanche près Piana, 500 m, 23 Apr 1938, Hilitzer s.n. (BRNM); Sotta Montagne de Cagna Chiralba, 770 m, Geissler 6651 (G). Haute-Corse: Vizzavone, 900-1100 m, 20 Apr 1938, Hilitzer s.n. (BRNM); Hétraie à Vizzavona, Apr 1938, Mosseray s.n. (BR); Castifao, Haut-Asco, N Cinto, 1600 m, Geissler 7036 & 7042 (G) and 1650 m, Geissler 7031 (COLO); Ghisoni, SE Col de Sorba, 1000 m, Geissler 6785 (G); Corte, Val Pestonica (Restonica), 1450 m. Geissler 6963 (G); Forêt de Zonza, Gabriel 2476 (PC); Forêt de Vizzavona, Pointe Grande, 1350 m, sine dato, Camus s.n. (PC); Sommes du Pigno (à Bastia), 1867, Debeaux s.n. (W); Col de Vizzavona, 1000-1100 m, 21 Apr, Schiffner s.n. (W); Cirque de Bonifatto (haute vallée de la Figarella), ca 550 m, Lambinon 67/C/168 (BR). FRANCHE-COMTÉ. Haute Saône: La Montagne 12 km S von Remiremont, "Moulin du Grand Saucis", 650 m, Jun 1980, Frahm s.n. (FLAS); Plancher-les-Mines, Rahin, 29 Jun 1924, sine collector (WTU). LAN-GUEDOC-ROUSSILLON. Gard: L'Espéron, 1200, Aug 1873, Boulay s.n. (BR). LIMOUSIN. Creuse: La Borne, près Aubusson, Loiseau 101 (BR). LORRAINE. Vosges: Défilé de Straiture, Le Valtin, 700 m, Bouharmont 2520 (BR); Val d'Ajol oberh. Cascade du Géhard, 1981, Philippi s.n. (JE); Gerbamont, 700 m, May-June 1867, Pierrat s.n. (US); Lac de Retournemer, 785 m, 21 June 1936, Duclos s.n. (PC). MIDI-PYRÉNÉES. Ariége: dans l'Etang Bleu dans la forêt des Hare, Aug 1901, Douin s.n. (BR).

Haute-Garonne: Bagnères-de-Luchon, près de la Cascade du Coeur, 1200 m, De Sloover 43474 (ALTA, BR, H, KRAM) [Herb. Bryol. No. 640]; Val d'Esquierry, Vallée d'Oo, pres de Luchon, 5 Aug 1965, Onraedt s.n. (BR); Luchon, Vallé du Lys, 20 Sep 1956, Casas s.n. (BCB); Hospice de France, 19 Sep 1956, Casas s.n. (BCB); environs de Luchon, Sept 1856, Zetterstedt s.n. (0) [Musci Pyren. No. 84]. Hautes-Pyrénées: Chaos de Coumély, Gavarnie, De Sloover 1059 (BR); forêt de Gabas au-dessus de Biches Artigues, SW of Lourdes, Aug 1901, Douin s.n. (BR); Cauterets (cascade du Lutour), 2 Jul 1933, Leroy s.n. (BR); Route de Lourdes à Cauterets, 600 m, Jun-Jul 1922, Vandenbroeck s.n. (BR); Lac de Gaube, 1800 m. Jun–Jul 1922, Vandenbroeck s.n. (BR), Tarn-et Garonne: Varen not far from Montauban (Mondarrá pres Vare), 29 Jun 1954, Casas s.n. (herb. Frahm). PAYS DE LA LOIRE. Maine-et-Loire: Noyant-la-Gravoyère, 31 Oct 1886 & May 1875, sine collector (BR). Sarthe: Sillé-le-Guillaume, sine dato, Monguillon s.n. (COLO). PROVENCE-ALPES-CÔTE D'AZUR. Var: Frégus, Vall on Saint-Jean, 150 m, 8 Apr 2006, Hugonnot s.n. (KRAM); Cannet-des-Maures, Saint-Daumas, 6 Apr 2006, Hugonnot s.n. (KRAM). RHÔNE-ALPES. Ardèche: Borne, Ardèche river, Borne river near St Etienne de Lugdarès, 18 Aug 1924, Dismier s.n. (BCB, BR, KRAM, NY, WTU) [Bryoth. Gall. No. 96,]; between Col de 4 Vios and Mézilhac, ca 1150 m, Lawalrée 12239 (G). Haute Savoie: Mont Blanc-Gruppe: St Gervais, Les Contamines-Montjoie, 1100-1400 m, 5 Jul 1981, Poelt s.n. (GZU); Massif du Mont Blanc, sine dato, Bescherelle s.n. (G). Loire: Chalmazel, de Cluzel, 1200 m, 15 July 1952, Cuynet s.n. (PC); Massif du Pilat, Saint-Régis-du-Coin, 1200 m, Cuynet 374 (BR); Tarentaise, au bord du Furan, May 1948, Cuynet s.n. (PC); Massif du Pilat, Rochetaillée, dans le lit du Furan, Gouffre d'Enfer, 28 Jun 1952, Cuynet s.n. (PC).

GEORGIA. CAUCASUS. *Adjarian Autonomous Republic*: distr. Khalvachauri, Agara, Khorulis-ckali river, 100–500 m, 29 Jul 1980, *Vašak s.n.* (BR, COLO, G); Bzani river, Bzaisan-Czakwiscchali, 10 km NE of Batumi, 15 Nov 1952, *Pietrow s.n.* (LE); Cichidziri (=Tsikhisdziri), 13 Jun 1938, *Pietrow s.n.* (LE); Egrisski khrebet, distr. Gegehkori, between Lebarde and Taleri, 10 km of Lebarde, Tekhuri river, 1200 m, 26 Jul 1979, *Vašák & Esvandzhia s.n.* (COLO).

GERMANY. BADEN-WÜRTTEMBERG. Schwarzwald: by the brook Haslach in Falkau near Titisee, 900 m, Hegewald 1150 (FLAS); Geroldsauer Wasserfall near Baden-Baden, 19 Sep 1860, Jack & Leiner s.n. (JE, M, POZG, W) [Krypt. Badens No. 746A] and 19 Sep 1859, Jack & Leiner s.n. (M) [Krypt. Baden No. 746]; St. Blasien, 15 Jul 1905, Janzen s.n. (JE); Baden, Feldberg, 25 Sep 1903, Janzen s.n. (JE); Triberg, sine dato, Reinecke s.n. (JE); Höllental by Freiburg, Jun 1886, Gotl s.n. (GJO); Freiburg, Zastlerloch/Feldberg, ca 1280 m, Sep 1849, Herzog s.n. (JE); Feldberg, Sep 1883, Haussknecht s.n. (JE); Simonswald, Ibichtal, Ibich, 540 m, Lüth 983 (herb. Frahm); Oberort, 960 m, Lüth 1071 (KRAM); Oberried, Steinwasen, 700 m, Lawalrée 11805 (BR) And ca 1000 m, Lawalrée 12793 (BR); between Utzenfeld and Wieden, Lawalrée 12820 (BR); Todtnau, Muggenbrunn Holzschlagbachtal, Lawalrée 20629 (G); Wehratal, Wehr, De Sloover 11577 (ALTA, BR). BAYERN. Hassenbach, Meinunger 18454 (JE); Kreis Hof, Dürsenwaid, Meinunger 17888 (JE); Spessart, Bischbrunn, ca 330 m, Düll 65/V (JE, KRAM, M); Böhmerwald, Riesloches by Bodenmais, 21 Sep 1953, Poelt (GZU); Grossen Schwarzbach, ca 915 m, 19 Aug 1984, Poelt s.n. (GZU); Böhmerwald, Seebach near Salnau, Hotzisäge, ca 700 m. 21 Oct 1897, Bauer s.n. (BRNM, PRC): Bayerische Wald, Rachelsee, 1090 m, Familler 183b (M); between Loisach and Kochelsee, Schwaiganger, ca 750 m, 15 May 1966, Lotto s.n. (M); Estergebirge, Neuglägerkopf/Südosthang, Wallgau, Kreis Garmisch-Partenkirchen, ca 1100 m, 30 Jun 1963, Lotto s.n. (M); Fichtelgebirge, Fichtelnaab between Unterlind and Ebnath, 550-600 m, 1901, Schwab s.n. (GZU, M) [Fl. Exs. Bavar. No. 183]; Frankenwald, 1867, Molendo s.n. (BR); Allgäu: Kreis Sonthofen, Wertachhorn, 11 Sep 1973, Düll s.n. (M); Langewang, 730 m, Oct 1863, Molendo s.n. (BR); Riedbergpass, 1520 m, Lüth 2126 (M); Obermeiselstein, road from Sessellift to Schwabenhaus, 1490 m, Lüth 3306 (M); Obermeiselstein, Wannenkopf, 1180 m, Lüth 2734 (M). BRANDENBURG. Alter Friedhof in Potsdam, 13 Aug 1967, Benkerd s.n. (B). HESSEN. Rhön, Münzkopf, near Holzberghofe in Schwarzbach, 750 m, 4 Aug 1908, Krüger s.n. (JE); Frankfurt a/M, iisine dato, de Bary albo Limingani (BR); Vogelsberg, near Wachtersbuch, 300 m, Hellsing 252 (COLO); Rhongebirge, Milseburg, 1872, Geheeb s.n. (BR, G, UC). NIEDERSACHSEN. Oldenburg near Neuenburg, 8 Oct 1897, Müller s.n. (herb. Koperski) and 23 Jul 1897, Müller s.n. (B); Nindorf, Hummigenbach, 24 Oct 1998, Koperski s.n. (herb. Koperski); Hannover - Mittelfeld, Seelhorster Fruedhof, 31 Aug 1966, Walsemann s.n.. (herb.

Koperski); Nordöstlich Hanstedt, Brackel, NE of Hochholzberg, 30 Sep 2000, Koperski s.n. (herb. Koperski); Lonau, 9 Jul 1905, Quelle s.n. (JE); Rehberger Graben, near Oderbrück, 10 Oct 1897, Quelle s.n. (JE); Oder, ca 550-600 m, 7 Nov 1965, Poelt s.n. (GZU); Radanthal near Harzburg, Jul 1896, Monkemeyer s.n. (GJO). NORD RHEIN-WESTFALEN. Krs. Aachen, Dreilägerbachtal NE of Roetgen, 450 m, 22 Oct 1977, Frahm s.n. (ALTA); Giersbach near Ellesinghausen, Olsberg, 1 Jan 1892, Schemmann s.n. (KRAM, POZG); between Guttrop and Kallenherd, Müller s.n. (CANM); Krs. Meschede, between Bracht and Gleierbrüc, "Hohe Lemberg", ca 410-30 m, 3 Jun 1972, Düll s.n. (BCB); Krs. Monschau, Eifel, Rurtal, 12 Oct 1974, Frahm s.n. (ALTA, CANM, DUKE). RHEINLAND-PFALZ. Höher Westerwald, Winterbachtal by Niederdresselndorf, ca 480-530 m, 14 Sep 1924, Ludwiget & Andres s.n. (BR); Westerwald, Mauden by Daaden, 10 Apr 1923, Ludwig s.n. (CAS); Hunsrück, Ehrenbachfälle by Brodenbach, ca 175 m, 22 Apr 1930, Andres s.n. (BR, M, W); Stegskopf, ca 580-620 m, April 1923, Ludwig & Andres s.n. (вк, м); Wuiterbachtal by Niederdresselundorf, ca 480-530 m, 14 Sep 1924, Ludwig & Andres s.n. (M). SAARLAND. Mettlach a/Saar, Winter s.n. (BR, G, JE, KRAM, M, UC) [Bryoth. Eur. No. 1178]; Hunsrück, Kreis Merzig-Wadern, Wadern-Steinberg, Wahnbachtal-Oberlauf, 380-450 m, Caspari, Heinrichs & Sesterhenn 3773 (KRAM); St. Arnual, Rothenfels, Aug 1865, Winter s.n. (WTU); Saargebiet, Taben, Wolfsbach, ca 300 m, Andres s.n. (BR, M, W). SACHSEN. Erzgebirge, Klingerbach by Tellerhäuser, Jun 1921, Kopsch s.n. (JE, KRAM) [Bryo. Sax. No 131]; Elbsandsteingebirge in Amselgrund by Rathen, 23 Apr 1966, Siegel s.n. (JE); Elbsandsteingebirge, Pirna, sine dato, Bauer s.n. (PRC); Vogtland/Erzgebirge, Jägersgrün, sine dato, Eckardt s.n. (JE); Vogtland, Geigenbach, Spindler 408 (BRNM); Vogtland, Schöneck, Görnitzbach, 13 Jun 1908, Spindler s.n. (JE); Hainicken, Arnsdorf, Meinunger 13884 (JE); Bielathal by Königstein, Apr 1895, Krieger s.n. (JE). SACHSEN-ANHALT, Harz, Friedrichsbrunn, Nesselbruch, Kreis, Quedlinburg, 9 Apr 1990, Rettig s.n. (JE); Wernigerode, Steinerne Renne, 28 May 1882, Janzen s.n. (JE); Ilsefälle, 29 Mar 1902, Janzen s.n. (JE); Holzemethal above Wernigerode, 25 Aug 1868, Schliephacke s.n. (JE); Wernigerode, Breites Thal, Jul 1894, Warnstorf s.n. (KRAM); Lonau, 9 Jul 1905, Quelle s.n. (JE); Bodethal, 1 Jun 1895, Quelle s.n. (JE); Brocken, Jun 1890, Naumann s.n. (JE); Ilsenbürg, Jul 1827, Beyrick s.n. (CANM). SCHLESWIG-HOLSTEIN. Kreis Bad Segeberg, Henstedt-Ulsburg, Meinunger 18883 (JE); Kreis Flensburg, Sieverstedt Kirchenholz, 7 Jun 1934, Saxen s.n. (B); Sachsenwald, Rev. Schadenbek, Bachgabelung, Reimers 0592 (B). THÜRINGEN. Eisenach, Landgrafenschlucht, 24 Oct 1916, Janzen s.n. (JE); Eisenach, Hohe Sonne, 390 m, 10 Oct 1925, Krüger s.n. (JE); Eisenach, Hohe Sonne, Fahrstrasse, 390 m, 10 April 1904, Krüger s.n. (JE); Hochwaldgrotte, 400 m, 3 Jul 1921, Krüger s.n. (JE); Annatal, 300 m, 14 Oct 1933, Krüger s.n. (JE); Inselsberg, 22 Jul 1894, Wuth s.n. (JE); Thüringer Wald, Wilden Gera (Schmücker Graben), 10 Sep 1921, Bornmüller s.n. (CANM, POZG); Schmücker Graben, 1952, Grolle s.n. (JE); Oberhof, 820 m, 5 Aug 1931, Koppe s.n. (JE); Oberhof, Zündorf 7942 (JE); Schmücker Graben, Bornmüller 32 (JE); Kreis Suhl, Vesser, 7 Oct 1974, Meinunger s.n. (JE); Kreis Schleiz, Untere Wisenta, Walsburg, Meinunger 1135 (JE); Kreis Neuhaus/Rwg, Alte Mutter S of Igelslieb, Meinunger 4432 (JE); Kreis Neuhaus/Rwg, Muters Franbachtal S of Katzhütte, Meinunger 17714 (JE); Schneetiegel by Gehlberg, 1952, Grolle s.n. (JE).

GREAT BRITAIN. ENGLAND & WALES. Anglesey (VC 52): Menai Bridge, Anglesev, sine dato, Griffith s.n. (NMW), Caernarvon (VC 49); Mt Snowdon, from pass of Llanberis, 200-800 m, Norris 52000 (UC); Cwmglas-mawr, Llanberis, 11 April 1979, Holyoak s.n. (herb. Holyoak); Snowdon, Llyn Glas, 670 m, 28 Mar 1963, Perry s.n. (US); Moel yr Ogof near Beddgelert, 520 m, 25 Nov 1950, Ratcliffe s.n. (E); Carnedd Llywelyn, Craig yr Ysfa, Sep 1951, Ratcliffe s.n. (E); Conway Valley, Afon Dulyn, Lawton 5268 (WTU). Cardigan (VC 46): Llwyngwair - Aberystwyth Road, 20 May 1954, Trotter s.n. (NMW). Carmarthen (VC 44): Nantymwyn, Rhanddirmwyn, 1954, Wade s.n. (NMW). E. Cornwall (VC 2): moor by Gimble, Commonmoor, Bodmin Moor, 17 Apr 1958, Laflin s.n. (FLAS); near Par, Jul 1921, Sherrin s.n. (NMW); near Tintagel, Aug 1922, Sutton s.n. (NMW): Camel River, Bodmin, 1878, Tellam s.n. (NMW): Seaton, Jun 1963, Field s.n. (NMW). W. Cornwall (VC 1): Castle Horneck, Penzance, 14 Sep 1993, Holyoak s.n. (herb. Holyoak); above Porthmeor Cove, 7 May 1996, Holyoak s.n. (herb. Holyoak). Cumberland (VC 70): New Gilsland, Jun 1931, Millar s.n. (NMW); Great End, 21 May 1945, Richards s.n. (NMW); Hillbeck, Skiddaw, Aug 1907, Tetley s.n. (NMW); Buttermere, 25 Mar 1883, Barker s.n. (UC); by River Derwent, near Rosthwaite, Borrowdale, 26 Mar 1942, Simmonds s.n. (E).

Brecon (VC 42): Cwm Graig Ddu, Mynydd Eppynt., 8 Jun 1968, Ambrose s.n. (NMW). Denbigh (VC 50): Rhiwlas, Jun 1898, Armitage s.n. (NMW). S. Devon (VC 3): Dartmoor, Jun 1920, Jackson s.n. (NMW); Dartmoor Park, 13 Sep 1971, Poelt s.n. (GZU); Bucka Falls, Mar 1946, Ravine s.n. (E); Dartmoor, near Post Bridge, Oct 1834, Powell s.n. (E); Dartmoor, 300 m, Raeymaekers 67 & 72 (BR); Teignbridge Distr., N Moretonhampstead, Fingle bridge, Weir near R. Teign, 150 m, Geissler 16111 (G). Derby (VC 57): Derbyshire, Padley Woods, Mar 1951, Evans s.n. (NMW). N. Essex (VC 19): Magdalen Laver, ca 80 m, Pyner 52/512082 (NMW). Glamorgan (VC 41): Mynydd Llangeinwyr, 7 Jun 1941, Banwell s.n. (NMW); upper Neath valley, ved Pont-Nedd-Fechan, 7 Apr 1963, Størmer s.n. (o). W. Gloucester (VC 34): Symond's Yat., 3 Jan 1912, Knight s.n. (NMW). Hertford (VC 20): Hunsdonbury, n. Hunsdon, Jan 1981, Diver s.n. (NMW); Welsh Newton, Feb 1898, Armitage s.n. (NMW). E. Kent (VC 15): East Sutton Park, 9 May 1982, Side s.n. (BBSUK, NMW). W. Lancashire (VC 60): Caton, Aug 1955, Garlick s.n. (NMW). Leicester (VC 55): between Colony Reservoir and Charnwood Lodge, Whitwick, 18 Jun 1963, Hallidav s.n. (BBSUK, NMW), Merioneth (VC 48): Dolgellau Cader Idris, Llyn y Garfr, 3 Jul 1948, Watson s.n. (BR): Harlech, Sep 1903, Thompson s.n. (NMW): Tvn-v-groes, Aug 1904. Chittenden s.n. (NMW); Falls Merioneth, Lyn y Groes, 4 Aug 1922, Bellerby s.n. (E); Blaenau Ffestiniog stream, Sep 1961, Field s.n. (CANM); S Bethesda, in Afon Oywen, 170 m, Geissler 3147 (G); Afon Llafar near Bethesda, Caerns, 490 m, 6 Oct 1950, Ratcliffe s.n. (E); Capel Arthog, 28 Jul 1919, Sutton s.n. (BBSUK, NMW). Merioneth/Caernarvon (VC 48/49): Beddgelert, 1865, Hunt s.n. (H). Monmouth (VC 35): Goetre, Garlick 3275 (NMW). Montgomery (VC 47): Lake Vyrnwy, Aug 1915, Armitage s.n. (NMW). N. Northumberland (VC 68): Chevcoli, Sep 1925, Duncan & Millar s.n. (NMW); Shielhope, W Challon, Jul 1927, Duncan & Millar s.n. (NMW). S. Northumberland (VC 67): near The Forks, Lewis Burn, Kielde, ca 210 m, Long 6047 (E); Hawk Burn near Byrress, Redesdale, Long 152 (E); Bizzle Burn, 4 Sep 1963, Pettifer s.n. (NMW); rock by R. Allen, Morralee Wood, Ridley, 22 Apr 1962, Perry s.n. (NMW); Keld, May 1937, F.E.M. s.n. (NMW). Radnor (VC 43): Elan Valley, 9 Apr 1965, Harrison s.n. (NMW). Shropshire (VC 40): Longmynd, Church Stretton, Salop, 3 Jun 1906, Duncan s.n. (E); Lyd Hole, Salop, 3 Jun 1892, Benson s.n. (NMW). N. Somerset (VC 6): Blackdown, Mendip Hills, sine dato, Ross s.n. (NMW): Black Down, 5 Mar 1968, Appleyard s.n. (NMW). S. Somerset (VC 5): East Lyn River, 6 Apr 1971, Harrison s.n. (NMW). E. Suffolk (VC 25): Wortham church 3.5 km from Diss, 15 Jul 1988, Smith s.n. (BBSUK, NMW). Surrey (VC 17): Wonersh churchyard, near Guildford, Dec 1980, Gardiner et al. s.n. (NMW); Tillingbourne Valley, near Wotton, 7 Mar 1925, Wallace s.n. (NMW) and 25 Sep 1927 (E). E. Sussex (VC 14): near Tunbridge Wells, SE of High Rocks,, Ramslye Rocks, 10 Feb 1951, Rose s.n. (NMW). Warwick (VC 38): Gills Corner, Monks Kirby, 3 Jul 1965, Laflin s.n. (NMW). Westmorland (VC 69): near Wray, Hoghouse Beck, Mar 1944, Wanstall s.n. (NMW); Grasmere, Aug 1948, Appleyard s.n. (NMW); Ralfland Forest, near Shap, 305 m, Bindless 18 (E); Durgeon Ghyll, Longdale, 2 Sep 1940, Catcheside s.n. (E); Lake District, Bowness, near Belsfield Hotel, Lawton 5427 (WTU); near Appleby, Hilton Beck, 11 Apr 1946, Watson s.n. (BR). N.W. Yorkshire (VC 65): Bleabeck Force, off River Tees, 335 m, Perry 56/2 (NMW); High Force, Teesdale, Aug 1899, Horrell s.n. (NMW); Kisdon Force, Swaledale, 15 Sep 1958, Fitzgerald s.n. (POZG). Mid-west Yorkshire (VC 64): Ingleton, Apr 1956, Garlick s.n. (NMW); River Ribble, Stainforth, Jul 1932, Milsom s.n. (NMW); near Ramsgill, 22 Sep 1873, Hobkirk s.n. (H); Bolton Woods, Blarington M.D., sine dato, Carrington s.n. (CANM); Lul Beck, Bouthwaite, Nidderdale, Pateley Bridge, O'Shea 56/2 (FLAS). S.W. Yorkshire (VC 63): Hebden Bridge, Hardcastle Crags, 14 Nov 1896, Needham s.n. (NMW). SCOTLAND. N. Aberdeen (VC 93): Fraserburgh, Aug 1932, Sherrin s.n. (BBSUK, NMW). S. Aberdeen (VC 92): NW side of Loch Etchachan, Cairngorms, 25 m, Long & Murray 14706 (E), Ballater, Aug 1879, Nicholson s.n. (NMW); Aberdeen, Ben-na-Mac-dhui, Jul 1855, Crundwell s.n. (E), Aberdeen, Rubislaw, Jun 1841, Kerr s.n. (E). Angus (VC 90): Glen Dale, Clova, 20 Jul 1853, Croall s.n. (CANM); Glen Esk, Inchgrundle, Sep 1947, Duncan s.n. (E), Caenlochan, Jul 1886, Smith s.n. (E); Dark Mountain Fruige Mofs, in Isla at Reekie Linn, 14 Apr 1919, Robertson s.n. (E); Reekie Linn, 30 Dec 1883, Smith s.n. (E); Guyud, Arbroath, Sep 1882, Smith s.n. (E); Sidlaw Hills, Apr 1842, Gardiner s.n. (E); Montreathmont Moor, Mar 1946, Duncan s.n. (E); Letham near Forfar, May 1946, Duncan s.n. (E); Airlie, Jun 1937, Duncan s.n. (E); Cannes gorge, Glen Isla, Jul 1945, Duncan s.n. (E); White Water, 5 Aug 1869, Christie s.n.

(E); Low of Denoon, Sidlaw Hills, 4 Jan 1921, Robertson s.n. (E). Argyll (VC 98): Inverary, Oct 1846, Stark s.n. (E); Near Dunoon, Sep 1847, Balfour s.n. (E). Ayr (VC 75): Knockdolian Hill, Sep 1915, Armitage s. n. (NMW). Berwick (VC 81): near Airhouse Quarries, Hartside, by Leader Water, ca 240 m, Long 17950 (E); Redpath Hill near Earlston, ca 220 m, Long 218 (E); Elba, 120 m, Graham 180 (E). Clyde Islands (VC 100): Arran, 1893, Salmon s.n. (NMW). Dumfries (VC 72): Moffatt Water, Carrifran Burn, Raven Craig, Jun 1951, Ratcliffe s.n. (E); Well Hill, Moffatt, Jul 1901, Duncan s.n. (NMW); Moffatt, Jul 1901, Duncan s.n. (E). Dunbarton (VC 99): Dumbartonshire, Stuckindroin, 19 Feb 1961, Clear s.n. (NMW). N. Ebudes (VC 104): Staffin area, Isle of Skye, 50-150m, Janssens 628 (ALTA); Uig area, Isle of Skye, 0-150 m, Janssens 777 (ALTA); Isle of Skye, Aug 1873, Boswell s.n. (s); Isle of Skye: Sligachan, 16 May 1939, Størmer s.n. (O); Glenbrittle, Skye, Jun 1933, Duncan s.n. (E). Fife (VC 85): near Orr Water, Aug 1847, Evans s.n. (E); Maspie Den, Falkland, 13 Apr 1925, Robertson s.n. (E); Fife, 1847, Evans s.n. (E); Swallowcraig Den, 24 May 1978, Caldwell s.n. (E). W. Inverness (VC 97): Fort William, 7 May 1939, Størmer s.n. (0); Laudale River on S shore of Loch Sunart, 0–75 m, Norris 51574 (UC); Morvern, N of Glenmorvern Cottage, ca 10 m, 16 Jun 1992, Coppins, James & Poelt s.n. (GZU); near Arisaig, road to Drimmindarrock, ca 15 m, 10 Apr 1972, Ballantyne s.n. (E); Larachmhor, Arisaig, 1 Nov 1965, Grierson s.n. (E); Ben Nevis, Aug 1908, Duncan s.n. (E). Kincardine (VC 91): Drumtochty, Jul 1834, Cruickshanks s.n. (E). Kirkcudbright (VC 73): New Galloway, River Dee, May 1890, sine collector (E); Bainloch Hill, 25 Mar 1949, Milne-Redhead s.n. (NMW). Lanark (VC 77): River Clyde, Falls of Clyde, Coppins 26/84 (E). E. Lothian (VC 82): Traprain Law, Long 2118 (E); N slope of Traprain Law, ca 120 m, Long 25034 (E); N side of Traprain Law, 12 Sep 1908, Evans s.n. (E). W. Lothian (VC 84): near Livingstone, 11 Apr 1914, Adam s.n. (E); Fairniehill near Philipstoun, ca 75 m, Long 15090 (E). Midlothian (VC 83): Pentlands, Harelaw Reservoir, 31 Oct 1908, Evans s.n. (E); Pentland Hills, Mar 1847, Laing s.n. (E); Logenulee Waterfall, Pentlands, Aug 1951, Fairley s.n. (E); near Glencorse, Pentlands, 31 Dec 1943, Watson s.n. (BR); Cock Burn near Balerno, 4 Apr 1915, Adam s.n. (E). Moray (VC 95): Carven, 15 Jul 1967, Shephard s. n. (E); Delliefure, n. Grantown-on-Spey, Sep 1908, Diver s.n. (NMW). Orkney (VC 111): Green Stamars, Cuilags, Hoy, Sinclair 381 (E); Braebuster Burn, Hoy, Sinclair 240 (E). Outer Hebrides (VC 110): St. Kilda, Hirta, N slope of Mullach Sgar above Village Bay, ca 230 m, Long 19748 (E); St. Kilda, Hirta, ca 40 m, Long 19701 (E); Barra Is., Heva; above Castlebay, Sinclair 337 (E); Alt Heiker, Barra, Sinclair 332 (E); Glen Nevis, 8 May 1939, Størmer s.n. (0); Isle of Harris, Loch Diraclett, Tarbert, 24 Apr 1938, Trotter s.n. (NMW); Barra, 1936, Watson s.n. (E). Peebles (VC 78): Cowies Linn, Long 1186 (E). E. Perth (VC 89): Glen Beag, Jul 1886, Smith s.n. (E). Mid Perth (VC 88): SW of Killin, Jury 6045 (BCB, BR); Ben Lawers, Sep 1908, Diver s.n. (NMW); Craig Chailleach, Jul 1883, Smith s.n. (E); Ben Chonzie, Jul 1909, Meldrum s.n. (E); Ben More, 15 Aug 1925, Bradshaw s.n. (NMW): Creag-an-Lochan, 15 Aug 1905, Evans s.n. (E); Rannoch Moor, Fairley 4/50 (E); Tarmachan Gorge, Lawers, Henderson 7760 (E); Inver, 4 May 1881, M'Intosh s.n. (E); Birnam Hill, Apr 1890, Meldrum s.n. (E); Callerfountain, Jan 1907, Meldrum s.n. (E); Stob Garbh, 7 Jul 1906, Meldrum s.n. (E); Cherrybank, 1887, Meldrum s.n. (E). W. Perth (VC 87): Ben Loch, Long 01709 (E); Dollar, 3 Jul 1869, Christie s.n. (E); Dollar, 23 Apr 1987, Evans s.n. (E); Ben Ledi, Long 1709 (E). E. Ross (VC 106): Coirean Ban, Glen Oykell, 16 Jun 1951, Crundwell s.n. (NMW); above Lochluichart, 21 Jul 1978, French s.n. (NMW); Allt Nan Caorach Valley, ravine along Allt Nan Caorach, Vitt 34638 (ALTA). W. Ross (VC 105): NW Bein Dearg, ca 760 m, Petteker? 56/2 (CANM); Beinn Eighe Reserve, Mar 1952, Fairley s.n. (E). Stirling (VC 86): Balmaha, on shore of Loch Lomond, Hermann 19516 (DUKE): Rowardennan, Lake Lomond, 1 Mar 1939, Walton s.n. (KRAM). E. Sutherland (VC 107): N of Lairg along A836 to Tongue, 122 m, Jury 5997 (BCB, BR). W. Sutherland (VC 108): above Loch nan Uan, Ben Klibreck, ca 550 m, Long 15163 (E); below Cean Garbh, Foinaven, ca 520 m, Long 5109 (E); Ben More Assynth, 21 Jul 1899, Nicholson & Dison s.n. (NMW). Wigtown (VC 74): Loch Ochiltree, Duncan & Crosland 56/2 (E).

GREECE. CENTRAL MACEDONIA. *Prov. Pella*: below Anopeternik, Voras NW Ardea, 1400 m, *Geissler 2121* (G). WEST MACEDONIA. *Prov. Kozani*: Pieria Mts, above Kataphygion, *ca* 1600–1900 m, 9–12 Jul 1956, *Rechinger s.n.* (W). ICELAND. Geysir, 15 Jul 1950, Holmen s.n. (ALTA); Reykianes, at Kleifarvatn, 27 Jul 1948, Holmen s.n. (ALTA); Sudvesturland, Litlimeitill östl., Lambafellshraun (Reykjanes), 27 Jun 1973, Frahm s.n. (COLO); Skápadalur v. Patolks fjörd, Jóhannsson 25359 (ICEL); Miklidalur, Jóhannsson 31238 (ICEL); Seljalandsfoss, V-Eyjefjöll, Jóhannsson 4924 (ICEL); Heidmörk, Reykjavik, Jóhannsson 4907 (ICEL); Veidileysa, Rrnhr. Strand, Jóhannsson 14984 (ICEL); Hemra Skaftartungum, Jóhannsson 30333 & 4914 (ICEL); Hnappavalla i Örafum, Jóhannsson 14671 (ICEL); Sidumannaafréttus v. Amundarbotna, Kristinsson 29661 (ICEL); Lónafjördes, Jóhannsson 11658 (ICEL).

IRELAND. Mid Cork (VC H4): Cork, sine dato, Carroll s.n. (E); Glengariff, May 1850, sine collector (E). E. Donegal (VC H34): Lifford, East, Mar 1889, Clarke s.n. (NMW). Down (VC H38): Tollymore Park, Jul 1901, Armitage s.n. (NMW); Donaghadee, 30 Jul 1935, Conard s.n. (TENN). Dublin (VC H21): Dublin, Foot s.n. (CANM). Fermanagh (VC H33): Correll Glen, 25 May 1907, Tetley s.n. (NMW); Brookfield, Florence Court, 20 May 1908, Tetley s.n. (NMW). W. Galway (VC H16): Kylemore River above Glencorbet, ca 150 m, Long 26250 (E); Longh Corrik, Jun 1842, sine collector (E). S. Kerry (VC H1): N of Dingle Peninsula, W of Castle Gregory, Jun 1989, Johnson s.n. (ALTA, CANM); Cloghane, 7 Aug 1935, Conard s.n. (CANM, WTU); Kenmare, Lough Clonee, 21 Jul 1949, Markgraf s.n. (M). N. Kerry (VC H2): Torc Falls, Killarney, 11 Aug 1935, Conard s.n. (TENN). Leitrim (VC H29): Glenade, Ballinlig, 210 m, 25 Jul 1963, Perry s.n. (NMW). Londonderry (VC H40): Downhill, Jun 1940, Irwin s.n. (NMW); Castlerock, Holyoak 99-112 (herb. Holyoak). W. Mayo (VC H27): Dugort, 15 Jun 1970, Vanden Berghen s.n. (BR). Meath (VC H22): Slane, 25 Sep 1950, Thomson s.n. (NMW). N. Tipperary (VC H10): Keeper Hill, S of the Silvermine Mountains and E of the River Shannon, Melick 79359 (NMW). Waterford (VC H6): Knockmeal Downs, 28 Jul 1933, Armitage s.n. (NMW).

ITALY. CALABRIA. Aspromonte (Prov. Reggio di Calabria), Pietra Impiccata, ca 1700-1750 m, 12 Jul 1988, Poelt s.n. (GZU); Serro Sgarrone, 1690 m, 3 Jul 1999, Privitera s.n. (KRAM). EMILIA-ROMAGNA. Piandelagotti, 11 Jun 1926, Lunardi s.n. (UC); Appennine Mountains, Lawton 518 (WTU); Piandelagotti, 12 Nov 1923, Lunardi s.n. (WTU); Piandelagotti, Gratticelli, Sbarbaro 528 (WTU); Piandelagotti di Modena, Apr 1926, Lunardi s.n. (WTU); Distr. Boscolungo, in Apenino Mutinesi Aemiliae, "Valle delle Pozze" supra Fiumalbo, 1200 m, Levier 352 (KRAM, TENN). LAZIO. Castelgandolfo, Rocca di Papa, Lackmann 22704 (PC). LIGURIA. Prov. La Spezia, Carro Grundgeb., ca 250 m, 24 Mar 1965, Düll s.n. (H); Varazze, Beigria, 5 Jul 1915, Gresino s.n. (WTU); Varazze, Mt Ermetta, Orberina, 11 Sep 1915, Sbarbaro s.n. (H) and 11 Sep 1916, Gresino s.n. (WTU). LOMBARDIA. Prov. Comensis, Alpe Darengo, Domajo, 15 Aug 1898, Artaria s.n. (CANM) and 2 Aug 1897 Artaria s.n. (GJO). PIEMONTE. Campello-Monti, Valdo, 1200-1250 m, Levier 799 (s). SARDINIA. Prov. Sassari: Monte Limbara by Tempio, ca 800 m, 8 Jun 1906, Herzog s.n. (JE). Prov. Nuoro: Punta la Marmora, Mt Gennargentu, ca 1750 m, 2 Jun 1906, Herzog s.n. (JE); Gennargentu Massiv, Lago Alto del Flumendosa by Villagrande-Strisaili, ca 715 m. 26 Jul 1971, Düll s.n. (KRAM). SICILIA. Prov. Catania: Sicily, Etna, Grotte delle Palombe, 1575 m, 1981, Privitera & Lo Giudice s.n. (KRAM, herb. Privitera). Prov. Messina: Monte Poverello, Nov 1904, Zodda s.n. (TENN); Itala presso Messina, 400 m, 1907, Zodda s.n. (s). TOSCANA. Presso Galleno, Vezza stream in Versilia, Jun 1883, Bottini s.n. (G, M, UC, W) [Erb. Critt. Ital. No. 1312]; Vallombrosa, E of Florentia, Secchietta, 1000-1100 m, 5 Sep 1884, Levier s.n. (GJO; M); Vallombrosa, E of Florentiae, Vicano river, near Paradisino, Levier 212 (PRC); in Apennino Pistoriensi Hetruriae, 1370 m, Levier 351 (s); in Apennino Pistoriensi Hetruriae, below "il Doccione" above Sestajone river, 1250 m, Levier 353 (s). TRENTINO-SOUTH TYROL. Adamellogruppe: Malga Monte, ca 1800 m, 19 Sep 1903, Baumgartner s.n. (W).

NORWAY. AKERSHUS. *Asker*: Rønningen, 25 Aug 1962, *Størmer s.n.* (0). *Eidsvoll*: Eidsvoll Verk, 6 Apr 1913, *Sørensen s.n.* (0). *Frogn*: Torkildstranda between Løkkedal and Elle, 9 Aug 1964, *Størmer s.n.* (0); Halaugs, 11 Aug 1935, *Størmer s.n.* (0); Håøya, Brudviken, 4 Jun 1934 and 5 Jul 1937, *Størmer s.n.* (0). *Nannestad*: Tømte, 15 Sep 1962, *Størmer s.n.* (0); Tømte-Vikseter, 28 Aug 1960, *Størmer s.n.* (0); Viksvangen, 28 Aug 1964, *Størmer s.n.* (0). *Oslo*: Aker, Bomva i Nordmarka, 6 Jul 1941, *Størmer s.n.* (0); Aker, Stygdal, 25 Aug 1889, *Conradi s.n.* (0); Sandefjord, Apr 1895, *Hoffstad s.n.* (JE, s); Nordmarken, Björnsaasen, 1866, *Blytt s.n.* (0); Hammeren I Maridalen, 26 Aug 1935, *Størmer s.n.* (0); Kolsans, *Fridtz 2390* (0); Risfjiedkaslet, 31 May 1887, *Fridtz s.n.* (0); Grefsenans, 19 Sept 1886, *Fridtz s.n.* (0); Egeberg, 19 Jun 1858, Zetterstedt s.n. (M, S); Skådalen, 9 Nov 1961, Størmer s.n. (O). Rælingen: Holt, 7 May 1971, Skofteland s.n. (0); Vesledammen W of Narvestad, 25 Jul 1953, Størmer s.n. (o). Vestby: Kjenn, 25 Jul 1958, Størmer s.n. (0). AUST-AGDER. Åmli: Fiskvatn, 11 Aug 1950, Størmer s.n. (0). Bygland: Breidablikk, 3 Oct 1915, Sørensen s.n. (0). Evje: Evjemyren, 2 June 1918, Sørensen s.n. (o). Gjerstad: Höggeto, 18 Aug 1950, Størmer s.n. (0). Gjövdal: Bergbudalen, 15 Aug 1950, Størmer s.n. (0). Herefoss: Ramnåsen, 7 Aug 1953, Jørstad s.n. (0). Lillesand: Lillesand, 28 Jul 1968, Størmer s.n. (0). Tvedestrand: ved Myre på Askerøya, 26 Jun 1976, Størmer s.n. (0); Furøya, 29 Jun 1976, Størmer s.n. (0); Vegusdal Hovlandsdalen, Kvikjern, 7 Jul 1918, Sørensen s.n. (0); Dypvaag, Borøen, 1 Aug 1891, Hagen s.n. (0). BUSKERUD. Eggedal: Øydegarden, ca 200 m, 28 July 1965, Størmer s.n. (0); Ertesprang-Tavstjern, ca 220 m, 30 Jul 1965, Størmer s.n. (0). Hurum: Striglevann, 27 Jun 1945, Størmer s.n. (0): between Barlindvandbekken and Tofte, 25 Jun 1945. Størmer s.n. (0); Knivsfjell, 3 Aug 1962, Størmer s.n. (0); Elgeton, 27 Jul 1959, Størmer s.n. (0). Krødsherad: Bjertnes, 10 Aug 1941, Størmer s.n. (0); Bjertnes, 4 Aug 1941, Størmer s.n. (0); Bratterud, 11 Aug 1941, Størmer s.n. (0); Olberg, 3 Aug 1941, Størmer s.n. (0). Lier: Øksnevoll, 24 Jul 1944, Størmer s.n. (o). Modum: Austad, 28 July 1947, Størmer s.n. (0); ved Kaggefoss, 17 July 1947, Størmer s.n. (0); Tanberg, 18 Aug 1940, Størmer s.n. (0); Askerud, 24 Jul 1947, Størmer s.n. (0); Engelstad, 31 Jul 1948, Størmer s.n. (0); Hornsjøvannet, 3 Oct 1970, Størmer s.n. (0). Øvre Eiker: Vestby-plassen-Langtjern, 4 Aug 1949, Størmer s.n. (COLO, O); ved Tryterud på Eikerens, 5 May 1973, Størmer s.n. (O); ved Tørrbekk ved Eikerens, 20 Sept 1978, Størmer s.n. (O). HEDMARK. Sør-Odal: Svarttjernbekkens munning ved Storsjøen, 30 Sep 1978, Størmer s.n. (0). HORDALAND. Åsane: Åstveit, 19 Feb 1961, Bødtker s.n. (0). Bomlo: Kalavåg, 20 Aug 1967, Størmer s.n. (0). Fana: Natlandsnuten, 9 Oct 1966, Bjørnstad s.n. (0); Espeland, 29 April 1956, Størmer s.n. (0). Fitjar: Rimbareid, 16 Jun 1946, Størmer s.n. (0); Vestbøstad, 20 Jun 1946, Størmer s.n. (0); Levåg, 21 Jun 1946, Størmer s.n. (0). Fjell: Apalvåg ved Sekkingstad, 4 May 1965, Størmer s.n. (0). Fusa: Kirkebygda, 11 Jun 1962, Bödtker s.n. (o). Granvin: Eide, 4 Aug 1943, Størmer s.n. (0); Eide i Hardangerfjord, 16 Jun 1936, Størmer s.n. (0); Nesheimshorgen, 20 Jul 1919, Havaas s.n. (DUKE); lake Nedre-Vasenden, Clarke 642 (WTU). Jondal: Berge, 20 Aug 1943, Størmer s.n. (0). Kinsarvik: Indre Kvalvik-Alsåker, 22 Apr 1954, Gjærum s.n. (0). Kvam: Aksnes, 20 Aug 1943, Størmer s.n. (0); Fosso, 26 Apr 1954, Gjærum s.n. (0); Norheimsund, 4 Aug 1943, Størmer s.n. (0); Kvanndalen, 20 Aug 1948, Lid s.n. (0); Øystese, 19 May 1954, Gjærum s.n. (0). Kvinnherad: Haaland, 11 Aug 1943, Størmer s.n. (0); Malmanger Nutens N-hell, 7 Aug 1943, Størmer s.n. (0). Odda: Odde, 12 Aug 1899, Clarke 459 (WTU). Skånevik: Skromme, Crundwell 286b/61 (S). Stord: Jekteviki, 11 Aug 1967, Størmer s.n. (o). Sveio: Lindøyni i Vigdarvatn, 3 Aug 1969, Størmer s.n. (0). Tysnes: Våge, 12 Aug 1964, Bødtker s.n. (0). Ullensvang: Gamleheimen, 15 Apr 1954, Gjærum s.n. (0). Valestrand: Valevåg, 21 Aug 1967, Størmer s.n. (0). Varaldsöy: Mundheim, 15 Aug 1943, Størmer s.n. (o), Voss: ved Bjørkebrua, 120 m, 24 July 1954, Lid s.n. (0). Vossestrand: Myrkdalsvatn, ca 230 m, 7 Oct 1974, Sandlund (0). MØRE OG ROMSDAL. Averøy: Averö, Jul 1867, Kiær s.n. (0). Bremsnes: Gløsvågen på Nordlandet, 2 Jul 1969, Baadsnes s.n. (0). Fræna: Eidem, 11 Apr 1965, Malme s.n. (0); Lindset, 21 Jul 1966, Malme s.n. (0); Talstadhesten, 7 Aug 1964, 12 Apr 1965 & 4 Aug 1966, Malme s.n. (0); Julset, ca 70 m, 13 Jul 1972, Malme s.n. (0); Slepskaret, 18 Jul 1966, Malme s.n. (0); Lindset, 21 Jul 1966, Malme s.n. (0). Kristiansund: Christiansund, Oct 1868, Lorentz s.n. (G, JE, M, O, S, UC). Midsund: ved Jenset på Otrøy, 11 Aug 1971, Størmer s.n. (0); Lundsbó I Sór-Aukra herres, 3 Jul 1934, Størmer s.n. (0). Molde: Molde, 1 Aug 1971, Størmer s.n. (0). Ørskog: Liafjell, Storvik, W of Sjøholt, 24 Sep 1953, Jørstad s.n. (0). Rauma: Nordsida av Gjersetvatnet, 1 Jul 1972, Malme s.n. (0); between Hjelvik and Hjelviksetra, 6 Aug 1971, Størmer s.n. (0); Grønningsætermyrane, 9 Aug 1951, 310 m, Lid s.n. (0). Stangvik: Stangvik, 5 Jun 1960, Mehls.n. (0). Sunndal: Hovsnebba, 16 Jul 1935, K. & G. Hygen s.n. (0). Sunnylven: Rindal, 15 Aug 1951, Lid s.n. (0). Vanylven: Grubsevatnet, 30 Jul 1973, Malme s.n. (o). Vatne: Fonneløp, 29 Jul 1971, Malme s.n. (0). Vestnes: Fiksdal, 9 Aug 1971, Størmer s.n. (0). Volda: Bjørkedalsvatnet, 26 Jul 1973, Malme s.n. (0). Voll i Möre og Romsdal: Voll, 28 Jul 1951, Lid s.n. (0); Tverrberg, 300 m, 2 Aug 1951, Lid s.n. (0). OPPLAND. Østre Toten: Leirsjøen, 6 Aug 1946, Størmer s.n. (0); between Stubdalen and Høgda, 9 Aug 1946, Størmer s.n. (0). ØSTFOLD. Fredrikstad: Onsø, Fosse, 29 Apr 1886, Rvan s.n. (0). Idd: Klo N of Berby, 14 Jul 1953, Störmer s.n. (O, POZG). Øymark: Ørje, 5 Aug 1963, Størmer s.n. (0). Marker: Rødenes, Ådal, 10 Aug 1963, Størmer s.n. (0). Råde: Ved Engene på halvøya i Vannsjø, 16 Jun 1969, Størmer s.n. (0). Trogstad: Flatebyvika, 5 Sep 1979, Størmer s.n. (0). NORDLAND. Bo: Mørk, Strømsjøen, 7 Aug 1955, Jørstad s.n. (0). Lurøy: Lurøy, 22 Jun 1961, Mehl s.n. (0). Nesna: Einmoen, Fransvikfiellet, Alava 10006 (BR, CANM, COLO, M, W); Nordvik: Bjvin, Jun 1823, Sommerfelt s.n. (0). Rana: Hemnaes, Børrestøllia, 16 Aug 1870, Arnell s.n. (s); Mo, Umbugten, 19 Jul 1933, Hülphers s.n. (s). Vågan: Svolvar, 10 Jul 1890, Jørgensen s.n. (0). Vega: Eidem, 25 Jul 1961, Vasshaug s.n. (0); Voldholmene, 22 Jul 1961, Vasshaug s.n. (o). NORD-TRØNDELAG. Lierne: Skutbakk, 23 Sep 1943, Mejland s.n. (0). Stjørdal: Mjølska-kløfta S of Flornes, 3 Aug 1974, Størmer s.n. (0). ROGALAND. Bjerkreim: Vikeså, 7 Jun 1951, Størmer s.n. (0). Eigersund: Helleland, ca 100 m, Hegewald 3342 (ALTA, FLAS, KRAM); Hesnes, 5 Jun 1951, Størmer s.n. (0); Helleland, 5 Aug 1975, Brettum s.n. (0); Rotveit, 1 Aug 1972, Størmer s.n. (0). Fister: between Hovda and Randøy, 20 Aug 1963, Lye s.n. (0). Gjesdal: Ryfylke, Frafjord, 1 Jul 1893, Nyman s.n. (s). Heskestad: Gya, 11 Aug 1938, Størmer s.n. (0). Hoyland: Gramstad - Stranden, 28 Apr 1958, Størmer s.n. (o); Sandvigen, 28 Apr 1958, Størmer s.n. (o). Karmøy: Skudenes, Hillesland, 9 Aug 1969, Størmer s.n. (0). Klepp: Vashus N of Grudevatn, 27 Apr 1958, Størmer s.n. (0). Lund: Hove, 6 Aug 1975, Brettum s.n. (0). Nærbø: Håelva N of Hå, 29 Apr 1958, Størmer s.n. (0). Sokndal: Eia, 22-26 Jul 1971, Ryvarden s.n. (0); Rekefjord, 13 Sep 1939, Hadač s.n. (o). Time: Søndre Kalberg E of Frøyland, 27 Apr 1958, Størmer s.n. (0). Torvastad: Bjørgjene, 6 Aug 1969, Størmer s.n. (0). SOGN OG FJORDANE. Balestrand: Dragsnes ferjested, 7 Aug 1970, Størmer s.n. (0): Balestråndi, 10 Aug 1970, Størmer s.n. (0). Davik: Förde, 24 Aug 1949, Størmer s.n. (0). Flora: Kinn, 5 Jul 1973, Störmer s.n. (0); Grytdalen, Kupevatn, 11 Jul 1973, Størmer s.n. (0); Sørsiden av Svardalsvatnet, SE of Osen, 9 Jul 1973, Størmer s.n. (0); Askrova, Devikbukta, 6 Jul 1973, Størmer s.n. (0); Florø, 8 Jul 1973, Størmer s.n. (0). Førde: Grøningstølvatn, 5 May 1972, Skulberg s.n. (0); Søöndfjord, 16-19 Jul 1869, Kiær s.n. (0). Gaular: Eldal, 5 May 1972, Skulberg s.n. (0). Hafslo: Okkleviki, 5 Aug 1970, Størmer s.n. (0). Innvik: Olden, Oldøyra, 16 Aug 1951, Lid s.n. (0); Faleide, Nordfjord, 22 Jul 1869, Kiær s.n. (0). Jølster: Paulen, 20 Aug 1951, 100 m, Lid s.n. (0). Lærdal: between Vindedalen gård and Hortu, 3 Aug 1970, Størmer s.n. (0). Leikanger: Skopasete E of Eitorn. 10 m. 27 May 1964. Wendelbo s.n. (0). Stryn: Visnes, 26 Aug 1949, Størmer s.n. (0); Hjelle, E of Strvnsvann, 15 Jun 1954, Jørstad s.n. (0). Vågsøy: Måløy, 18 Aug 1949, Størmer s.n. (0); S of Oppedal, 19 Aug 1949, Størmer s.n. (0). SøR-TRØNDELAG. Bjugn: Nes, Duvhellarn, 1 Oct 1960, Knutsen s.n. (0). Hitra: between Dolm and Bremnes, Dolmøya, Jørstad 15 (0). Kvenvar: Torsnes, 9 Oct 1936, Høeg s.n. (0). Ørland: Storfosen, 11 Oct 1936, Høeg s.n. (0). Rissa: Näbb, 8 May 1960, Størmer s.n. (0). Smøla: Insel Smølen, 8 Aug 1880, Geheeb s.n. (JE). TELEMARK. Bamble: between Ese and Vinterdalen, 10 Jul 1955, Størmer s.n. (o). Kviteseid: Bergsto ved Fjågesund, 8 Sep 1980, Størmer s.n. (0); Dalen i Dalane, 11 Sep 1980, Størmer s.n. (0); Bandaksøya, 14 Sep 1980, Størmer s.n. (0). Lårdal: Eirfjell, 700 m, 7 July 1956, Størmer s.n. (o). Mo: Nevestveit ved Børtevann, 450 m, 10 Jul 1956, Størmer s.n. (0); Barskårtveiten, 2 Jul 1956, Størmer s.n. (O); Bandaksli, 29 Jul 1936, Størmer s.n. (TENN). Notodden: Gransherad, Follsland, 22 Aug 1942, Størmer s.n. (0); Bolkesjø, 19 Aug 1942, Størmer s.n. (0); Dalen, Follsland, 22 Aug 1942, Størmer s.n. (0). Sannidal: Grønnåsen, ca 75 m, Bronger 0116 (0). Selfjord: Ojuvlandsdjuvel, 22 Jul 1885, Esmarks.n. (0). Skien: Gjerpen, Meitjern, 28 Jul 1966, Størmer s.n. (0); Holmbakken ved Kastet, 1 Aug 1966, Størmer s.n. (0). TROMS. Lyngen: Kjosen, 23 Sep 1966, Ulvinen s.n. (COLO, NMW, O, S, W). Tromsø: Kvaløy, Sandvik, 16 Aug 1966, Fagerstén s.n. (O). VEST-AGDER. Bakke: Strandeli, 9 Aug 1938, I. & P. Størmer s.n. (0); Lindeli ved Sirdalsvann, 6 Aug 1938, I. & P. Størmer s.n. (0). Farsund: Lista, E of Straumsland, 3 Aug 1954, Størmer s.n. (0); Planteskolen, 7 Aug 1954, Størmer s.n. (0); Sigersvoll, 6 Aug 1954, Størmer s.n. (0); Udal, 12 Aug 1954, Størmer s.n. (0). Feda: Nordvestvendt E of Feda, 18 Jul 1977, Størmer s.n. (0). Flekkefjord: Flekkefjord by Bergvegg, 24 Jul 1977, Størmer s.n. (0). Greipstad: Bertelsödegård-Trobbevann, 11 Aug 1959, Størmer s.n. (o). Halse og Harkm: Risøbank, 28 Jun 1947, Størmer s.n. (0); Sklernøya, 24 Jun 1947, Størmer s.n. (0). Herad: Sande, 9 Aug 1954, Størmer s.n. (0). Hidra: Midbö, 11 Jun 1951, Størmer s.n. (0); Ysteböbekken, 11 Jun 1951, Størmer s.n. (0); Abilsnes, 5 Aug 1939, Størmer s.n. (0). Holum: Sodeland, 22 Aug 1939, Størmer s.n. (o). Marnardal: Hommen i Bjelland, 21 Jul 1971, Skofteland s.n. (0); Laudal, Åksed nær Manflåvd., 24 Aug 1939, Størmer s.n. (0). Odd79

ernes: Gilsvannets, 12 Aug 1959, Størmer s.n. (0); between Mosby and Mestad, 8 Aug 1959, Størmer s.n. (0). Øvre Sidral: Rauå ved Tiørhom, 12 Aug 1938, I. & P. Størmer s.n. (0). Søgne: Try, 28 Aug 1939, Størmer s.n. (0); Ospedalen, 13 Aug 1959, Størmer s.n. (0). Spangereid: Våge, 19 Aug 1939, Størmer s.n. (0).

POLAND. Beskid Śląski: Nature Reserve "Barania Góra", in Czarna Wisełka River, 30 Jul 1981, Jędrzejko & Żarnowiec s.n. (ALTA, BR, JE, KRAM, M, POZG); Istebna-Prędowiec, Olza river, 22 Sep 1986, Jedrzeiko, Klama & Żarnowiec s.n. (ALTA, BR, COLO, JE, KRAM, M, POZG, w); Szczyrk-Biały Krzyż, Buczkowice commune, near Żylica river, 860 m, 8 Jul 2004, Stebel s.n. (KRAM) and 880 m, 8 Jul 2004, Stebel s.n. (KRAM). Beskid Wysoki: Babia Góra, 1430 m, 1 Oct 1959, Wojterski s.n. (BR, KRAM) [Bryoth. Pol. No. 1257]. Bieszczady Zachodnie: Solinka river between Dział and Jawornik, 680 m., 17 May 1955, Lisowski s.n. (BR, CANM, M) [Bryoth Pol. No. 112] and Ochyra 1553 (ALTA, KRAM). Góry Bialskie: Brusinek, 780 m., 12 Aug 1973, Berdowski s.n. (CANM, KRAM, W). Góry Izerskie: Izera stream near Orle, 780 m, 12 May 1957, Lisowski s.n. (BR, CANM, KRAM, M) [Bryoth. Pol. No. 540]; Czarny Potok river in Czerniawa Zdrój, W of Świeradów Zdrój, 650 m, 27 Sep 1981, Ochyra s.n. (ALTA, BR, CANM, JE, KRAM, TENN, UC) [Musci Pol. Exs. No. 629]. Góry Kaczawskie: Cieplice Śląskie Zdrój, 1 Aug 1904, Prager s.n. (CANM); Jelenia Góra, 1875, Lawrence s.n. (UC); Przesieka near Cieplice Śląskie Zdrój, 3 Aug 1892, Dresler s.n. (JE). Karkonosze: Karpacz, Sowia Dolina, 700-800 m, 13 Aug 1927, Bornmüller s.n. (CANM); Śnieżka, 1600 m, 12 Sep 1926, Wihan s.n. (PRC); Mały Staw, 2 Aug 1906, Krieger s.n. (JE); Jagniątków, 6 Apr 1882, Schoepke s.n. (PRC); Mały Śnieżny Kocioł, 15 Aug 2001, Fudali 4/2001 & 181/2000 (KRAM); Kocioł Małego Stawu, 1183 m, 16 Sep 2002, Żarnowiec s.n. (KRAM). Masyw Śnieżnika: Śnieżnik Kłodzki, Kamionka stream, 700 m, 3 Oct 1956, Lisowski s.n. (BR, CANM, KRAM, M, O) [Bryoth. Pol. No. 389]. Pogórze Kaczawskie: Bolesławiec, ca 150 m, 1 Apr 1868, Limpricht s.n. (BR, JE, KRAM, M, PRC, W) [Bryoth. Siles. No. 220]. Tatry Wysokie: Morskie Oko, ca 1700 m, De Sloover 16830 (BR).

PORTUGAL. Alto Alentejo: Marvão, estrada para Galegos vindo da Fronteira, afloramento junto á Penha da Esparoeira, 620-650 m, 3 Jun 1987, Sérgio, Brugués, Cros & Sim-Sim s.n. (LISU); Crato, Ribeira de Sôr, pr. de Sume, Monte das Cortiças, 450-180 m, Sérgio 8877 (LISU); Maravao, Penha da Esparveira, 650 m, 3 June 1987, Brugués, Sérgio & Sim-Sim s.n. (KRAM); S. Mamede, 820-840 m, 3 Jun 1987, Sérgio et al s.n. (BCB); Ribeira de Arronches, estrada para Vale Lourenço, 640-655 m, Sérgio, Casas, Brugués & Cros 19.1 (BCB); Marvão, Penha da Esparoeira, 650 m, 3 Jun 1987, Sérgio, Cros & Sim-Sim s.n. (KRAM). Beira Alta: Serra d'Estrella, Levier113 (G); Serra da Estrela, Ponte da Caniça e Buraco da Moura, 700-800 m, 25 Jan 1995, Sérgio, Brugués & Cros s.n. (KRAM); Rua dos Mercadores, 1400 m, 28 Mar 1990, Melo s.n. (LISU); Ponte do Soalheiro, a 10 km de Gouveia, descida das Penhas Douradas, 1150 m, Sérgio 8662 (LISU); Vale do Zêzere, 1200 m, Sérgio & Séneca 8120 (LISU); Covao da Ametade, 1450 m, 28 Mar 1990, Melo s.n. (LISU) and 1500 m, 26 May 1993, Greven s.n. (KRAM); Montes acima da Lagoa Comprida, 20 Jul 1941, Luisier s.n. (LISU); Covilha, bajo el Cantaro Raso, ca 1700 m, Muñoz 2042 (ALTA); Cantaro Raso, pr. do Túnel para Manteigas, 1700 m, Sérgio, Séneca & Jansen 8293 & 8296 (LISU): Serra do Caramulo, S. Joao do Monte, ca 600 m. Sérgio & Séneca 8769 (LISU); Entre Vila Nova do Paiva e Viseu pr. de uma ponte sobre o Rio Vouga, Sérgio 378 (LISU): d. Aveiro lim Viseu, Rio Texeiro, Werner 6071 (LISU). Beira Baixa: Serra da Estrela, a 1 km das Penhas da Saúde, 1400 m, Sérgio 7785 (LISU); Nave, 1600-1550 m, sine dato, Palhinha s.n. (LISU). Douro Litoral: Valongo, 1979, Newton s.n. (LISU); Maraõ, próximo da Pousada de São Gonçalo, Zona Florestal da Sapinha, Sérgio 285 (LISU). Minho: Serra de Gerês: Alberguria, Río Conha, 625 m, Schumacker 840619/46 (KRAM); Cascada do Arado, 970 m, Schumacker 840619/11 (KRAM); Laga waterfall, rio Gerês, Schumacker 840622/18 (KRAM); Albergaria, 1908, Luisier s.n. (LISU) [Bryoth. Lusit. No. 352]; Rio al Este de Portela de Hanen, ca 1100 m, 23 Aug 1990, Muñoz s.n. (herb. Frahm); Portela de Leonte, 900 m, Sérgio & Schumacker 5358 (LISU); Moledo do Minho, Sep 1915, Machado s.n. (LISU); Moledo do Minho, Paredez húmidas do "Monte do Padros", Sep 1924, Machado s.n. (LISU); Moledo do Minho, Azevedo, 200 m, Séneca & Sérgio 296 (LISU); Ponte de Lima, ribeiro do Moinho Velho, Aug 1915, Sampaio 985B (LISU); Serra de Arga, Sept 1915, Machado s.n. (LISU); Braga, Mata do Mosteiro de Tibães, 12 Aug 1931, Luisier 73.1 (herb. Frahm). Trásos-Montes e Alto Douro: entre Pitoes e Paradela, Carvalhal de Sezelhe,

1100 m, *Sérgio & Schumacker 5306* (LISU); Pitões das Junias, *ca* 1100 m, *Sérgio 11063* (LISU); Cascata do Cabril, Cabril, pr. de Roca Alta, 1100 m, *Sérgio & Schumacker 5238* (LISU); vila Real, Covelaes, ribeira de rio Mau, confluencia com o Cávado, 800 m, *Séneca & Sérgio 247 & 248* (LISU).

ROMANIA. *Bihorului Mountains*: Jadului valley between Remeti and Bulz, 400 m, 1 Jun 1941, *Boros s.n.* (BP). *Făgăraş Mountains*: Vâlsan Valley, *sine dato, Wallfisch s.n.* (herb. Wallfisch). *Retezat Mountains*: vallis Lepusnicul Mic, near Gura Api, 1000 m, 1 Sep 1971, *Vajda s.n.* (ALTA, BP, KRAM); Riu Mare river near Gura Zlata, 800 m, 9 Jul 1968 and 12 Jul 1968, *Boros s.n.* (BP); Turkului valley near Gura Zlata, 9 Jul 1968, *Vajda s.n.* (BP); Radesul valley near Gura Zlata, 800–900 m, 9 Jul 1968, *Boros s.n.* (BP); Lonticz patak, 800 m, Jul 1871, *Limkowicz? s.n.* (BP, KRAM).

RUSSIA. CAUCASUS. Karachaevo-Cherkessia: Teberda State Reserve, Buulgen Gorge, 28 Aug 1997, Onipchenko s.n. (KRAM, MW). Krasnodar Territory: Sochi, Mt Czamchatcha, 23 Jul 1912, Daniłow & Woronow (LE). Western Caucasus: Lagodiechskij Reserve, Lagodiechskoj gorge, 2 Jun 1951, Abramowa s.n. (LE). KARELIA. Suojärvi, Annantehdas, 10 Aug 1912, Koponen s.n. (H). MURMANSK PROV. Lapponia Imandrae: S of Khibiny Massif, SE of Lysaja Mt, 27 Jul 1956, Schljakov s.n. (Bryoph. Murman. Exs. No 89) (KRAM, MO); Khibiny Mountains, Ajkuajvenchjok river, SE of Lysaja Gora, Schljakov 1907 (KPABG, LE); Lavna-Tundra Mountains, Mt Lavnatundra, Belkina 79-4-87 (KPABG); Kola Peninnsula, Bialovsiha, Voronja river, 6 Jul 1887, Brotherus s.n. (GJO, H, LE); Umba River, Kihlman 604 (LE, S). Lapponia murmanica: Laplandskij Reserve, Salnyje tundry, Mt Elgoras, 856 m, Mt Tiacwaksz, Belkina 144-2-03 (KPABG); Salnyje tundry, between Pieczia-Wuwa Pass and N slope of Mt Cziartuaj, Belkina 35-1-04 (KPABG): Imandra Lake, 10 Jul 1940, Puszking s.n. (KPABG): Chiltald Mt. Chil Creek, Belkina 87-3-88 (KPABG); Chiltald Mt, Rossijoki Creek, Belkina 167-2-88 (KPABG); Rybachij Penninsula, Wolkowaja Bay, Likhachev 40/1 (KPABG). Lapponia petsamoensis: Pummauki, Poropellot, 11 Aug 1926, Häyrén s.n. (H). ARKHANGELSK PROV. Nenetskiy Autonomous Okrug: Terra Samoyedorum (= Nenetskiy Autonomous Okrug, NE part of Archangielsk Prov.), ?, Schrenck s.n. (LE). URALS. Bashkortostan, Beloretzk Distr., 3 km E of Zuyakovo, 23 Jul 1995, Baisheva s.n. (KRAM, MW). Komi Republic: Sverdlovskaya Oblast', Glavniy Khrebet Range, Khodowaja river, 20 Aug 1967, Storozhewa s.n. (KRAM, LE); Denezkin Kamen Reserve, Khozo-Tump Range, 13 Aug 1967, Storozhewa s.n. (KRAM); Piecziorsko-Ylitschkij Reserve, Ylitschia river, 7 Sep 1934, Korczagin & Bochtin s.n. (LE, KRAM). Perm Prov.: Basegi State Reserve, Korostelevka river, Bezgodov 130 (KRAM, MW).

SERBIA-MONTENEGRO. *Montenegro*: Ljubanjica potok at S foot of Kom, *Glowacki 21158* (GJO); Ljubanjica potok at N foot of Kom, 400–500 m, 16 Aug 1896, *Glowacki s.n.* (GJO).

SLOVAKIA. Malá Fatra: Kriváň, ca 1300 m, Jul 1934, Pilous s.n. (BRNM, KRAM, M, PRC) [Bryoth. Čech. No. 2]. Nízké Tatry: Vajskovská dolina, ca 720 m, 1 Sep 1987, Soldán s.n. (PRC); Vajskovská dolina, Kotliská, ca 1700 m, 30 Aug 1987, Váňa s.n. (PRC); Ďumbier at Mýto, ca 970 m, Aug 1949, Pilous s.n. (w) [Musc. Čechosl. Exs. No. 1161]; Tále, in Bystrá dolina, 1500 m, 29 Oct 1984, Irová & Soldán s.n. (PRC); Demänovská dolina, Široká dolina, ca 1220 m, 5 Oct 1984, Pokluda 3935 (BRNM); mons Kráľova hoľa near Čierny Váh, ca 1200 m, 7 Oct 1972, Vajda s.n. (BP). Roháče: Dolina Zuberska (pod Zubercom), 15 Aug 1882, Chałubiński s.n. (KRAM); Roháčské pleso, ca 1560 m, 22 May 1984, Váňa s.n. (PRC); Látaná dolina, ca 1150 m, 21 May 1984, Váňa s.n. (PRC); Zlomisková dolina below Popradské pleso, ca 1600 m, 14 Aug 1963, Vajda s.n. (BP); Malý Studený potok towards Malá Studená Dolina, 27 Aug 1919, Vilhelm (PRC - type of Racomitrium aciculare fo. fluviatile); Bielé pleso, 1620 m, 20 Jul 1922, Podpěra s.n. (TENN); Furkota, ca 1900 m, 3 Jul 1937, Šmarda s.n. (PRC); Podspády - Javorina, 12 Jul 1938, Pilous s.n. (BRNM); Mlýnická dolina, ca 1650 m. Doležal 79/5 (BRNM); Mengusovská dolina, u Hincova potoka, ca 1600 m, 28 Jun 1969, Pokluda s.n. (BRNM).

SLOVENIA. Slovenska Bystrica, 2 Nov 1896, *Glowacki s.n.* (GJO, GZU); Rakovec near Vitanje, 2 Nov 1897, *Glowacki s.n.* (GJO, GZU); "bösen Winkel" near St Lorenzen at Maribor, *Salzmann 3051B 3051C* (GZU); Celie, *Glowacki 337* (M); Oplotnica near Slovenske Konjice, 21 Nov 1897, *Glowacki s.n.* (GJO); Maribor, 21 Apr 1901, *Glowacki s.n.* (GZU); Lobnica near Ruše, 3 Sep 1899, *Glowacki s.n.* (GJO, GZU); near church in the vicinity of Maribor, 29 Apr 1876, *Breidler s.n.* (GJO) and 23 Dec 1900, *Glowacki s.n.* (GJO); near Reifnig, 25 Jul 1892, *Glowacki*

s.n. (GJO); Possruckgebirge, 21 Apr 1901, *Glowacki s.n.* (GJO); Pleschitzgraben am Bacher bei St Lorenzen, 1100–1200 m, 19 May 1892, *Breidler s.n.* (GJO).

SPAIN. Álava: Sarria, rio Larreakorta, ca 738 m, 29 Mar 1986, Heras s.n. (herb. Frahm) and 730 m, Heras 88/85 (VIT), 740 m, Heras 1374/85 (VIT); Lareakorta, 750 m, Heras 67/83 (VIT); Marquina, Barranco Ugalde, 800-950 m, Heras 1512/86 (VIT); Zárate, laderas orientadas al Sur de la cumbre del Gorbea. 1400 m. Heras 377/87 (VIT): Aspárrena, Arriola, Marojal, Rio Barrundia, 650 m, Heras 1660/89 (VIT); Ilárduya, río de La Lece, 820 m, Heras 553/85 (VIT); Cigoitia, Murua, hayedo del barranco Errekaseku, 1000 m, Heras 48/85 (VIT) & 394/83 (BCB); Zuya, Cara Sur de la cumbre de Gorbea, 1360 m, Heras 283/89 (VIT); río Bayas, en Higas, 660 m, Heras 36/86 (VIT); río Padrobaso, 750 m, Heras 1215/86 (VIT). Asturias: Villayón, 1ª Cascada de Oueta, pr. Linera, ca 280 m, Muñoz 1825 (ALTA, herb. Frahm); Castropol, pr. Aquillón, rio Porcia, 400 m, Muñoz 6705 (MA) & 6705 (herb. Frahm); Valdés, playa de Barayo (o de la Vega), rio Barayo, ca 10 m, 23 July 1993, Muñoz 4841 (herb. Frahm, KRAM); Leitariegos, 32 km S Cangas de Narcea, 1400 m, 13 July 1959, Rechinger 0-2135 (GZU, W); Bosc de Muniella, Parque Nacional Asturias, 800-900 m, 4 Sep 1980, Casas & Brugués s.n. (BCB); Valgranda, 1802, Lagasca, Garcia & Clemente s.n. (MA); Pico de Arvas, 9 Jul 1835, Durieu s.n. (BR, G) [Plant Select. No. 101]. Ávila: Sierra de Gredos, Laguna del Cervunal, 1820 m, Granzow, Oritz & Ron 36 (FLAS); Prado del Cervunal, 1800 m, Granzow, Ortiz & Ron 36B (DUKE); Bohoyo, Fuente de la Bajuela cami a la Font Seca, Aiguamolls, 9 Jul 1993, Brugués, Cros & Lloret s.n. (BCB, KRAM); Bohoyo, 1142 m, 9 Jul 1993, Brugués, Cros & Lloret s.n. (BCB); Navalperal de Tormes, 1725 m, 12 Jul 1993, Brugués, Cros & Lloret s.n. (BCB, KRAM); Navalperal de Tormes, 1600 m, 1820 m, 12 Jul 1993, Brugués, Cros & Lloret s.n. (BCB); Nava del Barco, Garganta de la Nava, 1500 m, 10 Jul 1993, Brugués, Cros & Lloret s.n. (BCB, KRAM); Circo de Gredos, 22 Sep 1976, Casas s.n. (BCB); Sierra de Gredos, 12 Aug 1878, Levier s.n. (GJO); Sierra de Béjar, Circo de Las Lagunas de El Trampla, 17 Jul 1985, Elías s.n. (BCB); Solana de Ávila, El Trampal, 2320 m, 9 Sep 1995, Muñoz 6725 (herb. Frahm); Sierra de Candeleda, 10 Dec 1983, Marquet s.n. (BCB). Barcelona: Aiguafreda, hacia Avencó, 18 Nov 1951, Casas s.n. (BCB); Santa Fe del Montseny, cerratera a Sant Marçal, 1200 m, 7 June 1984, Casas & Sergio s.n. (BCB) and 1100 m, 17 Aug 1951, Casas s.n. (BCB); Montseny, Turó de Morou, torrente cerca de Can Sac, 800 m, 10 Dec 1951, Casas s.n. (BCB); Torrent de Gualba, 1050 m, sine dato, Lloret s.n. (BCB). Burgos: Espinosa de los Monteros, Pico de La Miel, 1450 m, Heras 652/88 (VIT); Neila, glaciar de La Cascada, orientación Norte, 1820 m, Heras 863/87 (VIT); Neila, Hayedo junto a la carretera de subida a Las Lagunas, 1500 m, Heras 848/97 (VIT); Neila, bordes de la laguna de La Cascada, 1700 m, Heras 773/87 (VIT) and 23 Jul 1988, Casas s.n. (BCB); Neila, el desfiladero del Najerilla en La Cerrada, 1100 m, Heras 748/89 (VIT); Huerta de Arriba, borde del río Tejero, 1280 m, Heras 822/87 (VIT); Quintanar de la Sierra, 23 & 26 Jul 1988, Casas s.n. (BCB); Quintanar de la Sierra, Las Zabladas, 23 Jul 1988, Casas s.n. (BCB) and 1500 m. 26 Jul 1988, Casas s.n. (BCB), Cáceres: Castanar de Ibor, Rio de Viejas, 590 m, 23 May 1995, Casas et al. s.n. (BCB); San Martin de Trevejo, Sierra de Jalama, 20 Nov 1915, Luisier s.n. (KRAM); San Martin de Trevejo, Sierra de Eljas, 8 Oct 1915, Luisier s.n. (herb. Frahm); Guadalupe, Garganta de la Trucha, 615 m, 24 May 1995, Casas, Sérgio, Brugués & Cros s.n. (BCB); borde del rio Ibor, Las Villuercas, 20 Apr 1980, Viera s.n. (MA); Río Ibor, 710 m, 20 Apr 1980, Viera s.n. (MA); Gata, Rivera de Gata, 400 m, 2 Jun 1986, Brugues s.n. (BCB). Cádiz: Canâda de Candelá, mountains above Algeciras, 600 m, Allen 7416 (BCB). Cantabria: Camaleño, pr. Las Ilces, invernales de Mato, ca 1000 m, 8 Jun 19994, Muñoz 6327 (MA, herb. Frahm); Camaleño, Vega de Tarna, 1600 m. 7 Jun 1994, Casas, Cros & Brugués s.n. (BCB); Rionansa, Sierra de Peńa Sagra, pr. San Sebastián, Canal del Carro, ca 1700 m, Sedo 1141 (herb. Frahm); Santander, Puerto de las Estacas de Trueba, 1080 m, 5 Feb 1988, Brugués & Schumacker s.n. (BCB); Rionansa, Sierra de Peña Sagra, Collado Abellán, 900 m, Infante & Heras 783/93 (VIT); Hermandad de Campoo de Suso, Sierra de Peña Labra, 1700 m, Infante & Heras 760/93 (VIT); Soba, N del puerto de La Sia, 1180, Heras 687/88 (VIT); Canal de Sechugales E Cdo da Cámwa, 1500 m, Geissler 2926 (G). Gerona: Setcases, Torrent de Coma Ermada, 2050 m, 4 Jul 1984, Lloret s.n. (BCB); Setcases, Torrent de Pastuira, 1400 m, Jul 1985, Lloret s.n. (BCB); Setcases, Pinar de Carbones, 2000 m, 2 Jul 1985, Lloret s.n. (BCB); Valle de Núria, base de la Mare de Deu, 2050 m, 11 Aug 1949, Casas s.n. (BCB); Valle de Núria, 11 Aug 1949, Casas s.n. (BCB); En Riba, 13 Aug 1949, Casas s.n. (BCB). Gipuzkoa: Elduayen, río Leizarán, 210 m, Heras 1010/89 (VIT); Hernani, Valle del Urumea, riberas del arroyo Pagoaga, 100-150 m, Heras 1169/89 (VIT); Berástegui, valle de Leizaran, 550 m, Heras 809/92 (VIT); Irún, Lesaka, 160 m, 28 Oct 1982, Aizpuru s.n. (VIT). Granada: Sierra Nevada, Barranco de San Juan, 2600 m, 12 Jul 1973, Varo s.n. (PAMP). Guadalajara: Sierra Dealto Rey, 25 Oct 1975, Buades, Costa, Pajarón & Ron s.n. (BCB); Selas, Areniscas, Pinar de Selas, 1200 m, Heras 895/86 (VIT). Huesca: Panticosa, Ibones del Brazato, 1750 m, 12 Jul 1965, Casas s.n. (BCB); Panticosa, Balneario, 12 Jul 1965, Casas s.n. (BCB); Baños de Benasque, 1700 m, Jul 1969, Casas s.n. (BCB); Selva de Oza, 6 Jul 1989, Casas s.n. (BCB). La Coruña: Caveiro, 1 Mar 1980, Franco 1090 (BCB); Capela Caveiro, 150 m, Geissler 13059 (G); Santiago-Compostella, Dec 1910, Casares-Gil s.n. (GJO). La Rioja: Posadas Sierra de la Demanda, San Lorenzo, Casas 4857 (BCB); Ezcaray, hayedo en el barrancó Zetelurría, 1350 m, Heras 924/85 (VIT); Ezcaray, Negutia, 2000 m, Heras 919/85 (VIT); Ortigoza Cameros, 4 Jan 1983, Abigair s.n. (PAMP); Logroño, Hayedo bajo el Puerto de Piqueras, 15 Jul 1974, Casas s.n. (BCB). León: Puebla de Lillo, Pinares de Lillo, ca 1200 m, 7 Apr 1985, Muñoz s.n. (ALTA, herb, Frahm): Truchas, pr. Truchillas, El Lago, 1800 m. 5 Jun 1991, Muñoz 3643 (ALTA); Posada de Valdeón, pr. Caldevilla, rio Cares, ca 1150 m, 31 Jan 1993, Muñoz 4731 (BR, KRAM, MA, herb. Frahm); Villablino, Vallé du Sil, Weiller 88 (KRAM); Puerto de la Magdalena, Weiller 111 (KRAM); Valles de Cuiña, Ancares de Leon, 900-1000 m, 11 Jul 1984 and 1100 m, 10 Jul 1984, Cros & Lloret s.n. (BCB). Lleida (Lérida): Areu, Vall Ferrerá, 1700 m, Heras 1069 (VIT); Areu, Vall Ferrerá, La Farga, 1500 m, 6 Mar 1992, Casas s.n. (BCB); Vallferrera, 26 Sep 1981, Casas s.n. (BCB); Val d'Aran, Valarties, era Restanca, 2015 m, 14 July 1998, Brugués, Cros, Barrón, Badia & Ruiz s.n. (BCB); Pallars Sobirrà, Vall de Cardós, entre el pla de Negua i Cossibrós, 1550 m, 29 Jun 1998, Casas & Ruiz s.n. (BCB); montes Pirineo Catalán, Pallars Sobira, vallis Vall de Cardós, lacus Llac de Certascans, ca 2236 m, 6 Sep 1988, Váňa s.n. (PRC); Vall de Cardós, Zavascau, 1200 m, sine dato, Casas s.n. (BCB); Zavascau, pujada a l'estany de Certascan, 2100 m, 5 Jul 1988, Casas s.n. (BCB); Canejan, 780 m, 4 Sep 1988, Casas et al. s.n. (BCB); Tabescan, Plans de Boavi, rierol pujant a Broate, 23 Jul 1975, Casas s.n. (BCB); Plans de Boavi, 1600 m, 8 Aug 1969, Casas s.n. (BCB): Garganta de los Caballeros. 11 Aug 1989. sine collector (BCB). Lugo (Galicia): Serra de Xistral, Xestido, 600 m. 22 Sep 1995, Casas, Sérgio & Brugués s.n. (BCB); Belesar, 380 m, 21 Sep 1995, Casas, Sérgio & Brugués s.n. (BCB); Carretera a Piornedo, 1100 m, 5 Jun 1986, Ederra & de Miguel s.n. (PAMP). Madrid: El Chaparral, Montejo de la Sierra, 18 Oct 1980, Ron, Blanco & Toboso s.n. (MA); Siete Picos, alto del Telégrafo, 8 Dec 1929, sine collector (MA); Sierra de Guadarrama, Mar 1802, Lagasca, Garcia & Clemente s.n. (MA). Navarra: Olaldea, 25 Nov 1982, Miguel & Ederra s.n. (PAMP); Urdax, 26 Jun 1985, Miguel & Ederra s.n. (PAMP); Quinto Real, 26 Nov 1981, Ederra s.n. (PAMP); Leyre, 23 Sep 1980, Ederra s.n. (PAMP); en hayedo Fabrica Orbaiceta, Jun 1980, Ederra s.n. (PAMP); Penās de Aya, 28 Jun 1974, Arraisa s.n. (PAMP); Saira, 22 Dec 1974, Arraisa s.n. (PAMP); Artikuza, 4 Apr 1983, Heras s.n. (VIT); Artikuza, Erroiharri, Erreka, 430 m, Aizpuru 591 (VIT); Artikuza, Erroharri, 520 m, Heras 426/83 (VIT); Lezaun, Hoya de Lezaun, 870 m, Heras 21/83 (VIT). Orense: Parque do Xurés, Requiás, subiendo a la Sierra de Pisco, 880 m, 24 Sep 1995, Casas, Sérgio & Brugués s.n. (BCB); Parque do Xurés, Rio Caldo subiendo a la Portela do Home, 530 m, sine dato, Casas, Sérgio & Brugués s.n. (BCB). Palencia: Velilla del Rio Carrión, supra Cárdano de Arriba, laguna de Las Lomas, 2060 m, 17 June 1995, Muñoz 6703 (herb. Frahm); sobre el Pozo de Curavacas, 2000 m, 27 Jul 1950, Losa & Monserrat s.n. (KRAM); Curavacas, 1550 m, Geissler 2997 (G). Pontevedra: Pontevedra, Aug 1912, Casas s.n. (BCB); Vale do Tamezji, perto de Lezneja, 21 Apr 1924, Luisier 73.1 (herb. Frahm); Bords des Rio Leres au Lessvus de Fuente de Bora, 9 Sep 1917, Luisier 73.1 (herb. Frahm); El Grove, Jul 1930, Buch s.n. (H); Fornelos, 20 Aug 1930, Buch s.n. (H); Lerez, 9-10 Aug 1930, Buch s.n. (H); in Monte Cibal, San Vincente, 6 Aug 1930, Buch s.n. (H). Salamanca: El Travieso, 1900 m, Muñoz 6758 (herb. Frahm); Dehesa de Candelario, Elias 363 (BCB); entre Navasfrias i Valverde, 800 m, 31 May 1986, Casas s.n. (KRAM); Navasfrias, Puerto de la Mezas, 1080 m, 19 Jun 1986, Casas, Brugués, Cros s.n. (BCB); Aldeadávila de la Ribera, arroyo del Ropinal, pr. Salto de Aldeadávila, 400 m, 26 Mar 1993 Rupidera s.n. (KRAM, herb. Frahm); Valle de Las Batuecas, 21 Dec 1984, Elías s.n. (BCB). Segovia: Navafria, parque del Chorro, 1 Sep 1988, Garilleti & Lara s.n. (MA); Rio Frio de Riaza, Puerto de la Quesera, 26 Jan 1982, Fuertes & Rojas s.n. (MA) and 1340 m, 26 Nov 1982, Fuertes s.n. (BCB); Riaza la Pinilla, 1550 m, Geissler 13999 (G); N Puerto de la Aneseso, Hayedo de la Pedrosa, piedra en Arroyo, 1720 m, Geissler 14017 (G). Soria: Laguna Negra, Sierra de Urbion, 1650 m, 11 Jul 1974, Casas s.n. (BCB); Sierra de Urbión, ca 50 km NW of Soria, road from Duruelo de la Sierra to the Sierra, 1500 m, Goyder & Jury 720 (H). Tarragona: Prades, Tossal de la Baltassana, 1175 m, sine dato, Casas s.n. (BCB). Teruel: Puerto de Orihuela, sine dato, Varo s.n. (BCB); Orihuela del Tremedal, turbera en Los Ojos, 1400 m, 4 Apr 1974, Casas s.n. (BCB) and 5 Apr 1974 (BCB). Valencia: Estaguas, 1802, Lagasca, Garcia & Clemente s.n. (MA). Vizcaya: Bakio, Barranco del Infierno, Guinea 182 & 186 (MA) and 50 m, Heras 41/91 (VIT); Bakio, Monte Jata, 27 Aug 1941, Guinea s.n (MA); Ubidea, río Zubizola, 580 m, Heras 1703/85 (VIT); Ubidea, 720 m, Heras 67/84 (VIT); Ceanuri, Neveros de Igitegi, 1375 m, Heras 1335/86 (VIT); Abadińo, Rio Urkiola, 600 m, Infante & Heras 232/92 (VIT); Carranza, Pando, 420 m, Robledal, Rio Escaleras, Heras 1153/92 (VIT); Carranza, La Calera del Prado, 620 m, Heras 617/92 (VIT); valle de Carranza, Lanzas Agudas, 350 m, Heras 1609/89 (VIT); Barmeo, Artike, 140 m, Infante 1324/95 (VIT); Meńaca, Sollube, Bco. del Infierno, 320 m, Heras 1378/95 (VIT); Orozco, río Arralde, 900 m, Heras 1289/84 (VIT).

SWEDEN. ÅNGERMANLAND. Säbrå: between Långsjön and Nässjön, 29 Oct 1944, Tuomikoski s.n. (s). ÅSELE LAPPMARK. Vilhelmina: Skikkisjöberget, 22 June 1933, Malmström s.n. (s); Marsfjällen, 31 Jul 1914, Möller s.n. (s). BLEKINGE. Asarum: Granefors, 8 Mar 1918, Medelius s.n. (DUKE, S). Foss: Atorp, 23 Jun 1933, Stenholm s.n. (M). Grinneröd: Ljungskile, 17 Nov 1935, Krusenstjerna s.n. (s). Jämshögs: Baggeboda, 31 Oct 1934, Halle s.n. (s); Gränum, 30 Nov 1917, Medelius s.n. (s). Ronneby: Djupadal, 1860, Winslow s.n. (s). BOHUSLÄN. Högås: Tånga, Nov 1916, Palmer s.n. (s). Kville: Hamburgsund, 23 Jul 1922, Möller s.n. (s). Stenkyrka: Rösselvik, Selling 104 (s); Tyft, 22 Sep 1945, Selling s.n. (s); Blekets hamn, 21 Sep 1945, Selling s.n. (s). DALSLAND. Bäcke: Bjärtveten, 13 May 1913, Bergström s.n. (s). Bolstads: Kvantensburg, Vänern, 16 Jun 1920, Larsson s.n. (KRAM). Dalskogs: Tamshed, 31 Jul 1913, Larsson s.n. (s). Edsleskog: Strand, 17 Jul 1933, Larsson s.n. (s); Rådane, Gulliden, 15 Jun 1913, Larsson s.n. (s). Frändefors: Djupedalen, 7 Sep 1916, Larsson s.n. (s). Fröskogs: Lilla Strand, 2 Aug 1917, Larsson s.n. (s). Gunnarsnäs: Backa, 20 Sep 1914, Larsson s.n. (s). Mo: Öjersbyn, 28 Apr 1912, Larsson s.n. (s); Hasserås, Harsjön, 6 Oct 1913, Larsson s.n. (s). Ödeborgs: Bråten, Torp, 29 Jun 1920, Larsson s.n. (s). Tisselskogs: Buterud, 24 Jul 1938, Larsson s.n. (s). Tõftedals: Mon, 21 May 1916, Larsson s.n. (s). DALARNA. Gagnefs: Mockfjärd, Säl, 19 Jul 1953, Fries s.n. (s). Idre: Häflingkällornas, 31 Jul 1928, Halle s.n. (s); Sjöhöjden, Grövelsjön, 3 Aug 1928, Halle s.n. (s). Leksand: Tibbleberget, 1 Jul 1909, Arnell s.n. (S). GÄSTRIKLAND. Ockelbo: Granbo, 18 Jun 1941, Halle s.n. (s). HALLAND. Fagered: Hackarp, 27 Jun 1926, Stenholm s.n. (s). Hanhals: Hammargård, 23 Mar 1922, Stenholm s.n. (s). Hishult: Hishults, 1 Jun 1926, Stenholm s.n. (s). Tölö: Höglunda, 12 Jun 1922, Stenholm s.n. (s). Vallda: Ysby, 12 Apr 1926, Stenholm s.n. (s). HÄRJEDALEN. Storsjö: Ljungdalen, 600-650 m, 27 Jun 1931, Florin s.n. (s); Dunsjöfjällets, ca 700 m, 16 Jul 1931, Florin s.n. (s). Sveg: Lake Stortjärnen, 13 Jul 1989, Hedenäs s.n. (s). Tännäs: Anåtjärnarna, 16 Aug 1936, Halle s.n. (s); Funnesdalsb, Hellbom 98 (G, JE, M, S). JÄMT-LAND. Åre: Mullfjället, 10 Jul 1916, Hasslow s.n. (BR). Kall: Storvallen vid Rutälven, 400-450 m, 1 Aug 1924, Halle s.n. (s); Strådalen, 30 Jul 1924, Halle s.n. (s). Undersåkers: Ottfjället, 19 Jul 1936, Krustenstjerna s.n. (S). Frostviken: Jormlien, Becking 500715 (UC). LYCKSELE LAPP-MARK. Tärna: village Tärnaby, 600 m, 22 Jul 1916, Möller s.n. (DUKE). LULE LAPPMARK. Sarek National Park, Pårtefjäll, 13 Jul 1902, Arnell s.n. (s). NÄRKE. Kil: Ullaviklint, 18 Sep 1993, Hakelier s.n. (s); between Nya dammen and Klockarhyttan, 25 Oct 1975, Hakelier s.n. (s). Viby: Tystingsbergen, Zetterstedt 72 (s). ÖSTERGÖTLAND. Motala: Lemunda, 1869, Ekstrand s.n. (BR). Risinge: Häradstrop, 21 Jun 1896, Westerberg s.n. (CANM). Torpa: Häradsbäcken above Trantorpet, 21 Jul 1933, Florin s.n. (ALTA, s); Svalön in Sommen, 20 Jul 1933, Florin s.n. (DUKE, s); Brandnäs, 13 Jul 1933, Florin s.n. (s); Björkvik, 15 Jul 1933, Florin s. n. (s). Västra Ny: Gopö, 1863, Holmgren s.n. (KRAM). SKÅNE. Bosarp: Hjälmarod, 23 Jul 1934, Hovgard s.n. (s). Hästveda: Hästveda, 4 May 1914, Hasslow s.n. (KRAM). Höör: Vaxsjön, Jul 1886, Berggren s.n. (S); Höör, 15 May 1891, Möller s.n. (s). Vånga: between Bögesta, Sågmnölla and Västervik, 30 Oct 1934, Halle s.n. (ALTA, S). SÖDERMANLAND. Botkyrka: Övre Tumba, 9 Apr 1928, Florin s.n. (s). Huddinge: Balingsta, 30 May 1899, Arvén s.n. (s); Vårby källa, 14 Apr 1943, Krusenstjerna s.n. (s); Vårbydalen, 19 Oct 1958, Krusenstjerna s.n. (s); Ågestaberget, Krusenstjerna 105 (s). Nacka: Saltsjö-Duvnäs, 17 Sep 1927, Florin s.n. (ALTA, S); Saltsjö-Duvnäs, 24 Jun 1919, Möller s.n. (CANM). Örno: Örno, Jun 1941, Persson s.n. (S). Sorunda: Stora Vika, 27 Aug 1933, Florin s.n. (s). Svärta: Svärtagård, 1 Sep 1929, Florin s.n. (s). Turinge: Näs, 10 Sep 1933, Florin s.n. (s). Tveta: Agdala, 2 Sep 1928, Florin s.n. (s). Tyresö: Långsjöns norra strand, 8 Oct 1933, Florin s.n. (S). Västerhaninge: Presttorp, 22 Sep 1929, Florin s.n. (DUKE, GZU, KRAM, WTU); Vitså, 9 Oct 1927, Florin s.n. (s). SMÅLAND. Algutsboda: Krysseboda, 30 Jun 1942, Florin s.n. (s); Gransjösjöns, 21 Jul 1942, Florin s.n. (s). Aneboda: Frejen, 7 Jul 1938, Santesson s.n. (s). Bankeryd: Alefors, 2 Jun 1897, Arvén s.n. (s). Eksjö: Bjässarp i Skurugata, 26 Aug 1874, Vetterhall s.n. (s). Gladhammar: Gunnebo, 25 Sep 1914, Möller s.n. (s). Gryteryd: between Skogsgärde hållplats and Hensjön, 26 Aug 1938, Halle s.n. (s). Hult: Hesslås, 29 May 1906, Löfvander s.n. (s); Hesslås, 11 Sep 1941, Larsson s.n. (s). Kristdala: Mjölkulla, 15 Dec 1934, Evers s.n. (s). Långaryd: Landeryd, vid Österån mellan stationen och järnvägsbron vid Gårdshult, 25 Aug 1938, Halle s.n. (s). Ljunga: Berget, 14 Jun 1959, Christoffersson s.n. (s). Lofta: Segersgärde, 13 May 1915, Möller s.n. (ALTA, S). Ödestugu: Hohult, 1 Jul 1927, Florin s.n. (s). Pelarne: Massebo, 1 May 1921, Issén s.n. (s). Ramkvilla: Hulu, 16 Jul 1970, Nicklasson s.n. (H). Ryssby: Strättö, 20 Jul 1951, Christoffersson s.n. (s). Törnsfalls: Tjust Blekhem, 10 Aug 1948, Stenar s.n. (KRAM). Tingsås: Ygden Lake, Jul 1926, Halle s.n. (CANM, POZG); Tiken, Jul 1926, Halle s.n. (s). Vissefjärda: Kjessjöns, 2 Jul 1942, Florin s.n. (s); Ansjöns, 2 Jul 1942, Florin s.n. (s). TORNE LAPPMARK. Karesuando: along Merasjoki, below the inflow of the brook Niittyjoki, Hedenäs & Aronsson NT90-338 (s). UPPLAND. Angarns: Nära Kyrkan, 2 Oct 1927, Florin s.n. (s). Blidö: Bergstup, Vagnunda, Yxlan, Jansson 220 (S). Gustavsbergs: Skeviks, 17 Sep 1933, Florin s.n. (KRAM); Skeviks, 17 Sep 1933, Florin s.n. (s). Össeby-Garns: Hackstad, 2 Oct 1927, Florin s.n. (CANM, S); Garnsvikens, 12 Aug 1928, Florin s.n. (S). Östra Ryds: Söderby, Holmingeviken, Krusenstjerna 79 (s). Djurö: Hafsnäo, 24 May 1902, Möller s.n. (CANM). Edebo: Skälby, 7 Oct 1927, Florin s.n. (s). Fresta: Skällnora, 11 Sep 1927, Florin s.n. (s). Ingarö: Tjällmora, Hedenäs B11956 (s). Kärsta: between station and kyrkan, 25 Sep 1927, Florin s.n. (s). Länna: Slängbodaströmmens, 24 Aug 1941, Florin s.n. (s). Lidingö: Kyrkviken, 7 Jun 1928, Möller s.n. (CANM, KRAM, POZG, s); Skärsätra, 7 June 1928, Möller s.n. (s); Ekholmsnäs, Ekholmsnässjön, 10 Nov 1957, Weber s.n. (COLO, DUKE, POZG, UC, WTU), Liusterö: Kornäs. 2 Sep 1928, Möller s.n. (s); Linanäs, 27 May 1928, Tärnlund s.n. (s). Lovö: Kungshattsön, 7 Apr 1927, Florin s.n. (s). Närtuna: Berga, 27 May 1928, Florin s.n. (s). Rasbo: Karlslund, 6 May 1928, Florin s.n. (s). Riala: Rumsättra, 3 Jul 1943, Halle s.n. (s). Sollentuna: Tunberget, 29 Apr 1928, Florin s.n. (s). Solna: Bergshamra, 30 Oct 1927, Florin s.n. (s). Spånga: Rinkeby, 19 Aug 1928, Florin s.n. (s), STOCKHOLM, Värtan near Maceraanstalt, 1 Oct 1927, Florin s.n. (DUKE); Djurgården, 1846, Thedenius s.n. (s); Norra Djurgården, 19 June 1954, Krusenstjerna s.n. (s); Brännkyrka, Flatsjon, 1855, Cleve s.n. (s); Haga, 28 Oct 1887, Thedenius s.n. (s). Vallentuna: Lingsberg, 20 May 1928, Florin s.n. (s). Vaxholm: Vaxön NE of Eriksö, 17 Jun 1962, Krusenstjerna s.n. (s). Wada: Wada by, 25 Mar 1927, Florin s.n. (s); Kråktorp, 25 Mar 1927, Florin s.n. (s). VÄRMLAND. Frykerud: 800 m W of Saxebyn, 3 Sep 1928, Johansson s.n. (s). Långeruds: Kyrkebol, 10 Aug 1936, Larsson s.n. (s). Östmarks: Rõna, 23 Aug 1936, Larsson s.n. (s). Sunne: Stöpafors, Jul 1914, Hülphers s.n. (s). VÄSTERGÖTLAND. Billingen: Simsjön, Aug 1937, Hülphers s.n. (s); Björsjö, 28 Jun 1939, Hülphers s.n. (s). Brandstorp: Vättern between Hästebäcken and Rödån, 19 Aug 1939, Halle s.n. (s). Dimbo: Dimmingedalen, Aug 1937, Halle s.n. (s). Gustav Adolfs: Gagnån between Vättern and Landsvägen, 19 Aug 1939, Halle s.n. (s). Habo: Västra Kärr, 19 Aug 1944, Halle s.n. (s). Haggum: Myggberget, Nov 1933, Hülphers s.n. (s). Härja: between Hackebo and Kvillan, 18 Aug 1944, Halle s.n. (s); Kringelaruder, 18 Aug 1944, Halle s.n. (WTU). Hössna: Rönnåsen, 22 Sep 1933, Halle s.n. (s). Medelplana: Hällekis, Oct 1921, Hülphers s.n. (s). Otterstad: Kållandsö, 1919, Hülphers s.n. (s). Trökörna: Tamstorp, 20 Aug 1937, Hülphers s.n. (s). Tufve: Göteborg, Hisingen, Glöstorp, 12 Apr 1922, Stenholm s.n. (s). Utvängstorp: between Kyrkekvarn and Amurliden, 22 Aug 1929, Halle s.n. (s). Velinga: Ettak, 13 Sep 1946, Hülphers s.n. (s). VÄSTMANLAND. Arboga: Tjurlangens, 10 Sep 1933, Tärnlund s.n. (DUKE). Järnboås: Loberget, 21 Aug 1976, Hakelier s.n. (s). Ljusnarsbergs: Hörken, 12 May 1928, Tärnlund s.n. (s).

SWITZERLAND. Bern: Guttannen, 1080 m, Maier 10591 (G) and 1170 m, Maier 10557 (G); Guttannen, Boden, 900 m, 29 Sep 1995, Maier 10573 (G). Obwalden: Engelbeg, Firnalpeli, 1620 m, Geissler 550 (G). Schwyz: Muotathal, Urwald-Reservat-Bödmeren, 1510 m, Bertram 1164B (G). Ticino: Orello, 1800 m, Geissler 10587 (G). Valais: Oberwald, Gletsch, 1600 m, Maier 10622 (G); Bovernier, gorge du Durnand, 800 m, Maier 10725(G); Cocovier du Salentin, 2000 m, 16 Sep 1900, Amann s.n. (WTU); Strasse to Giètroz, 1250 m, Maier 10374 (G).

TURKEY. ANATOLIA. *Prov. Balikesir*: Edremit, 2 km to Kogaro valley, 850 m, 30 Dec 1993, *Erdag s.n.* (KRAM). *Prov. Trabzon:* Karadul-baraji river near Trapieson near Karadul-baraji village, 8 Nov 1916, *Muriubur s.n.* (KRAM, LE); Ardeşen, Zil Kale castle, 700 m, 20 Jul 2001, *Papp s.n.* (BP).

UKRAINE. Bratkowska, 16–18 Aug 1886, *Wołoszczak s.n.* (KRAM); *Ivano-Frankowskaja Oblast'*: Czarnohora, 1865, *Rehman s.n.* (KRAM); Pozhyzhevska, 24 Sep 1963, *Ulyczna s.n.* (POZG).

MACARONESIA. AZORES. *Fayal Island*: Caldeira, 500 m, *Goncalves 362* (BM), 4 May 1937, *Persson s.n.* (0, s). *Saint Miguel Island*: Capelas ravine near Capelas, 26 Jun 1937, *Allorge s.n.* (PC). *Pico Island*: above Arrife, Riberinho, 330 m, *Frahm Az-247* (herb. Frahm). *San Jorgè Island*: Ribeira Funda, Rinnande, 16 Jun 1938, *Cedercreutz s.n.* (H).

CANARY ISLANDS. *El Hierro Island*: Mountain Ridge above Frontera, 1400 m, 18 Mar 1957, *Lid* (o). *La Palma Island*: Cumbre Neuva, near Cumbre Tunnel, *ca* 1300 m, *Long* 7364 (E, G, NY).

MADEIRA. Bonaventura, Pico Ruivo, 5 Jun 1952, Persson s.n. (CANM, MO, S) and 6 Jun 1952, Persson s.n. (ALTA, DUKE, H, S); Pico Ruivo, 1861 m, 6 Jun 1952, Persson s.n. (ALTA, S); Pico Arieiro, 3 Jun 1926, Hoock s.n. (M); Ribeira Brava, Jun 1937, Persson s.n. (NY); Serras da Boaventura, 15 Sep 1934, Luisier s.n. (herb. Frahm); Pico do Arreiro, Vale de Ribeira do Cidrão, 1750 m, 12 Nov 1994, Greven s.n. (herb. Frahm); Pico do Arieiro, Casa do Arieiro, 1550 m, 16 Jun 1952, Persson s.n. (s); Pico Arieiro towards Pico Ruivo, ca 1700 m, 4 Nov 1976, Eggers MD6/16 (KRAM); Ribeiro Frio, Levado do Furado, 850 m, 15 Nov 1994, Greven s.n. (herb. Frahm); Ribeiro Frio, valley S of the village, ca 900 m, Long 25118 (E); Poiso-Ribeiro Frio, Persson B11955 (s); Fuechal Serras da Ribeira da Janela, 12 Mar 1934, Luisier s.n. (herb. Frahm).

NORTH AMERICA. CANADA. BRITISH COLUMBIA. Lynn Creek Canyon, Schofield & Godfrey 67647 (ALTA, CANM, DUKE, NY); Cheam View, Faser River, Schofield 16517 (CANM); Bella Coola River, near village of Bella Coola, Norris 2351B (COLO) & 2351A (UC); Vancouver, Cypress Creek, Schofield 35749 (CANM); Cheackamus River, S of Garibaldi Station, Ireland 69-200 (CANM); Wadhams, near mouth of Johnston Creek, Schofield 85955 (ALTA, CANM, DUKE); Lausmann Creek, head of Queen's Reach, Jervis Inlet, Schofield 38270 (DUKE); Deserted Bay, Princess Royal Reach, Jervis Inlet, Schofield 38192 (DUKE); Kanaka Creek, E of Haney, Schofield & Bohm 59637 (CANM, DUKE); Haney, Blaney Creek Gorge near University Forest, Schofield 16376 (CANM, DUKE); Mt Noohalk, Norris 2279 (UC); Assanany Creek near Atnarko River, 150-450 m, Norris 2391A (UC); Ocean Falls, Schofield 86312 (DUKE); Bowyer Island, Howe Sound, Schofield 20737 (CANM, DUKE); Calvert Island, Mt Buxton, Schofield & Williams 27929 (CANM); Gambier Island, Mannion Creek, Howe Sound, Schofield 38126 (DUKE); Pitt Island, Holmes Lake, Schofield, Vitt & Horton 72640 (DUKE); Prince Rupert Area, Wyndham Lake, 130 m, Vitt 24644 (ALTA); Monckton Inlet, Schofield 86788 (MO); Selkirk Mountains, Creston Dist., "Summit Creek", 530-600 m, Düll 54 (ALTA); Eagle Pass, near Revelstoke, 9 May 1890, Macoun s.n. (BM, CANM, COLO, DUKE, FH, H, NY, UC, US) [Canad. Musci No. 485]; Mt Revelstoke, 1920 m, Landals & Scotter 810 (ALTA); Ten Mile Creek, Silverton District, Slocan Lake, MacFadden 4122 (CANM, MO); Mill Creek, Slocan Lake, New Denver District, MacFadden 4115 (NY); Indian Creek, Slocan Lake, MacFadden 866 (MO): Yard Creek, E of Sicamous, Schofield & Tan 60491 (ALTA, CANM, DUKE); Hot Springs Kootenay Lake, 7 Jul 1890, Macoun s.n. (BM, FH, US) [Canad. Moss. No. 98]; Sanca Creek, near Boswell, Kootenay Lake, Schofield 14611 (MO); Nelson Area, Kokanee Creek at Redfish Campground, 550 m, Shaw 2762 (ALTA, DUKE); Clear Water plateau, N of Kamloops, 2000-2300 m, Oct 1936, Buckell s.n. (BM); Wells Gray Provincial Park, Murtle Lake Trail, Schofield 76297 (CANM, DUKE); Murtle Lake, Diamond Lake, by start of Murtle River, Ahti 13735 (H); Coffee Creek, Kaslo, MacFadden 869 (NY, WTU); Fraser River, Yale, Schofield & Boas 17745 (CANM); Harrison Hot Springs, E Fraser Valley, Schofield 105419 (DUKE); ca 15 km E of Agassiz, Schofield & Belland 84529 (ALTA, CANM, DUKE, H, MO, NY, TENN); Sumas Mt, Schofield, Chuang & Zales 43161 (DUKE); Trail to Lindeman and Greendrop Lakes, S of Chilliwack Lake, Schofield 57915 (BR, O). QUEEN CHARLOTTE ISLANDS. Chaatl Island: Schofield & Boas 18962 (CANM, DUKE). Graham Island: Dawson Inlet, Schofield & Vaarama 24648 (CANM, DUKE); Image Point, between Skidegate and Skidegate Mission, Schofield & Vaarama 23523 (CANM); Skidegate Mission, Schofield 29755 (DUKE); Marie Lake, near source of Gold Creek, Yakoun River, Schofield 14234 (DUKE); Nercer Lake, near Athlow Bay, Schofield & Krajina 39669 (DUKE); Tow Hill, NE of Massett, Schofield 14309 (CANM, DUKE, NY). Louise Island: Mt Carl, Skedans Creek, Schofield & Spence 83583 (CANM). Lyell Island: Beljay Bay, Schofield & Vaarama 24001 (CANM). Moresby Island: Upper Victoria Lake, 31-46 m, Vitt 12426 (ALTA); Copper River, Schofield 15198 (CANM, DUKE); Crescent Inlet, Schofield 45261 (COLO); Antiquary Bay, Schofield & Krajina 39432 (DUKE). STRAIT OF GEORGIA. Mayne Island: Laura Point, facing Active Pass, Schofield & Boas 17563 (CANM, DUKE); Bennett Bay, Schofield & Boas 17500 (CANM, DUKE). Read Island: NE coast, Schofield 38538 (DUKE). VANCOUVER ISLAND. Goldstream, 180 m, Flowers 4001 (ALTA, COLO, NY); Malahat Highway, Schofield 77342 (ALTA, CANM, DUKE, MO, TENN); Cowichan Lake NE of Duncan, 22 Oct 1976, Hübschmann s.n. (ALTA, herb. Frahm); Mesachie Mt near Cowichan Lake, Schofield 13670 (CANM, DUKE); Pachena River mouth area, Pachena Bay, Schofield 55596 (FLAS); Cook Creek, near Qualicum, Boas 1703 (DUKE); Elk Falls, near Campbell River, Schofield 16194 (DUKE); Arrowsmith trail, 1525 m, Boas 1503 (DUKE); Sooke Hills, MacKenzie 205 & 206 (MICH); Mills Peninsula, near Bamfield, Halbert 4086 (DUKE, FH): Oualiton Falls, ca 180 m. Redfearn 38653 (MO): Old Baldy Mt. Shawinigan Lake, Halbert 4503 (COLO, CANM, DUKE, FH, H, MO); Victoria, Highland District, MacKenzie 203 & 204 (MICH); Port Hardy area, Cheslakee Campsite, Nimpkish River, Horton 640 (ALTA); Port Alice, Frye 275 (WTU); Banks Island, Kooryet Bay, Schofield 86834 (DUKE); Evans Island, Port San Juan, Eyerdam 5169 (WTU); Raza Island, Raza Passage, Schofield 64038 (ALTA, DUKE); Saltspring Island, Mt Bruce, Boas 393 (CANM, DUKE). NEW BRUNSWICK. Albert Co.: Point Wolf, Habeeb 1631 (ALTA, F, NY); Fundy National Park, trail to Third Vault Falls, Ireland 11472 (ALTA, COLO, CANM, DUKE, H, MICH, NY, TENN, US, WTU); trail to Laverty Falls, Ireland 11603 (ALTA, CANM, DUKE, H, MICH, NY, US); Dickson Falls, Ireland 10791 (COLO, CANM, DUKE, H, MICH, NY, TENN, WTU); Dickson Falls, Belland & Schofield 17555 (CANM, DUKE); Kinnie Brook Trail, Ireland 10906 (CANM, MICH). Charlotte Co.: Digdeguash, Ireland 17036 (ALTA, CANM, DUKE, FH, H, MICH, NY, TENN, US, WTU). St. John Co.: Lepreau Falls, SE of Lepreau, Ireland 13392 (CANM, MICH). Victoria Co.: Grand Falls, Hand 55-010 (CANM). York Co.: Fredericton, University Forest, Habeeb 273 (F, NY). NEWFOUNDLAND. Avalon Peninsula: Placentia Bay, Hancock 228 (ALTA, CANM); Conception Bay, Brassard 7122 (ALTA, BR); Long Harbour, Schofield 100994 (DUKE); Black Ridge, Holyrood, Harbour Main, Bell Island, Tuomikoski 669 (CANM, H, MICH); Biscay Bay, Ferryland, Tuomikoski 375 (CANM, H, MICH); Aquaforte, Ferryland, Tuomikoski 616 (H); Content, Trinity Bay. Waghorne 68 (BM); Logy Bay N of St Johns, Norris 3492, 3493, 3494 & 3524 (UC); Waterford Bridge, Tuomikoski 167 (H). West Coast: Bonne Bay area, Gros Morne, 300 m, Brassard, Hancock & Mitchell 7463 (ALTA); Table Mountain near Cape Ray, Burgeo-La Poile, Tuomikoski 2061 (CANM, H); Rencontre West, Burgeo-La Poile, Tuomikoski 1029 (H, MICH); Curzon, Belland 702 (H); Barachois Pond Provincial Park E of Stephenville, Norris 3359 (UC). Central & NE Coast: Gander Lake, Gillett 396 (CANM); Mont Brook near Gambo Pond, Gambo, Bonavista North, Toumikoski 6027 (CANM, H, MICH); Grand Falls District, 23 km SW of Grand Falls, Caledonia Brook on Sandy Lake road, Ahti 7920 (H). South Coast: Pushthrough, Fortune Bay and Hermitage, Tuomikoski 1558 (CANM, H, MICH); Burin Peninsula, Little Harbour East, Hancock & Butler 400 (CANM, H). Northeast Coast: Trinity North District, N of Georges Brook, 75 m, Brassard 7078 (ALTA, BR, CANM, herb. Frahm, H); at mouth of Northwest River near Port Blandford, Norris 3850 & 3903 (UC). North Coast: Northern Peninsula, East River ca 9 km E of Port Saunders, Norris 4425K (UC); Bartlett's River, Schofield, Belland & Hedderson 89125 (DUKE); White Bay North District, Martinique Bay, Conche Harbour, Fife 1765 (MICH, NY). LABRADOR. Battle Harbour, 26 Aug 1891, Waghorne s.n. (CANM). NOVA SCOTIA. Anapolis Co.: Kejimkujik National Park, Kejimkujik Lake, Ireland 12550 (ALTA, COLO, CANM, DUKE, H, MICH, NY, TENN, US, WTU); Mill Falls on Mersey River, Ireland 12529 (ALTA, CANM, MICH, NY, US); W of Hampton, Ireland 17812 (COLO, CANM); Lamb's Lake, Fernald, Bartram & Long 772 (DUKE, FH). Colchester Co.: Lynn, Ireland 17366 (ALTA, CANM, DUKE, FH, H, MICH, NY, US); North River Road, Smith S23 (MICH). Cumberland Co.: Damp rock face, Schofield & Bentley 4851 (CANM). Halifax Co.: Waverley, 22 May 1925, Brown s.n. (CANM); Upper Sackville, 25 Jun 1932, Brown s.n. (CANM); Halifax, 20 Jun 1883, Macoun s.n. (CANM) [Can. Musci No. 97]; Blueberry Point, Grand Lake, Fernald, Bartram & Long 701 (DUKE, FH). Inverness Co.: Cape Breton Highlands National Park, Beulach Ban Falls, Ireland 11863 (ALTA, CANM, MICH); at Third Pool on Cheticamp River, Belland 15701 (CANM); Morrison's Brook, Schofield & Belland 88775 (DUKE); Fishing Cove, ca 6 km SW of Pleasant Bay, Allen 2211 (MO). Kings Co.: Cambridge, Sharpe Brook, Webster 21 (CANM); Blomidon, Ireland 17436 (CANM, MO, TENN, WTU); Long Beach near Baxter's Harbour, Schofield 42445 (CANM, DUKE, MICH); Cape Split, Scots Bay, Allen 2387 (MO). Lunenburg Co.: New Germany, Ireland 17697 (ALTA, CANM, DUKE, FH, H, MICH, MO, NY, TENN, US, WTU); Gold River, S of Beech Hill, Ireland 17622 (COLO, CANM, FLAS, POZG); Gold River at New Ross, Belland & Schofield 10286 (DUKE). Richmond Co.: Irish Cove Brook, S of Irish Cove, Richmond Municipality, Shchepanek & Dugal 84-B-131 (CANM); Cape Breton, below Irish Cove, 4 Aug 1931, Smith S97 (MICH). Victoria Co.: Cape Breton Highlands National Park, trail to South Point, Ireland 11934 (ALTA, COLO, CANM, DUKE, H, MICH, NY, US); trail to Franey Peak, 430 m, Ireland 11685 (ALTA, COLO, CANM, DUKE, H, MICH, NY, US); Cape Breton Island, near Sunset Cape North, 85 m, Mackenzie Lamb 6961 (COLO, CANM, DUKE, NY); Skir Dhu, Schofield 6100 (CANM, NY, US); Indian Brook, Schofield 6052 (CANM, DUKE, MICH, POZG, WTU) and Nichols 77 (NY); Ingonish, about 3.5 km along Cliburn Trail, 1 Aug 1966, Erickson s.n. (DUKE); Jigging Cove Lake, Ireland 11761 (ALTA, CANM, MICH); Mary Ann Falls, Ireland 10406 & 10545 (CANM, MICH). Yarmouth Co.: Goven Lake, Fernald, Bartram & Long 738 (DUKE, FH). ONTARIO. Algoma District: Lake Superior Provincial Park, Orphan Lake Trail, Ireland 15013 (ALTA, CANM, COLO, DUKE, FH, H, MICH, MO, NY, TENN, US, WTU); Sand River, Ireland 14998 (CANM, F); Towab Hiking Trail along Agawa River to Agawa Falls, Ireland 24374 (CANM, WTU); Mamainse Hill, Batchawana Bay area, Williams 1516 (CANM). Haliburton Co.: Haliburton District, Buttermilk Falls, Hand 61-28 (CANM); 10 km N of Minden, Maple Lake, Allen 8531(MO, NY). Hastings Co.: Barry's Bay, ca 14 km SW of Madawaska River, Ireland 22846 (ALTA, CANM, H, MICH, MO, NY). Lennox and Addington Co.: Mellon Creek, Sheffield Twp., Mellon Lake, Ireland 22699 (F, FLAS, CANM, POZG, TENN, WTU). Muskoka District: Rosseau, E of Cardwell Township, Ireland 23056 (ALTA, CANM, CAS, DUKE, F, FH, FLAS, H, MICH, MO, US, TENN, WTU); Foot's Bay, Moon River, Freeman Township, Ireland 23981 (ALTA, CANM, H); Kashi River, Cain 1297 (CANM, DUKE, NY, TENN, WTU). Nipissing District: Algonquin Provincial Park, Highland Hiking Trail, Lake of Two Rivers, NW of Whitney, 395 m, Ireland, Koponen & Inoue 15687 (ALTA, CANM, FH, H, MICH, NY); Algonquin Park, Costello Lake, Cain 2550 (CANM); Rutherglen, Ireland 20828 (COLO, CANM); Bear Island, Lake Timagami, Cain 745 (CANM, MO). Parry Sound District: Sequin River, ca.3 km N of Orrville, Ireland 20735 (ALTA, DUKE, F, FH, FLAS, H, MICH, MO, NY, TENN, US, WTU); Bigwood, French River, Mowat Township, Ireland 22196 (ALTA, CANM, DUKE, F, FH, H, MICH, MO, NY, TENN, WTU); Sprucedale, McMurrich Township, Ireland 23011 (CANM, DUKE, F, FH, FLAS, POZG, TENN, US, WTU); South River, Hand 842 (CANM); McKellar Township, Ireland 24107 (CANM, DUKE, F). Sudbury District: Chutes Provincial Park, along Aux Sables River, near Massey, Ireland 14703 (CANM); ca 12 km S of Espanola, Curtin Township, Ireland 22309 (COLO, CANM); Wanapitei River, ca 25 km SW of Estaire, Ireland 22272 (FLAS, CANM, KRAM, POZG, UC); Long Lake, 12 km S of Sudbury, Cain 3882 (H). QUEBEC. Argenteuil Co.: Grenville Twp., Fasset, Petite Riviére, about halfway up to Lac Fabré, Ley 224 (CANM). Brome Co.: Mont Sutton, Faubert 250.1 & 250.5 (herb. Frahm). Dorchester Co.: Morisset, riviére Famine, Masson 5273 (TENN). Gatineau Co.: Luskville Falls, Luskville, Ireland & Ley 10016 (COLO, CANM, FLAS, MICH) and Trucco & Ireland 78 (CANM): Cantley, Gatineau River near Ottawa, Schofield 14911 (CANM, DUKE WTU). Pontiac Co.: Mansfield Twp., Coulonge, Ley 25 (CANM). Matane Co.: Mt Blanc, LaPage 3504 (WTU). Montcalm Co.: Comté de Montcalm, Lac des Femmes, SE of Petit Lac Monroe, Hermann 16518 (BM, DUKE); Comté de Montcalm, Parc du Mont Tremblant, on shore of Riviére La Diable, Le Vieux Camp, Lac Monroe, Hermann 16667 (MICH, US, W); Parc du Mont Tremblant, NE of Lac des Femmes, Lac Monroe, in Ruisseau des Ormes, Hermann 16804 (CANM, US). Saguenay Co.: Petit lac Manicouagan, Lavoie 80-179 (CANM). Terrebonne Co.: Rivière La Diable below La Chute, Lake Monroe, Parc du Mont Tremblant, *Hermann 16647* (BR, COLO, US); Mont Tremblant Park, *Flowers 5826* (COLO); Mont Tremblant Lodge, *Crum & Anderson 10071* (CANM). **YUKON.** Lake Lindeman, *Williams 601* (F, MO, NY, US).

USA, ALABAMA, Cherokee Co.: Cherokee National Forest, Dennis Cove Campground, SE of Hampton, along Laurel Fork River, ca 790 m, Buck 1040 & 1126 (NY): at Little River canvon Bowers, Havnes & Timme 14594 (DUKE, MICH). De Kalb Co.: at Little River Gorge, 600 m, Churchill 19645 (DUKE, MO); De Soto State Park on Lookout Mountain, West Fork Little River, 430 m, Allen 21202 (MO); De Soto State Park, NW of Mt Payne, ca 430 m, Pursell 3632 (MO); Buck's Pocket, S of Langstone, Guntersville State Park, Harvill 5376 (NY). Jackson Co.: Flat Rock, Pursell 12072 (PAC). ALASKA. Aleutians East Co.: Alaska Peninsula, Izembek National Wildlife Reserve, Swan Lake, Cold Bay Area, Schofield & Talbot 99471 (DUKE); Port Moller, Sharp & Iwatsuki A354a (TENN, WTU); Nagai Island, Macoun 129 (CANM); Simeonof Island, Shumagin Island, Schofield 105887 (DUKE, MO, NY). Aleutians West Co.: Adak Island, Finger Bay, Schofield, Talbalt, Talbolt & Schofield 101402 (ALTA, DUKE); Mitt Lake, Smith 3604 (TENN); Atka Island, Eyerdam 535 (BM, FH, MICH, WTU); St Paul Island, Macoun 83 (NY); Unalaska Island, Summer Bay, Schofield 104550 (DUKE); Unalaska Island, Eyerdam 553 (WTU); Attu Island, Sarana Valley, Bell Howard 58bis, 60bis, 61bis, 62bis & 63 (MICH, US); Holtz Bay, Moore Ridge, Bell Howard 712 (MICH); Amchitka Island, (Rat Islands), lakes on Infantry Road near Cyril Cove, Shacklette 7186 (MICH). Juneau Co.: Juneau Ouadrangle. Montana Creek, 200 m, Viereck 8682 (COLO, CANM, NY); Gold Creek Canon near Juneau, 31 Jul 1891, Cooley s.n. (FH, US); Juneau, Coville & Kearney 573 (NY, US) and Trelease 2174 (MO, NY); E of Juneau, along Basin Road, Gold Creek Valley, Worley 12459 (MICH). Kenai Peninsula Co.: Chisik Island, Snug Cove Cannery, Schofield 99173 (ALTA, DUKE, TENN). Ketchikan Gateway Co.: Ketchikan, 25 m, Eyerdam 551 (CANM, DUKE, MO, NY, WTU, TENN), 554 (COLO, FH, NY, UC, TENN, WTU), 672 (MO, WTU) & 689 (MICH); Revillagigedo Island, George Inlet, Mahoney Creek, ca 15 m, Shacklette 4932 & 4971 (MICH). Kodiak Island Co.: Kodiak Island, Trelease 1849 (MO, NY, PC); Kassaan, Looff & Looff E16 (FH, MICH); Alitak, Looff E67 (FH, MICH); Fort Greely, Smith 42 (CAS, FH); Anton Larsen Bay beyond Buskin Lake, ca 30-50 m, Sharp 219 (NY, TENN); Olga Bay region, Cannery Lake, 10 Jul 1940, Looff s.n. (WTU); Pasagshak State Recreation Area, Pasagshak Bay, Darigo 2781 (MO); Sitkalidak Island, Eyerdam 37 (BM, FH). Prince of Wales-Outer Ketchikan Co.: Morse Cove, 14 June 1913, Frye s.n. (WTU); Prince of Wales Island, Lower End of Klawak Lake, Half Mile Creek, Worley & Hamilton 6874 (UC); Prince of Wales Island, 15 Sep 1937, Looff s.n. (OSC). Sitka Co.: Baranof Island, Sitka, sine dato, Rischoff s.n. (FH); Old Russian Cemetery near Blockhouse, 18 Aug 1969, Yuncker s.n. (NY); Norfolk Sound, 1830, Katalsky s.n. (F); Indian River, 150-240 m, Sharp & Iwatsuki 5485 (TENN); Sawmill Creek, Blue Lake, Hamilton 9452 (BR, DUKE). Skagway-Hoonah-Angoon Co.: Admiralty Island, Deep Bay, 30 m, Eyerdam 563a (WTU); Yakobi Island, Lake Iakanis, 75 m, Shacklette 3933 & 3933a (MICH). Valdez-Cordova Co.: Knight Island, Thum Bay, Prince William Sound, Eyerdam 834 (NY, WTU). Wrangell-Petersburg Co.: Union Bay, Baxter 3B (MICH); Mitkof Island, S of Petersburg, Worley & Schofield 8764 (F). ARIZONA. Pima Co.: Bear Canyon Picnic Area, Mt Lemmon, 2440 m, McCleary 520 (COLO). ARKANSAS. Newton Co.: Alum Cove Natural Bridge, Ozark National Forest, 550-640 m, Redfearn & Shimizu 33201A (ALTA, COLO, CANM, herb. Frahm, MICH, MO, NY, TENN); Alum Cove Natural Bridge, Redfearn & Düll 32707 (MICH, MO) and Allen & Magill 4726 & 4728 (MO); Alum Cove Natural Bridge Recreational Area, Ozark National Forest, 590-640 m, 12 Oct 1996, Redfearn s.n. (herb. Frahm, KRAM) [Moss Int. High. No. 75]; Alum Cove, "Natural Bridge", ca 6 km NW of Deer, 700 m, Düll & Redfearn 2023 (DUKE, NY). CALIFORNIA. Alpine Co.: Toiyabe National Forest near end of Blue Lakes Road, Tamarack Lake, 2400 m, Norris 82770 & 82778 (UC); Central Sierra Nevada, Stanislaus National Forest, Carson-Iceberg Wilderness, Sword Lake, N of County Line Trailhead and the Dardanelles, 2100 m, Shevock 21047 (CAS, KRAM). Amador Co.: Eldorado National Forest, Bear River Reservoir, Devil's Lake Trailhead, 2100 m, Norris 82698 (H, UC), 82710 (UC) & 82694 (KRAM). Butte Co.: Bidwell Bar, Feather River, Schofield 23135 (CANM); Powell Creek mouth, Enterprise, Schofield 23188 (CANM, DUKE). Del Norte Co.: Redwood Forest, Smith River near Jedediah Smith State Park, Koch 3799 (BM, H, MICH, NY, UC, US). Six Rivers National Forest: Hardscrabble Creek at Smith River, Norris 10866 & 10872 (UC); North Fork of Smith River S of Stony Creek, 150 m, Norris 9668 (MICH, NY, UC); along Smith River at Jones Creek, Norris 46209 (UC); along Smith River, Pappas Flat, ca 4 km W of Gasquet, 1400 m, Norris 7815 & 7816 (UC); Prescott Cabin, 1370 m, Norris 9025 (UC); Bear Basin, 1500 m, Norris 9009 (UC). El Dorado Co.: Desolation Wilderness of Eldorado National Forest: between Wrights Lake and Grouse Lake, 2200-2500 m., Norris 76715, 76740, 76743, 76750 & 76761 (UC) & 76754 (ККАМ, МО, UC); Desolation Lake, ca 2400 m, Norris 71122 (UC); Ropi Lake, ca 2300 m, Norris 71111 (UC); American River at Bridal Veil Falls Campground, 1000 m, Norris 58362 (UC) and 1100 m, Norris 58383 (UC); Eagle Falls at Lake Tahoe, Koch 1979 (MICH). Fresno Co.: Kings Canyon National Park, Ranger Lakes at Silliman Pass, 2900-3350 m, Norris 46593 (UC); Sierra National Forest, Cow Creek, N of Dinkey Creek, 2100 m, Norris 88217 (UC); Rock Creek Road along Rock Creek, a tributary to Dinkey Creek, 2040 m, Shevock & York 13934 (CAS, KRAM); Courtright Reservoir road near Clear Lake about 4 km N of Short Hair Creek crossing, Shevock & York 18322 (CAS, KRAM); Short Hair Meadow Creek below Short Hair Meadow, 2620 m, Shevock & York 18347 (CAS, KRAM); along Dinkey Creek at the junction with the McKinley Grove Road toward Wishon Reservoir, Kings River drainage, 1700 m, Shevock & Ertter 13446 (CAS, KRAM). Humboldt Co.: Way County Park, 30 m, Norris 56289 (UC); Redwood Creek, 245-275 m, Norris 47051 & 47078 (UC); Freshwater Creek SW of Kneeland, 600 m, Norris 68268 (UC); Six Rivers National Forest: East Fork of Willow Creek S of East Fork Campground, 365 m. Norris 53337 (UC); Mad River at Graham's, Howe 1060 (NY); Quinby Creek, N of Denny, 610-760 m, Norris 52692 (UC); Oregon Creek N of Trinity Summit Guard Station, 1710-1830 m, Norris & Creek 50161 (UC); Tish Tang Campground, S of Hoopa, 150 m, Norris 47311 (UC). Lake Co.: Mendocino National Forest, Eel River W of Lake Pillsbury, 550 m, Toren 7443 (CAS, KRAM); Crabtree Hot Springs, along Rice Fork of Eel River, 700 m, Toren & Dearing 5239 (CAS, KRAM). Madera Co.: Central Sierra Nevada, Sierra Nevada National Forest, Owl Creek ESE of Whisky Falls, Shevock, Norris, Beyer & Price 20221 (CAS, KRAM); Little Shuteye Pass, Chiquito Ridge, 1950 m, Shevock 24128 (CAS, KRAM); Beasore Road E of Portugese Creek, SW slope of the Balls, 2225 m, Shevock & Kellman 19682 & 19689 (CAS, KRAM); Chilkoot Lake E of Cold Springs Saddle and Beasore Road, 2260 m, Shevock 21212 (CAS, KRAM); Ansel Adams Wilderness, Vanderburg Lake, 2650 m, Shevock 24186 (KRAM). Mariposa Co.: Yosemite National Park: Yosemite Valley near Mirror Lake, 1280 m, Flowers 6528 (ALTA, COLO, KRAM, NY); Merced River near Pohono Bridge, 1180 m, Flowers 6522 (COLO, MO, NY); Yosemite Creek, Vitt 1857 (ALTA, H); Wawona Road S of Wawona Tunnel below Turtleback Dome, 1490 m, Shevock & Norris 20179 (САS, КRAM); Middle Chain Lake, 2775 m, Ikenberry 1292 (мо). Mendocino Co.: Frank and Bessie Smythe Grove, Schofield 93199 (ALTA, CANM, DUKE); Eel River, Branscomb 22824 (MO); N of Branscomb, along South Fork of the Eel River, 400-1000 m, Bourell 551 (CAS, MO); North Fork, Little River, Howe 627 & 645 (UC). Mono Co.: Mammoth Lakes, Inyo National Forest, 3200 m, Norris 86801 (UC); Mill Creek, S of Walker, N of Bridgeport, 2225 m, Lavin 86 (NY). Monterey Co.: Los Padres National Forest: S of Santa Lucia Memorial Park and Indians Ranger Station, 690 m, Shevock et al. 24762 (CAS, KRAM). Nevada Co.: Tahoe National Forest, South Fork Yuba River, 820 m, Shevock & Toren 20738 (CAS, KRAM); Washington Road, below Washington Creek, 875 m, Shevock & Toren 20741 (CAS, KRAM); Feeley Lake, trail to Island Lake, Koch 2016 (MICH); trail from Donner Pass Rest Area to Summit Lake, 2225 m, Whittemore & Whittemore 3036 (CAS). Placer Co.: Dutch Hat District, Canyon Creek, Monte Vista Inn, MacFadden 9596 (CANM); American River near Rawhide Mine, 590 m, Jul 1934, Mac Fadden s.n. (BM, BR, COLO, DUKE, FH, H, JE, M, MICH, MO, NY, O, TENN, UC, US, W, WTU). Plumas Co.: Chipps Creek W of Belden, 1300 m, Norris 69982& 69985 (UC); Gurnsey Creek E of Mineral, 1370 m, Norris 48088 (UC); Buck's Ranch, 1000 m, Leiberg 3478 (US). Shasta Co.: Dog Creek Road, 450 m, Norris & Hermann 22532 (UC); Sacramento River, Sims, Howe 112B (CAS, NY, UC); Lakehead, Dog Creek, Chase Gulch, Hermann 2421A (F, FH); Lassen Volcanic National Park, Hat Creek below Paradise Meadows, Showers 2284 (WTU), Siskivou Co.: Klamath National Forest: Salmon Trinity Alps, Sugar Creek E of Eaton Peak and NE of Russian Peak, 1500 m, Spjut, Norris & Koponen 6277 (OSC, UC); Rainy Creek Canyon, along Elk Creek Trail, 1430 m, Spjut 979 (UC); trail from Wilderness Falls toward Doe Flat, 800-950 m, Norris 67767 (UC); Big Duck Lake, 2010 m, Norris 23308 (UC); Duck Lake Creek, 1670 m, Norris 23302 (FLAS, UC, WTU); South Sugar Lake, 1830 m, Norris & McGrew 45578, 45596 & 45583 & 45608 (UC); Sugar Creek, 1800 m, McGrew 10, 15, 19, 21, 22 & 64 (UC); Russian Lake, 2135 m, McGrew 537, 578, 549 & 550 (UC); Bingham Lake, 2135 m, McGrew 657 (UC); Horse Range Creek, W of Callahan, ca 1830 m, Aug 1969, Sawyer s.n. (UC); Terrace and Upper Cliff Lakes, 1890-1950 m, Norris 53020 (UC). Sonoma Co.: Gualala River near Lee Noble Road, 120 m, Norris 86964 & 86968 (UC). Tehama Co.: Battle Creek E of Mineral, 1675 m, Norris 48168 (UC). Trinity Co.: Shasta-Trinity National Forest: Trinity River, at Swede Creek, 365 m, Norris 10696 (UC); Trinity River at Willie Jack Trail E of Burnt Ranch, 300 m, Norris 10562 & 10572 (UC); Hayfork Creek W of Hayfork, 650 m, Norris 56133, 56139 & 56141 (UC); Bridge Camp W of Clair Engle Lake, 800 m, Norris 68837 (UC); Canyon Creek between Ripstein Camp and McKay Camp, 700-1100 m, Norris 8023 (UC); Weaver Lake, ca 2165 m, Norris 9392 & 9411 (UC); Browns Meadows, ca 1830-2010 m, Norris 23144 (UC); Swinging Bridge E of Burnt Ranch, 8 Apr 1978, Pintler s.n. (MO). Tulare Co.: Sequoia National Park: trail from Panther Gap to Emerald Lake, 3000 m, Norris 67831 (UC); Marble Fork Kaweah River at junction with Little Deer Creek, along Crystal Cave road, 1590 m, Shevock & Tseng Yen-Hsueh 15773 (CAS, KRAM, MO); Mineral King, East Fork Kaweah River drainage, Mosquito Lake, 2745 m, Shevock & O'Brien 15948 (CAS, KRAM); Paradise Creek Trail near Buckeye Campground along the Middle Fork Kaweah River, 915 m, Shevock 15194 (CAS, KRAM); Heather Lake, 2800 m, Shevock 16487 (CAS, KRAM). Sequoia National Forest: Slate Mountain Botanical Area, Middle Fork Tule River, NW of Slate Mt, 2560 m, Shevock 15691 (CAS, KRAM, MO); South Mountaineer Creek, Little Kern River Drainage, Golden Trout Wilderness, 2440 m, Shevock 14242 (CAS, KRAM); Golden Trout Wilderness, Maggie Lake, Pecks Canyon, 2745 m, Laeger 411 (CAS, KRAM). Tuolumne Co.: Stanislaus National Forest, Mill Creek below Cascade Creek Campground, 1700 m, Norris 78813 (UC): Burst Rock Trail E of Strawberry, 2700 m, Norris 82961 (UC); Chewing Gum Lake on Burst Rock Trail in Emigrant Wilderness, 2700 m, Norris 82992 (UC); Donnell Vista Overlook above Donnell Lake, 1900 m, Shevock 21029 (CAS, KRAM): Columbia, South Fork of Stanislaus River, Ikenberry 51 (CANM, MICH, MO,NY, WTU, WVA). Yosemite National Park: Olmstead Point off of Tioga Road, 2500 m, Kellman 505 (CAS, KRAM). COLORADO. Jackson Co.: Lone Pine Creek Trail, Mt Zirkel Wilderness, Park Range, W of Walden, 3200 m, Hermann 26734 (COLO, DUKE, F, FLAS, MICH, NY, US, WTU); Roxy Ann Lake Trail, S of Roxy Ann Lake, NE of Mt Ethel, 3292 m, Rolston 82185 (COLO); between Rainbow Lake and Slide Lake, W of Walden, 3170 m, Rolston 81099 (COLO); Upper Slide Lake, Rainbow Lake Trail, NE of Mt Ethel, 3267 m, Rolston 82205 (COLO). CONNECTICUT. New Haven Co.: Hamden, Allen 265 (FH); Branford, 30 Apr 1920, Nichols s.n. (NY); Wintergreen Falls near New Haven, 22 Apr 1879, Allen s.n. (NY); Mt Carmel, 15 May 1880, Allen s.n. (NY). GEORGIA. Rabun Co.: Canyon at Tallulah Falls, Aug 1893, Small s.n. (NY). IDAHO. Benewah Co.: S of Chatcolet, Bird & Mahler 6523 (CANM). Bonner Co.: Priest Lake, Indian Creek, Ireland 8566 & 8581 (CANM); Lake Pend d'Oreille, Leiberg 230 (CANM, DUKE, MICH, NY, O, US); Boundary Co.: Smith Falls, NW of Copeland, Anderson 22677 (CANM, DUKE, MICH, MO). Clearwater Co.: confluence of North Fork of Clearwater River and Beaver Creek, Steele M36 (US). Gem Co.: Boise National Forest, along South Fork of Payette River at junction with North Fork near Banks, 1150 m, Norris 85287 (COLO, UC). Idaho Co.: Tenmile Creek with South Fork of Clearwater River, 1035 m, Dewey 821 (UC); Clearwater National Forest, Lochsa River, NE of Lowell, Anderson 22.952 (DUKE, NY); Selway Falls, Young 818 (WTU). Kootenai Co.: without closer locality data, Leiberg 19 (NY). Shoshone Co.: St Joe National Forest, Squaw Creek, Avery Ranger District, Mueggler, Anderson & Robinson 8M-5 (DUKE). KENTUCKY. Bell Co.: Cumberland Mt, Varilla Quad, Shillalah Creek, 450 m, Risk & Davison 7494 (DUKE). Letcher Co.: Pine Mt, Poor Fork of the Cumberland River, 915 m, Risk 4910 (DUKE); Bad Branch, SE of Whitesburg, Risk 776, 777 & 968 (DUKE); Bad Branch Nature Preserve, along Bad Branch of Poor Fork of the Cumberland River, Buck 20747 (NY); Bad Branch, SE side of Pine Mt, Fife 3889 (MICH). Mc-Creary Co.: Eagle Falls, Cumberland Falls State Park, Norris 63-215A (TENN, UC). Morgan Co.: WSW of Dehart, Kay Creek, 250 m, Risk & Ousley 10949 (DUKE). Rowan Co.: Passenger Br., SE of Morehead, Risk 4155 (DUKE). MAINE. Androscoggin Co.: Durham Township, Androscoggin River below Lisbon Falls, Allen 14715 (MO). Aroostook Co.: Mody Bridge over St. John River, 330 m, Pursell 12014 (PAC). Cumberland Co.: West Gray, 10 Nov 1935, Lowe s.n. (MAINE). Franklin Co.: N of Weld Township, Tumbledown Mt, West Brook, Chimney Trail and summit, 935 m, Allen 15888 (MAINE, MO); Avon Township, Mont Blue, NE of Weld, Allen 10310 (MO, NY) & 10230 (MO); Madrid, 10 Sep 1933, Nortens & Braum s.n. (MAINE). Hancock Co.: Mt Desert Island, S of the Tarn, Dorr Mt, Senter 106852 (DUKE); Mt Desert Island, Denning Creek, Patterson 139 (NY); Mt Desert, Fernalds Point, Taylor 3301 (MICH); Hulls Cove, Breakneck Road, 23 Nov 1980, Greene & Lee s.n. (DUKE); Acadia National Park, Schodic Point, SE of Winter Harbor, Pedano 574 (MO); Champlain Mt, Allen 2048 (MICH, MO). Knox Co.: Camden Township, Mt Megunticook, Maiden Cliff trail, Camden State Park, Allen 20039 (MO). Lincoln Co.: "Roaring Brook", Bremen, Chamberlain 5630 (FH); Boothbay Harbor Township, Linekin Bay, Spruce Point SE of Boothbay Harbor, Allen 9260 (MO). Oxford Co.: Hartford, Parlin 9178 (DUKE); Ragged Kock, N. Hartford, Parlin 11688 (NY); Canton, Parlin 8325 (DUKE); Trask, Mt Pern, Adams 14341 (DUKE); Mexico, Parlin 11646 (MAINE, NY); Byron Township, Coos Canyon, Swift River at Byron, Allen 16760 (MO); Hebron, Hills Duarry, 18 Jun 1939, Lowe s.n. (MAINE); Andover, 14 Jul 1934, Nortens & Perkins s.n. (MAINE); Grafton Township, Old Speck Mt, Grafton Notch State Park, NW of North Newry, Allen 22593 (MO, KRAM). Piscataquis Co.: Schoodic Lake, N of Milo, Hermann 19134 (BR, CANM, F); Mt Katahdin, 1065 m, Hermann 19294 (BM, DUKE, US); Katahdin Stream, 520 m, Hermann 19577 (NY); Mt Katahdin, Basin Pond, Collins 2151a (FH); Great Basin Trail, Mt Katahdin, Habeeb 2041 (F); N of Waldo Patent Schoodic Lake, Italian Cove SW of West Seboois, Allen 16581 (MO). Somerset Co.: Moxie Gore Township, Moxie Falls, Allen 9343 (MO); Skowhegan, 18 Jul 1928, Lowe s.n. (MAINE); Houston Brook Falls, Pleasant Ridge, Collins 5909 (FH). Waldo Co.: Lincolnville Township, Bald Rock Mt, Camden Hills State Park SW of Lincolnville, Allen 10376 (MO); Liberty, N of South Liberty, 140 m, Solomon 20176 (MO). Washington Co.: Eagle Hill Wildlife Research Station, Dyer Bay Road, Steuben, Pedano 335 & 364 (MO). York Co.: West Hollis, Gleason 3202 (MICH, NY); York, Fernald 211 (FH). MARYLAND. Frederick Co.: Fishing Creek, Catactin Mt, NW of Bethel, Hermann 14283 (CANM, NY) & 13730 (DUKE, MICH, NY, US). Garrett Co.: Swallow Falls, NNW of Oakland, 730 m, Hermann 14892 (CANM, DUKE, MICH, NY, US); Swallow Falls, 13 Sep 1950, Conard s.n. (NY, WTU); Swallow Falls State Park, along Muddy Creek Falls, Reed 62571 (US); Whiskey Hollow, Big Run Road SW of New Germany, Hermann 17615 (DUKE, US); Little Savage River, below Bear Hill, SE of Grantsville, Anderson 25595 (DUKE). MASSACHUSETTS. Berkshire Co.: Mt Washington, brook at Alander, 12 Aug 1901, Britton s.n. (FH); Bash-Bish Falls, 9 Jul 1918, Beals s.n. (NY). Esex Co.: Manchester, Aug 1906, Stevens s.n. (FH). Franklin Co.: Shippee Brook, 13 Nov 1896, Williams s.n. (FH). Middlesex Co.: Melrose, 20 Nov 1911, Kingman s.n. (BM, DUKE, FH); Horn Pard Mt, Woburn, Kingman 1886 (FH). Norfolk Co.: Edith Cascade Ravine, Blue Hill, 23 Apr 1895, Kennedy s.n. (FH); Edith Cascade, Blue Hill, Milton, 28 Feb 1896, Kennedy s.n. (FH); Blue Hill Reservation, Milton, Collins 1808 (FH). Suffolk Co.: Boston, Oak Ridge, ca 80 m, 12 Jul 1980, Frahm s.n. (herb. Frahm). Worcester Co.: The Harvard Forest land, near Petersham, Moccasin Brook, ca 280 m, Brian 10A (MO). MICHIGAN. Alger Co.: Train Point, Steere 472 (BM, COLO, FH, MICH, NY, WTU). Keweenaw Co.: SW of Copper Harbour, Lake Medora, Hermann 16122 & 16123 (DUKE, US); Esrey Park, along Lake Superior, 8 Jul 1962, Sharp s.n. (TENN). Marquette Co.: NNW of Champion, at East Falls, Yellow Dog River, Hermann 23740 (CANM, MICH, W) & 23741 (CAS, NY); Dead River Gorge, W of Marquette, 9 Jul 1962, Sharp s.n. (CANM, TENN). Ogemaw Co.: Rifle River area, Sharp 64713A (TENN). Ontonagon Co.: Little Union Gorge, Porcupine Mountains State Park, Ireland 5181 (US) & 5188 (CANM, US); Porcupine Mts., road to Nonesuch Mine, 20-27 Aug 1935, Nichols & Steere s.n. (FH, MICH). MINNESOTA. Cook Co.: Lake Superior, Grand Marais, 16 Jul-7 Aug 1902, Holzinger s.n. (ALTA). MONTANA. Flathead Co.: Glacier National Park, Jackson Creek on Fish Lake Trail, 1250 m, Hermann 22330 (US, WTU); Glacier National Park, trail to Fish Lake, 1160 m, Yucker & Yucker 7095 (NY); MacDonald Lake, Williams 311 (ALTA, BM, COLO, MO, NY); Lake Terry, 3 Aug 1895, Williams s.n. (ALTA, COLO, KRAM); Avalanche Basin, above Macdonald Lake, 10 Aug 1895, Williams s.n. (CAS); Sperry Glacier, 25 Jul 1898, Holzinger s.n. (NY). Ravalli Co.: Bitterroot Mountains, Hidden Lake, McCune 612 (OSC) and 2020 m, McCune 4046 (OSC). NEVADA. Washoe Co.: Toiyabe National Forest, Lower Tahoe Meadows, Ophir Creek, 2590 m, Shevock et al. 26158A (CAS, KRAM). NEW HAMPSHIRE. Belknap Co.: Mt Belknap, Gilford, 5 Sep 1904, Carter s.n. (DUKE, F, FH, NY, WTU) & 107 (US); Lake Waukewan, Meredith, near Lake Winnipesaukee, 1 Sep 1966, Sutcliffe s.n. (DUKE). Carrol Co.: Pinkham Notch, Lampton 1139 (DUKE); White Mountains, Crawford Notch, James 39-1 (US). Cheshire Co.: Mt Monadnock, 1915, Rathbum & Kite s.n. (US); Marlow, near Sand Pond, Allen & Stair 178 (MICH). Coos Co.: Shelburne, Ingall's Brook, Sep 1891, Farlow s.n. (DUKE, F, OSC); Mt Washington, Greenman 2742 (MO); King's Ravine, Randolph, Rickett 125 (MO); Mt Jefferson, 1740 m, 13 Aug 1939, Wickes s.n. (NY, WVA); Cascades, Tuckermans Ravine, Mt Washington, 10 & 15 Aug 1898, Grout s.n. (DUKE). Grafton Co.: Grafton, Brundage Covered Bridge, ca 520 m, Sep 1963, Hutchinson s.n. (CANM, DUKE, MO); Franconia Notch, 3 Oct 1900, Seymour (F, UC); Holderness, Jun 1915, Dunham s.n. (DUKE, FH); Canaan, Powell's pasture, 530 m, 10 Oct 1947, Hutchinson s.n. (DUKE); North Woodstock, 7 Oct 1884, Summers s.n. (FH) and Jul 1892, Cummings s.n. (MO). Merimack Co.: Concord, Oct 1900, Sanburn s.n. (DUKE). NEW JERSEY. Bergen Co.: Palisades, Austin s.n. (CANM, CAS, MICH, MO, NY, O, US) [Musci Apall. No 147]. Warren Co.: Del. River, Flatbrookville, E.B.B. & E.B.C. 1049 (FH). NEW YORK. Cattaraugus Co.: Allegany State Park, at "Science Lake", 600 m, Düll 875/5 (ALTA, KRAM); Mcarty Hill, Mutton Hollow Road, Great Valley, Glowny 5086 (ALTA, DUKE, MO). Dutchess Co.: Clove, Standley & Bollman 12470 (US). Essex Co.: North Elba, Heart Lake, 670 m, Hermann 13926 (DUKE, MICH, US) and Redfearn 13514 (MICH); North Elba, above Cascade Mt, 825 m, Slack 4485 (herb. Frahm); Adirondacks, Ray Brook, ca 670 m, Düll 1171/1 (KRAM); trail from Adirondak Loj to Algonquin Peak of the MacIntyre Mountains, ca 670 m, Redfearn 13307 (MO); Schroon lake, ca 250 m, 23 Sep 2001, Frahm s.n. (herb. Frahm); Rainbow Falls near Lower Ausable Lake, ca 610 m, Phelps 584 (MICH) and 640-670 m, Smith. Phelps & Marble 38592 (FH): Ausable River, Wilmington Notch. Smith & Baim 16239 (NY); between Whiteface and Esther Mountains, Chamberlain 4447 (FH); St Huberts, 430 m, Ketchledge 724 (MICH, NY); NE of Averyville, ca 550 m, Smith, Miller & Rogerson 38740 (NY); Marcy River near Adirondack Lodge, 29 Aug 1892, Britton s.n. (NY, WTU); Marcy Falls, 3 Aug 1894, Britton s.n. (NY); Lake Avalanche, John Brown Trail, sine dato, Dudley s.n. (NY). Franklin Co.: Camp Wenonah, Upper Saranac Lake near Wawbeck, Chamberlain 4448 (FH). Greene Co.: Kaaterskill Falls, Smith & Blackman 40635 (ALTA, BM, BR, CANM, COLO, F, FLAS, H, KRAM, MICH, O, POZG, TENN, UC) [Moss. N. Am No. 227]; Kaaterskill Creek, below Kaaterskill Falls, Smith et al. 43037& 43041 (NY): Stony Clove, 655 m. Smith & Hammond 40263 (MICH) and 670 m. Smith, Rogerson & Moore 43965 (KRAM, herb. Frahm); Kaaterskill Clove, ca 280 m. Smith. Crum & Miller 47697 (NY). Hamilton Co.: Adirondack Mountains, Gables Cottages, 520 m, Hermann 14584 (CANM, NY); Long Lake Village, Buttermilk Falls, Raquette River, 520 m, Hermann 14480 (DUKE, NY) & 14476 (F); N of Speculator, Hermann 15825 (NY); along Lake Placid Trail, E of Long Lake Village, 550 m, Hermann 15718 (NY, TENN, US). Herkimer Co.: Little Falls, 1868, Austin s.n. (NY). Lewis Co.: Boonville, 1927, Laubengayer s.n. (NY). Orange Co.: Tuxedo, Lawton 1617 (WTU); Montanville, Levy 1398 (DUKE); Arden, Lawton 597 (WTU). Rockland Co.: Sloatsburg, Lawton 3566 (WTU); Ramsey, Levy 1831 & 1982 (DUKE). St Lawrence Co.: Cranberry Lake area, Sixmile Creek, Breisch 113 (ALTA); Cranberry Lake, Chair Rock, 460 m, Ketchledge 539 (MICH, NY); Indian Mountain Bluffs, Cranberry Lake, Allen 47 (MO). Saratoga Co.: Spier Falls, Smith & Ellett 40215 (ALTA, BM, BR, CANM, COLO, F, FLAS, H, KRAM, MICH, MO, O, POZG, TENN, UC) [Moss. N. Am No. 220]; Schunemund Mt, 23 Sep 1917, Beals s.n. (NY). Tompkins Co.: Ithaca, Cornell Falls, 14 May 1941, Hand s.n. (CANM); The Cayuga Lake Basin: Roan Mt, 1 Sep 1885, Dudley s.n. (NY). Ulster Co.: New Paltz, 5 Jul 1964, Yarrow s.n. (NY); Catskill Mountains, Long Path from Upper Cherrytown Road to Vernooy Kill Falls, along Vernooy Kill, 400-550 m, Buck 23087 (NY); trail from Giant Ledge Parking Area to Giant Ledge, 700-975 m, Buck 23128 (NY); Watson Hollow, 305 m, Haring 88 (NY, WVA); Rondout Creek, ca 560 m, Smith, Dunbar & Larson 26058 (MICH). Warren Co.: Tounge Mt, Lake George, Schmitt & Slack 911 (ALTA); Sugar Loaf Mt, 15 May 1918, Burnham s.n. (CANM, MICH); Glen, Hudson River, ca 750 m. Smith & Herrick 49539 (NY), Washington Co.: Lake George Region, Peaked Mt, Fort Ann, 7 Jul 1918, Burnham s.n. (CANM, MICH); Bluff Head, Lake George, ca 100 m, Smith, Lewis & Ogden 43735 (MICH, NY). NORTH CAROLINA. Buncombe Co.: Mineral Creek, NW of Craggy Gardens, 1220 m, Zander 3299A (DUKE); Montreat, Standley & Bollman 10415 (NY); Asheville, Lehman 1042 (F). Burke Co.: Linville River, N of Lake James, 610 m, Anderson & Jones 9331 (DUKE). Clay Co.: Barnett Creek, Perry Gap, Shooting Creek, 1130 m, Anderson 8003 (DUKE). Forsyth Co.: along southbound railroad, Schallert 2894 (DUKE). Jackson Co.: Whitewater Falls, S of Cashiers, 854-976 m, Vitt 22625 & 22627 (ALTA); Cashiers, Anderson 6628 (DUKE); Whitewater Falls, ca 610 m, Pursell 3498 (MO); Upper Falls, 730 m, Anderson 8677 (DUKE); Whitewater Falls, Almeda 1401 (CAS); Nantahala National Forest, Upper Falls of Whitewater River, 700-825 m, Ireland 2824 (CANM, US); Wolf Creek, near junction with East Fork of the Tuckaseegee River, 790 m, Anderson 10193 (DUKE); E of Healy Mt Gap, ca 960 m, Anderson 26350 (DUKE); Pigeon River, below Green Knob Balsam Mountains, 1220 m, Anderson 11261 (DUKE); Devil's Elbow, East Fork, Tuckasegee, Panthertown, 1040 m, Anderson 26330 (DUKE, herb. Frahm); Tuckaseegee Falls, Sylva, Anderson 689 (DUKE); Robinson Creek, near junction with Slattern Branch, 15 km E of Glenville, 975 m, Anderson 10484 (DUKE); Lower Rock Bridge, above Bonas Defeat East Fork of the Tuckaseegee River, 915 m, Anderson 10566 (DUKE); Jenkins Lake, 1100 m, Sharp & Wagner 1866 (TENN); Trays Island Creek, above Fairfield Lake, 1070 m, Wagner 1981 (TENN). Macon Co.: SE of Highlands, Big Creek, S of Horse Cove, 790 m, Anderson 10474 (CANM); Cullasaja River Gorge SE of Cullasaja, Norris 53480 & 53487 (UC); Lower Cullasaja Falls, Cullasaja River, Anderson 882 (DUKE, FH); Chattooga River, between junction of Scotsman Creek and Forest Services bridge, Anderson 26430 (DUKE); Highlands, Chatooga River, 730 m, Hermann 15299 (FH); Chattooga River, Horse Cove near Highlands, Steere 10078 (MICH); Scotsman's Creek, Bull Pen, S of Cashiers, 760 m, Anderson 7879 (DUKE); The Narrows, Chattooga Bluffs Highlands, 820 m, Anderson 8585 (DUKE); Crow Creek, Little Fishhawk Mt, Highlands, 1130 m, Anderson 7984 (DUKE); Piney Knob Creek, 1160 m, 20 Jun 1979, Flisser s.n. (DUKE). Mitchell Co.: Blue Ridge Parkway, Crabtree Falls, below Crabtree Meadows, 945 m, Anderson & Jones 9420 (DUKE). Stokes Co.: Cascades, Moores Springs, Anderson 5757 (DUKE); Lower Cascades Waterfall, Hanging Rock State Park, Dorr 1184 (MO). Swain Co.: Great Smoky Mountains National Park, below Heintooga Overlook, 1460 m, Anderson 20992 (CANM, DUKE); Bunch Creek, Blomquist 2354 (DUKE); Flat Creek Falls near Heintooga, Sharp 4959C (TENN). Transylvania Co.: Toxaway Creek, 550 m, Anderson 9033 (DUKE); Rainbow Falls, Horsepasture River, 820 m, Anderson 8295 (DUKE); Nantahala National Forest, Whitewater River, Corbin Creek, Allen 17811 (MO). Watauga Co.: Blowing Rock, Blomquist 315 (DUKE); Watauga River, W of Sugar Grove, 820 m, Anderson 13133 (DUKE); Grandfather Mt, 25 Jul 1891, Small & Heller s.n. (DUKE, NY). OHIO. Hocking Co.: Hocking Hills State Park, Cedar Falls, Snider 2774 (DUKE). OKLAHOMA. McCurtain Co.: Broken Bow, 15 May 1929, Sharp s.n. (MO). OREGON. Benton Co.: Alsea Falls, Schofield & Lyford 59827 (CANM, DUKE) and Lyford 690 (OSC); W of Alpine on Fall Creek Road, Schofield & Lyford 59872 (DUKE). Clackamas Co.: Mt Hood, Anderson 14481 (DUKE); Camp Creek, SE of Rhododendron, Mt Hood, 915 m, Hermann 18706 (US, WTU); Salmon River, 20 Jun 1901, Foster s.n. (WTU); Oregon city, Willamette river, 12 May 1883, Henderson s.n. (NY); Milwaukie, High Water, 14 May 1883, Henderson s.n. (MICH); Estacada, Leiberg 1150 (US); Clackamas River, 1525 m, Leiberg 1149 (US); Goble, Columbia River, Foster 275 (WTU). Clatsop Co.: Saddle Mt State Park, Saddle Mt, Schofield & Godfrey 67955 (CANM, DUKE); Saddle Mt, 240-305 m, Norris 81290 (UC); Arch Cape, Schofield & Lyford 72302 (DUKE). Columbia Co.: St Helen, May 1875, Macoun s.n., (CANM). Curry Co.: Elk River Road, Norris 21976 & 21980 (UC); Siskiyou National Forest, Elk River Road E of Port Orford, 300 m, Norris 84632 (UC); Hunter Creek Road SE of Gold Beach, 200 m, Norris 84622 (UC); S of Gold Beach, N of Pistol River, Sundberg 171 (WTU). Deschutes Co.: Tumalo Falls, Deschutes National Forest, Tumalo Creek, 1536 m, Christy 1139 (OSC). Douglas Co.: Umpqua River at Susan Creek, E of Roseburg, 500 m, Norris 81839 (UC); Cow Creek, West Fork, Henderson 125921/2 (OSC). Jackson Co.: Prospect, Rogue River, Henderson 12156 (NY, OSC, WTU). Jefferson Co.: Cascade Mountains, Monon Lake, 1525 m, Prescott P-48 (MICH). Klamath Co.: Alsea area, Arsea Falls Creek, Lyford 695 (KRAM); Cherry Creek Basin Research Natural Area, W of Chiloquin, Up Cherry Creek, E of White Pine Lake, 1546 m, Wagner 8524 (osc); Cherry Creek Basin Research Natural Area, W of Chiloquin, above Trapper Lake, 1817 m, Wagner 8357 (osc); W of Valsetz, Siletz River, 240 m, Lyford 45 (NY, OSC); Mack Creek, Lyford 41, 42 & 43 (OSC); Upper Mack Creek, 760 m, Lyford 72 (OSC); Saddle Creek, Lyford 68 & 69 (OSC). Lane Co.: Rainbow, McKenzie River, Schofield & Lyford 60132 (ALTA, DUKE); Blue River, McKenzie River, Henderson 16924 (KRAM, NY, OSC); junction of Walker Creek and S. Fork McKenzie River, Henderson 17132 (OSC); Redsides, Henderson 17829 (OSC); E of Eugene, Fall Creek, 300 m, Sundberg 102 (WTU); Cooks Creek Trail, E of Cape Perpetua, 450 m, Norris 84023 (UC); Springfield, Willamette River, Henderson 17349 (OSC); Leaburg, Leiberg 1591 (US). Linn Co.: Packers Gulch, W of Quartzville, Willamette National Forest, Norris 83980 (COLO, UC); Willamette National Forest, along Pamelia Lake Trail, Pamelia Creek, 976 m, Halse 5692 (KRAM); Rainbow, Schofield & Lyford 60132 (CANM); Old Growth Trail at Echo Creek, 1350 m, Norris 78532 (UC); Green Peter lake, 300 m, Norris 78095 (UC); Gordon Meadows and Lakes, Schofield & Lyford 73736 (DUKE). Marion Co.: Silverton, 1871, Hall s.n. (FH, MICH, MO). Multnomah Co.: Columbia River, E of Crown Point, Ireland 7035 (CANM); Shepperd's Dell, along Columbia River E of Portland, Ireland 6985 (CANM); McCleary Cannon, Portland, 13 Apr 1906, Foster s.n. (BM, CANM, DUKE, F, FH, H, M, MICH, MO, NY, US, WTU, WVA) [Musci Acr. Bor.-Am. No. 238]; Magoon's Landing, Willamette River, 6 Aug 1905, Foster s.n. (OSC); Willamette River above Portland, Elk Rock, Sheldon S11956-2 (OSC); Portland, McClay Park canyon, Flinn 313 (OSC); Oneonta Creek, 23-25 Aug 1962, McCleary s.n. (MO). Polk Co.: Coast Range, Valley of the Giants, North Fork Siletz River, 307 m. Halse 5798 (KRAM). Tillamook Co.: Oswald West State Park, N of Manzanita, 15 m, Griffin C211, C217 & C229 (FLAS); Hug Point, 65 m, Lyford 2165 (OSC). PENNSYLVANIA. Butler Co.: Stone House, Brady Twp, Big Run, 24 Oct 1936, Eastwood s.n. (DUKE, MO, WVA). Cambria Co.: Alleghany Mt., Oct 1859, James s.n. (TENN). Cameron Co.: Wykoff Run, SSW of Sinnemahoning, Pursell 10143 (MO) and 305 m, Manuel 2132 (MO); Shippen Township, Elk State Forest, Fourmile Run Road, Fourmile Run, N of Emporium, Pursell & Allen 11199 (MO); Grove Township, Jerry Run, S of Wyside, Pursell et al. 11257 (MO). Centre Co.: Auxilary State Game Refuge SW of Pine Grove Mills, 240 m, Allen 4855 (DUKE, herb. Frahm); Tussey Mt, 22 Nov 1924, Roberts s.n. (TENN, WVA); Wallace Run, between Bear Knob and Ganderstep Knob, NW of Unionville, Pursell 9801 (MO); Stone Creek, Penn Roosvelt Dam, SE of State College, Allen 133 (MO). Clearfield Co.: Laurel Run, N of Mehaffy, Bell Twp., 30 May 1937, Eastwood s.n. (DUKE); N of Clearfield, Goshen Twp., 4 Jul 1936, Eastwood s.n. (DUKE, MO, WVA). Clinton Co.: Kettle Creek State Park, NW of Westport, Pursell 6146 (MO); Grugan Township, along Eagleton Road, Allen 15959 (MO). Fayette Co.: Cucumber Run just above falls Ohiophyle, 13 Oct 1935, Boardman s.n. (DUKE); upper Cucumber Run, Ohiopyle, Boardman 971 (DUKE); Ohio Pyle Falls, Ohiopyle, Ammons 6433 (WVA); E of Elliotsville, Stony Fork, Allen 275 (MO); Meadow Run, Ohiopyle, Jennings 13254 (MO); Cucumber Run Ohio Pyle, 20 Oct 1940, Jennings s.n. (MO). Huntington Co.: Furnace Gap, SE of Pennsylvania Furnace, Allen 5960 (CANM, herb. Frahm, MICH, MO); Leading Ridge Watershed, Becking 57070036 (CANM). Lackawanna Co.: Stafford Meadow Brook, Glowenke 772 (WTU). Luzerne Co.: E of Glendale above Spring Brook, Rothrock 590 (MO). Lycoming Co.: Cummings Township, Upper Pine Bottom State Park, Upper Pine Bottom Run, WNW of Waterville, Allen 20073 & 20074 (мо); Larry's Creek, NE of Salladsburg, Pursell 10252 (мо). McKean Co.: Willow Creek, ESE of Corydon, 490 m, Moul 4439 (NY); Bennett Brook, Burnett 430 (NY). Pike Co.: Egypt Mills, Bartram 19 (FH); Bushkill Falls, Bartram 436 (FH). Somerset Co.: Shafer Run, Laurel Ridge, 16 Jul 1947, Boardman s.n. (DUKE, MO); Clear Run, Laurel Hill, 620 m, Boardman s.n. (DUKE); Clear Run, Laurel Ridge, W of Miller School, Boardman s.n. (DUKE); Blue Hole, Blue Hole Creek, Laurel Ridge, 5 Jul 1948, Boardman s.n. (DUKE, MO); Sheepskin Run, SE of Ohiopyle, 6 Nov 1943, Boardman s.n. (DUKE, MO); Darlington, 7 Oct 1944, Boardman s.n. (DUKE, MO); Laurel Run, Chestnut Ridge, Dunbar Twp., Boardman s.n. (DUKE, MO); NW of Somerset, Allen 1997 (MO); S of Buckstown, 27 Sep 1937, Jennings s.n. (MO). Sullivan Co.: Sonestown, Moul 2903 (F). Union Co.: White Deer Township, White Deer Creek, W of White Deer Furnace, Tiadaghton State Forest, Allen 16827 (MO). RHODE ISLAND. Providence Co.: Natick (Meshanticut) Falls, Cranston, Collins 6006 (FH, MICH). SOUTH CAROLINA. Oconee Co.: E Fork, Chattoonoga River, 850 m, Anderson 8348 (DUKE). TENNESSEE. Carter Co.: Roan Mt, between upper Little Cove Creek and Carvers Gap, 1525 m, Churchill 13882 (COLO, NY); Cherokee National Park, 1370 m, Ireland 1586 (CANM, US); Carver's Gap, along tributary of Little Cove creek, Risk 582 (DUKE). Cocke Co.: Low Gap, 610 m, Sharp 39187 (FH, TENN). Cumberland Co.: Daddys Creek, N of Crab Orchard, Sharp TM-681 (TENN). Monroe Co.: Sycamore Creek, 730 m, 19 Sep 1954, Sharp s.n. (COLO, TENN); Tellico River, 760 m, Griffin 15878 (FLAS, herb. Frahm); Tellico River below Bald River, 380 m, 18 Sep 1954, Sharp s.n. (DUKE, TENN); Cherokee National Forest, Falls Branch Falls, Falls Branch Trail, Citico Creek Wilderness, Big Junction Quad., Allen 16170 (MO).

Morgan Co.: Clear Fork River E of Clarkrange, 14 Oct 1961, Pringle s.n. (TENN). Sevier Co.: Great Smoky Mountains, Ramsay Falls in Porter River, Voth V462A (COLO, MO); Alum Bluffs Trail, 915 m, 3 May 1972, Griffin s.n. (FLAS); Ramsay Cascade Trail near Greenbrier Pinnacle Fire Tower Trail, 820 m, Norris 57 (TENN, UC); between Mt Buckley and Clingmans Dome, Anderson 10819 (DUKE, MO, NY); between Newfound Gap and Walkers Prong, ca 1370 m, Curry 38 (MO); Mt LeConte, 1280 m, Crum 1516 (CANM); Mt LeConte, Alum Cove Trail, Welch 2175 (NY); Indian Gap Road, 1220 m, Sharp 80 (FH); Mt LeConte, Rainbow Falls trail, 1525 m, Steere 10578 (MICH); Arch Rock, below Alum Cave, Mt LeConte trail, ca 1220 m, Steere 10374 & 10381A (MICH); W of Elkmont, 8 Feb 1931, Johnson s.n. (TENN); below Chimney's Parking Area, 1100 m, 6 Feb 1949, Redfearn s.n. (TENN); Buck-Eagle Rocks Forks, Greenbrier, Cain 636 (TENN); Ramsay Cascades above Gatlinburg, ca 1220 m, Steere 10318 & 10358 (MICH); Gatlinburg, 13 Jun 1934, Conard s.n. (MO). VERMONT. Bennigton Co.: Dorset, 1 Sep 1934, Thompson s.n. (FH); Manchester, 2 Sep 1934, Thompson s.n. (FH). Caledonia Co.: Hardwick, 11 May 1913, Kaiser s.n. (CAS). Chittenden Co.: Mt Mansfield Region, 7 Feb 1896, Grout s.n. (DUKE). Franklin Co.: near Rossier's Farmhouse, Tan 9 9-103 (FH). Lamoille Co.: along Bear Pond Trail, Smuggler's Notch, ca 660-945 m, Pursell 3784 (MO). Rutland Co.: Appalachian Trail, Pico peak, W of Killington, Holcombe 396 (DUKE); West Rutland, 19 Jun 1910, Kirk s.n. (FH). Windham Co.: Newfane, Flowers 4374 (COLO); Newfane, Baker Brook, 20 Apr 1927, Grout s.n. (CANM, CAS, FH, MICH, MO, NY, UC, US) [N. Am. Musci Perf. No. 90]; Newfane, Grout Pond, 240 m, 12 Aug 1935, Haring s.n. (NY); Black Brook, Newfane, Stratton Mt, 610 m, 25 July 1936, Haring s.n. (NY); Stratton, Grout 179 (F); Black Brook, Stratton Mt, Schnooberger 3424 (MICH) and Wareham 1608 (MO). Windsor Co.: Ouechee Gorge, W of White River, Holcombe 375 (DUKE); Mt Ascutney, sine dato, Thompson s.n. (FH); Rochester, Dutton 689 (MO). VIRGINIA. Floyd Co.: Twin Falls, 760 m, Patterson R-497 (NY). Giles Co.: Cascades, Blomquist 3452 (DUKE); Cascades, Mountain Lake, Blomquist 3452 (FH); Little Stony Creek, 24 Jun 1978, Steere s.n. (NY); along Little Stony Creek to Cascades Falls, Redfearn 31798 (MO). Lee Co.: Cumerland Mt, Rose Hill, ca 820 m, Patterson SW-5 (NY). Madison Co.: Blue Ridge Mountains, Whiteoak Canyon, below Third Falls, ca 640 m, Hermann 14841 (DUKE, US); Shenandoah National Park, Hogcamp Branch, Dark Hollow Trail, 915 m, Hermann 14382 (CANM, MICH, NY, US). Scott Co.: Norton, Patterson 2544 (NY). Shenandoah Co.: Massenutten Mt, Three Top Mt, Patterson 2142 (NY); Massanutten Mt, Passage Creek, Elizabeth Furnace, SW of Waterlick, Hermann 18401 (US). Smyth Co: Dickey Creek, 820 m, 17 Jun 1892, Small s.n. (GJO, DUKE, NY, US); Dickey Creek, Sugar Grove, Patterson 2456 (NY). WASHINGTON. Chelan Co.: Cascade Mountains, upper valley of the Nisqually, 18 March 1898, Allen 27 (CANM, COLO, DUKE, F, FH, M, MICH, MO, NY, TENN, UC, US) [Exs nr 30]; Upper Valley of the Nisqually, 18 March 1898, Allen 30 (WTU); Icicle Creek Canyon, W of Leavenworth, ca 365 m, 23 May 1964, Ireland 8739 (CANM); Washington Pass on North Cascade Hwy, trail to Blue Lake, 23 Aug 1976, Schofield 63362 (ALTA, CANM, DUKE); Chelan-Kittitas Counties boundary, Blewett Pass, April 1932, Bailey s.n. (WTU); Wenatchee National Forest, 19.06.1956, McFarlin A1513 (FLAS). Clallam Co.: Olympic National Park, Bogachiel River, Harthill 3509 (COLO); Appleton Pass, Ireland 6789 (CANM); Lake Crescent, North Olympics, Schallert 738 (DUKE) & 701 (MICH); Port Angeles, Elwha River, Harthill 7A (DUKE, FH, H, NY, TENN); trail from Olympic Hot Springs to Boulder Lake, 1220 m, Lawton 4179 (WTU); Olympic Hot Springs, Svihla 821 (WTU) and Smith 2032 (MICH, MO); Soleduck River road to Sole Duck Hot Springs, Welch 20621 (NY); Hobo Creek, Schofield & Spence 77687 (CANM, DUKE); Deer Lake, Mt Bogachiel, Eyerdam 3650 (WTU); La Push, Schallert 1042 (MICH). Cowlitz Co.: Cedar Creek, Eyerdam 262 (NY); Kelso, Rakestraw 16 (WTU); Coweman River NW from Kelso, 5 Jul 1911, Frye s.n. (WTU). Franklin Co.: Connell, 9 Apr 1903, Bailey s.n. (WTU). Grays Harbor Co.: Quinault Ranger District, Gatton Creek Campfround on Lake Quinault, 180 m, Buck 30297 (NY); Montesano, 22 Mar 1917, Grant s.n. (DUKE, FH, MO, US). Jefferson Co.: Lake Quinault, 60 m, Griffin C316 (FLAS); Lake Constance, Ireland 6450 & 6627 (CANM); Hoh River, W of Ranger Station, Lawton 2491 (W54 181) (WTU); Elwha River, 1220 m, Frye 560 (WTU) and 1370 m, Frye 470 (WTU). Lewis Co.: Mt Rainier, Stevens Canyon Road, Box Canyon, Lawton 4870 (WTU). King Co.: W of Snoqualmie Pass, Denny Creek trail, Lawton 5627 (KRAM, WTU) and 760 m, Ireland & Lawton 9431 (CANM); Stevens Pass, ca 1065 m, Ireland 8112 (CANM) and Schofield 12391 (CANM); North Bend, Ireland 5836 (CANM); Palmer, Eagle Gorge, 10 Oct 1921, Frye s.n. (WTU); Snoqualmie Falls, Frye 364 (WTU). Kittitas Co.: Wenatchee River near Swift Water Camp, Lawton et al. WER24 (TENN); Lake Kachess, Svihla 1062 (WTU). Klickitat Co.: Klickitat River, Klickitat, NE of Lyle, Lawton 5102 (ALTA, COLO, H, KRAM, UC, WTU) and Ireland & Lawton 8355 (CANM, DUKE, H). Mason Co.: Lake Cushman, Staircase Creek, Svihla 6417 (WTU); Shelton, Wynoochee Big Canyon, Tree Farm Camp, Becking 52080621 & 52080621b (WTU). Pierce Co.: Summit Lake, 1000 m, Norris 83658 (H, OSC, UC); Paradise Valley on Alta Vista trail, Schofield & Boas 22276 (CANM, DUKE); Mt Rainier, trail to Berkeley Park, ca 1950 m, Ireland & Lawton 8303 (CANM); Mt Rainier, Paradise Park, Bailey 132 (NY); Paradise Valley, 1525 m, Frye 274 (WTU) and 1830 m, Frye 1681 (WTU); Spray Park, S of Mowitch Lake, Hermann 22909 (E, MO); Cayuse Pass near Dewey Creek, Lawton 2430A (H, US, WTU) & W54110 (WTU); Van Trump Park, Becking 5308P12411 & 5308P12413 (WTU); Stevens Canyon Road, Narada Falls, Young 267 (WTU); Mt Rainier, 1980 m, Piper 247 (WTU); Mt Rainier, Stephens Canyon Road, Reflection Lakes, ca 1525 m, Svihla 4921 (WTU); Carbon River above Fairfax, Brinker 4307 (MO); Glacier Basin, Rainier National Park, Grant 402 & 405 (NY). Skagit Co.: Hamilton, South Fork of Nooksack River, Ireland 5914 (ALTA, CANM, MICH, NY, US); Hamilton, Cumberland Creek, Foster & 266 (WTU). Skamania Co.: Wind River at Stabler, Weber 2809 (COLO); Wind River, N of Carson on road to Lookout Mt, Ireland & Lawton 8481 (CANM); Trout Creek, Weber 2688 (COLO). Snohomish Co.: Black Creek between Silverton and Verlot, Ireland 5705 (ALTA, CANM, MICH); Stilliquamish River, between Verlot and Silverton, Lawton 3755 (WTU); Stilliquamish River, E of Wisconsin Creek at Slide Camp, Lawton 5669 (UC, WTU); Mt Pilchuck, 320 m, 3 Dec 1947, Larrison s.n. (MICH); Troublesome Creek campground, 610 m, 23 Oct 1997, Taylor s.n. (UC); Silverton, Ireland 5668 (CANM, NY, US); Stilliquamish River, Gold Basin Campground, Lawton 4748 (WTU); Mt Pilchuck road, Rotary Creek, ca 760 m, Lawton 4507 (WTU); Granite Falls, 16 Sep 1923, Frye s.n. (CANM, WTU) and 3 Dec 1925, Roberts s.n. (FH, MO, WVA); Sulphur Creek Campground near Glacier Peak, Largent 245 (CANM); Thurston Co.: Deschutes River Park, along Deschutes River, W of Rainier, Ireland 5734 (CANM); Olympia, Tumwater Falls, 10 Feb 1912, Foster s.n. (MO). Wahkiakum Co.: Cathlamet, Foster 1686 (WTU). Whatcom Co.: Goodell Creek Campground, North Cascade Mountains, Horton 8037 (ALTA); Schreibers Meadow, Mt Baker area near Concrete, Schofield 71384 (ALTA, CANM, DUKE); Glacier, road to Mt Baker Lodge, Ireland 7582 (COLO, CANM); Bellingham, near Nooksack Falls, Bailey 267 (WTU); between Mt Shuksan and Mt Baker, Schofield 16089 (CANM, DUKE); Glacier Creek, Glacier Point, Hermann 22806 (MICH) & 22807 (BM, E, MICH, NY); Mt Baker, Excelsior Camp, Svihla 1099 (WTU). Yakima Co.: Mt Adams, Bird Creek Meadow, ca. 2010 m, Lawton 5154 (UC, WTU). WEST VIR-GINIA. Marion Co.: Glady Run, Cross Roads, 1 Aug 1937, Ross s.n. (US). Mercer Co.: Flat-top Mt, Aldrson, Gray 1646 (NY, WTU). Mineral Co.: Alleghany Front, 410 m, 17 Nov 1934, Roberts s.n. (MO). Pocahontas Co.: Cold River, Cass, 18 Jan 1928, Gray s.n. (DUKE); Cold Run, Cass Quad., Gray M1023 (WVA); Hill Creek Falls, 17 Jun 1966, Fisher s.n. (MICH). Tucker Co: Blackwater River, 1 Jun 1957, Boardman s.n. (DUKE, MO); in Blackwater Fork, Davis, Gray 4038 (WVA) and Ammons 828 (WVA); Hunters Branch, 22 Aug 1934, Hitche s.n. (DUKE); Blackwater Falls, Cheat River, 5 Jul 1878, Smith s.n. (US). WISCONSIN. Chippewa Co.: Chippewa Falls, 5 Aug 1955, Robinson s.n. (DUKE) and 23 July1955, Robinson et al. s.n. (US). Jackson Co.: Hatfield, 25 Oct 1907, Holzinger *s.n.* (NY).

2. *Codriophorus aduncoides* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra (Figs 32–34)

Codriophorus aduncoides (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. \equiv Racomitrium aduncoides Bednarek-Ochyra, Fragm. Florist. Geobot. 44: 278, f. 1–3. 1999. — TYPE CI-TATION: U. S. A. Tennessee, Sevier Co.: Great Smoky Mountains National Park, Alum Cave Creek, near Arch Rock, Mt. LeConte, 25 Jul 1959, Schofield 10585 [H. A. Crum & L. E. Anderson, Mosses of North America No. 870] [Holotype: "Mosses of North America Howard A. Crum • Lewis E. Anderson University of Michigan •

Duke University 870. Racomitrium aciculare (Hedw.) Brid. c.fr. Common on boulders in creek. USA. Tennessee. Sevier County: Alum Cave Creek, near Arch Rock, Mt. Le Conte, Great Smoky Mountains National Park. Wilfred B. Schofield 10585 July 25, 1959" – KRAM!; isotypes: ALTA!, BR!, CANM!, COLO!, FLAS!, MO! POZG!, TENN!, UC!].

Plants medium-sized to large and robust, rather stiff and rigid, dull, light to dark olive-green to golden-brown, occasionally blackish-brown, in loose tufts or mats. Stems creeping or more frequently ascending, (1-)3-7 or sometimes up to 17 cm long, irregularly forked, brown to goldenbrown, without short tuft-like horizontal branchlets, in transverse section rounded or oval, without central strand, comprising 3-4 layers of small, sclerenchymatous epidermal cells with strongly incrassate walls and very small lumina surrounding the 5-6-layered medulla composed of large, hyaline to yellowish-hyaline cells with moderately to strongly thickened walls; rhizoids infrequent, mostly scattered in clusters at stem bases, long, branched, brown, smooth; axillary hairs numerous at stem or branch tips, filiform, hyaline throughout, consisting of 18-21 relatively short, barrel-shaped cells. Stem and branch leaves similar in size and shape, crowded, evenly set, appressed, imbricate, erect to secund on drying, erect-spreading on wetting, ovate-elliptical, lingulate to oblong-lanceolate, (1.9-)2.3-3.0(-3.2) mm long, 0.8-1.1 mm wide, narrowly subacute to broadly rounded at the apex, obtusely keeled below to somewhat concave or nearly flat above, without hair-point; margins unistratose throughout, usually broadly recurved on one side and flat to narrowly recurved on the other in the lower ³/₄, the upper part plane or frequently incurved at the apex giving it a subcucullate appearance, entire below, distantly bluntly or sharply eroso-dentate to almost entire at the apex; costa single but frequently spurred and forked at the tip, concolorous or usually sharply demarcated from the laminal cells, bright to dark yellow, yellow-brown to dark or reddish-brown, pronounced but very variable on the same plant, usually vanishing in mid-leaf but sometimes extending ³/₄ of the way up the leaf, (80-)90-180 (-220) µm wide near the base, usually gradually tapering upwards, lying in a shallow furrow below, in cross-section flattened and not very prominent dorsally, plane or canaliculate ventrally, bistratose in the upper and median parts, tristratose below, with 2-4, 2-6 and 8-10 large ventral cells in the upper, median and lower parts, respectively, with relatively large dorsal cells in the upper and median parts and small, stereid cells in the basal parts; laminal cells unistratose throughout, densely covered on both surfaces with large, flat papillae extending over the cell walls and leaving only a small pit over the centre of the cell lumen, with moderately to strongly sinuose or nodulose, firm to thick walls; upper cells irregularly rounded-quadrate, rhombic to short-rectangular, 10-15(-20) µm long, 10-14 µm wide, becoming short-rectangular in mid-leaf, 10-25(-30) µm long, 10-14 µm wide, and long rectangular, up to 65 µm long, 8-10 µm wide below; cells at the insertion rectangular in 2-3 rows, 30-80 µm long, 10-15 µm wide, with strongly incrassate and porose walls, intensively yellow- to golden-brown, forming a distinctive



FIGURE 32. Codriophorus aduncoides. — 1. Habit, wet. 2. Portion of stem, wet. 3–5. Axillary hairs. 6–15. Leaves. 16–26. Cross-sections of costae and leaves, sequentially from base to apex. — [1-2, 12, 18-19 from Schofield 10585, KRAM (holotype); 11 from Schofield 10061, KRAM; 3–5, 8–9 Voth V467a, COLO; 6–7 from Rolston 81086, COLO; 10, 16, 20, 23 from Ketchledge 101, ALTA; 13 from Judd s.n., 26 Oct 1975, FLAS; 14 from Griffin III s.n., 3 May 1972, FLAS; 15, 17, 21–22, 24–26 from Whitten 14, FLAS]. — Scale bars: a – 1 mm (6–15) and 100 µm (3–5); b – 100 µm (16–26); c – 1 cm (1) and 2 mm (2). (Reproduced from Fragmenta Floristica et Geobotanica, 44: 279, 1999, with permission).

strip sharply demarcated from the adjacent laminal cells; alar cells short-rectangular to subquadrate, larger than the other basal cells, 20-30 µm long, 20-30 µm wide, with incrassate, esinuose to moderately sinuose walls, usually forming distinct, yellow-green to brown, flat or swollen, pellucid, shortly decurrent auricles, or sometimes almost undifferentiated and not forming distinct auricles; basal marginal cells quadrate to short-rectangular, 9-11 µm wide, 10-16 µm long, thick-walled, sinuose, not pellucid, not particularly different from the adjacent laminal cells and not forming a distinct border. Dioicous. Perigonia bud-like, to 1.2 mm long; outer perigonial bracts similar to vegetative leaves, but smaller; inner perigonial bracts orange-brown, ovate, broadly and shortly acute, to 0.9 mm long, strongly concave, with a rather firm costa ending well below the apex; antheridia 12-15 per perigonium, club-shaped, pale brown; paraphyses very few, pale brownish, aout half the length of the antheridia. Outer perichaetial leaves lanceolate to oblong-lanceolate, gradually narrowly acuminate, 3.1-3.3 mm long, 1.0-1.1 mm wide, with narrowly obtuse or acute apex, usually distinctly eroso-dentate often well down the leaf margins, with upper laminal cells thick-walled and sinuose, generally similar to those in the vegetative leaves and lower cells, rectangular, rather thin-walled and weakly sinuose; inner perichaetial leaves oblongovate to lingulate, rounded-obtuse to broadly subacute at the apex, 2.0-2.2 mm long, 0.9-1.0 mm wide, entire, strongly concave, hyaline, composed of thin-walled cells. Setae single or geminate in the perichaetium, straight, 8-11 mm long, reddish when young, becoming reddishor blackish-brown with age, smooth, dextrorse when dry; vaginula reddish-brown, ca 1 mm long, with rectangular, sinuose-walled epidermal cells. Capsules erect, straight, obloid to shortly cylindrical, gradually narrowed towards the seta and orifice, without neck, 2.0-2.3 mm long, 0.9-1.0 mm wide, smooth, dull, brown, pachydermous; operculum erect, long rostrate, with a straight rostrum to 1.3 mm long; annulus separating, biseriate, composed of pellucid, yellow- to orange-brown, very thick-walled cells with an outer row of elongate, vesiculose cells and basal rows of short, isodiametric cells; exothecial cells isodiametric to elongate, oblong-elliptical, quadrate to rectangular, disposed in rather regular longitudinal rows, 20-60 µm long, 10-20 µm wide, with thick to strongly incrassate walls and distinct collenchymatous thickenings in the angles, becoming quadrate to oval below the mouth forming a distinct, 5-7-seriate orange-brown rim; stomata quite numerous, usually about 20, near the base of the urn in 3-4 rows, superficial, bicellular with rounded pori; peristome single composed of 16 teeth, 480-520 µm long, orange- to yellow-brown, split nearly to the base into 2 filiform, terete, clearly barred and nodose branches, densely papillose with tall, needle-like papillae; basal membrane short, to 50 µm, finely papillose; preperistome present, equaling the basal membrane. Spores globose, finely papillose, pale yellowish-brown, 14-17 µm in diameter. Calyptra conic-mitriform, somewhat roughened at the apex, naked, not plicate.

Etymology — The name of the species derives from the Latin aduncus = curved or hooked (on one side) and the Greek suffix *–ides* which designates affinity. It refers to the falcate-secund leaves and the tips of the stems and branches, giving the plants a characteristic facies.

Diagnostic characters and differentiation — Codriophorus aduncoides is diagnosed by the following set of characters: (1) plants medium to large and robust, rather stiff and rigid; (2) stem often ascending, irregularly sparingly to moderately branched; (3) leaves ovate-elliptical, ligulate to oblong-lanceolate, usually falcato-secund; (4) leaf apex epilose, broad, obtuse or subacute to broadly rounded, flat or tubular to subcucultate owing to inflexed margins; (5) costa broad, (80-)90-180(-220) µm wide, bistratose in the distal and median parts, tristratose, strongly flattened and weakly convex dorsally in the proximal part, spurred on both sides and forked at the apex, sometimes extending $\frac{3}{4}$ of the way up the leaf, but often terminating at mid-leaf; (6) leaf margins unistratose throughout, broadly recurved on one side and flat on the other, usually incurved at the apex, entire below, distantly bluntly or sharply eroso-dentate to subentire at the apex; (7) laminal cells unistratose throughout; (8) setae 8-11 mm long, reddish- to blackishbrown, dextrorsely twisted when dry; (9) capsules obloid to short-cylindrical, 2.0-2.3 mm long; (10) peristome teeth divided nearly to the base into 2 filiform, terete, densely papillose branches.

Codriophorus aduncoides is closely related to C. acicularis and the two species have similar leaf shape and areolation as well as similar ecological requirements. It is, however, well-defined and easy to distinguish by the structure of the costa which, although variable in length, even on the same shoot, is generally shorter and ceases well below the apex, extending at most three quarters of the way up the leaf. However, some minor deviations in length occur, and leaves with the costa vanishing in mid-leaf are not uncommon. If the costa does reach the upper half then it is rather weak and much narrower than in the basal part and is represented there by a single branch of the forked costa. Additionally, the costa is distinctly spurred on both sides in the distal portion and is mostly forked at the apex, although this distinctive character is sometimes only occasionally present, as for example in the specimens from Maine (Allen 22191, MO). In general, the costa is more pronounced, wider and shorter than in C. acicularis. In transverse section, the costa of C. aduncoides is less prominent dorsally and rather flattened in the proximal half. It is situated in a relatively shallow groove, resulting in the leaves possessing a less distinct, obtuse keel. In the distal portion, the leaves are slightly concave to nearly flat because of the lack of a costal groove and the weakness of the costa itself.

In contrast to *Codriophorus acicularis*, the leaves in *C. aduncoides* are often narrowly subacute at the apex and are frequently secund. In addition, the leaf margins are usually distinctly incurved in the latter, giving a tubular to subcucullate shape to the leaf apex. These macroscopic features, taken together, give a characteristic appearance to the species which, after some field training, can be sep-



FIGURE 33. *Codriophorus aduncoides.* — 1–3. Leaf apices. 4. Upper laminal cells at margin. 5. Mid-leaf cells. 6. Basal juxtacostal cells. 7–8. Alar cells. 9. Portion of stem cross-section. — [1, 5–6 from *Rolston 81086*, COLO; 2, 9 from *Voth V467a*, COLO; 3–4, 7–8 from *Schofield 10585*, KRAM (holotype)]. — Scale bar 100 µm. (Reproduced from *Fragmenta Floristica et Geobotanica*, 44: 280, 1999, with permission).



FIGURE 34. Codriophorus aduncoides. -1. Perigonium. 2. Perigonial bracts. 4. Perigonial bract and antheridia. 5. Outer perichaetial leaf. 6. Innermost perichaetial leaf. 7. Apical cells of the innermost perichaetial leaf. 8–9. Operculate capsules, wet. 10. Deoperculate capsule without peristome, wet. 11–12. Deoperculate capsules with peristomes, wet. 13. Young calyptra. 14–15. Lower exothecial cells and stomata. 16–17. Exothecial cells in mid-urn. 18. Portion of peristome, annulus and spores. - [1–4, 10–13 from *Schofield* 10585, KRAM (holotype); 5–7, 14, 16, 18 from *Voth V467a*, colo; 8–9 from *Judd s.n.*, 26 Oct 1975, FLAS; 15, 17 from *Griffin III s.n.*, 3 May 1972, FLAS]. - Scale bars: a – 1 mm (8–12); b – 1 mm (5–6, 13); c – 100 µm (7, 14–18); d – 1 mm (1–4). (Reproduced from *Fragmenta Floristica et Geobotanica*, 44: 282, 1999, with permission).

arated without difficulty, even with the naked eye, from *C. acicularis*. This is especially true when the two species grow in mixed stands as occasionally happens, for example from Long Lake Village in New York (*Hermann 14584*, NY) and Ramsay Falls in the Great Smoky Mountains, Tennessee (*Voth V462a*, COLO).

Codriophorus aduncoides is unlikely to be mistaken for the other two species of the type subsection of *Codriophorus*, namely *C. norrisii* and *C. mollis*. Apart from their entirely different geographical ranges, the former is immediately distinct in its partially bistratose laminal cells and the latter is made unmistakable by its elliptical to oblong-elliptical leaves which are broadly rounded, flat and almost entire at the apex.

Variability — Codriophorus aduncoides is a well-defined species that shows little interpopulational variation in its essential diagnostic characters, although like the other aquatic species of this group, it exhibits some phenotypic plasticity induced by the environmental conditions. In the collections examined specimens have differed in dimension, with the largest plants, from Mt Chocorua, New Hampshire (Lowe s.n., MAINE, TENN), reaching 17 cm in length. In contrast, the smallest known specimens have stems only about 1 cm long, for example the plant from Oxford County, Maine (Allen 22191, MO). However, the majority of specimens have medium-sized stems 3-7 cm long. The colour of the tufts depends on the insolation of the plants and whether they are submerged or not. It varies from dark olive-green to golden-brown and very rarely submerged plants are black (Hermann 15701, DUKE, FH, us). The plants are generally sparingly irregularly branched and only seldom are the shoots more regularly branched. In the researched collections some variability in the dimension and shape of leaves was apparent. Leaf length generally ranged from 2.3 to 3.0 mm, but in extreme cases it could be as little as 1.9 mm and extends to 3.2 mm. The apex is flat in some leaves but often it is tubular to subcucullate due to distinctly incurved leaf margins in the distal portion. It is mostly broadly rounded to narrowly subacute and the leaf margin towards the apex varies from bluntly or sharply eroso-dentate to almost entire.

As far as microscopic characters of Codriophorus aduncoides are concerned, the costa is subject to considerable variation. In most leaves it extends three quarters of the way up the leaf but sometimes it vanishes higher or more often earlier, reaching only to mid-leaf. It also varies markedly in robustness, its width usually ranging from 90 to 180 µm in the proximal part (though occasionally it is as wide as 220 µm or as narrow as 80 µm). However, the anatomical structure of the costa is quite stable. It is bistratose distally and medially and tristratose in the proximal portion, with occasional 4-stratose spots. Enlarged ventral epidermal cells vary in number from 7 to 10. Additionally, there is some variation in the shape of the alar cells which often form distinct, swollen, pellucid and shortly decurrent auricles, but on some leaves, even on the same plant, they are almost uniform and do not form these distinct decurrencies.

Codriophorus aduncoides is usually found in fruiting condition. The sporophytes exhibit remarkable uniformity and only minor variations in the length of the setae and capsule size are observed.

Reproduction — The majority of populations produces fully mature sporophytes, usually one or two per perichaetium, but seldom are the fruits found in great profusion.

Taxonomic and nomenclatural notes — Codriophorus aduncoides has a short and simple taxonomic history. Only recently was it segregated from the C. acicularis complex and described as a species in its own right, Racomitrium aduncoides (Bednarek-Ochyra 1999a). Subsequently it was transferred to the genus Codriophorus (Ochyra et al. 2003). The species was described from material collected by W. B. Schofield in Alum Cave Creek on Mt LeConte in the Great Smoky Mountains of Tennessee and distributed by H. Crum and L. E. Anderson in their exsiccati Mosses of North America No. 870 as Racomitrium aciculare. Ten specimens of the exsiccati from various herbaria have been examined and nine of them consist of pure samples of C. aduncoides. Only the specimen from COLO has a small admixture of C. acicularis and represents a typical mixed stand. Following its description, C. aduncoides was discovered in Maine (Allen 2002).

Chromosome number — Not available.

Habitat — *Codriophorus aduncoides* is a hydrophilous acidophilous moss which can tolerate periodic desiccation. It predominantly grows on acidic, primarily granite rocks, boulders and blocks in and close to streams, creeks and brooks that are periodically water-splashed, on damp or wet cliffs, sometimes on wet soil over rock outcrops. Quite often it grows on boulders entirely submerged in swiftly running water or on rocks in waterfalls as a typical rheophytic moss. It is usually found in shady places in various types of coniferous or mixed forest but sometimes it also occurs in open and more xeric sites on rock outcrops where it is seasonally submerged. The species usually forms pure stands and only occasionally grows mixed with C. acicularis. Its most frequent associates are Scapania and Marsupella spp., but these grow close by and are not intermixed with C. aduncoides.

Geographical distribution — *Codriophorus aduncoides* is an eastern North American endemic species which is restricted in distribution to the US Appalachian Mountains. It is widely distributed, though rather scattered, ranging from western Maine, New Hampshire, Vermont and New York in the north to Tennessee and North Carolina in the south (Fig. 35). It is widespread in most mountain ranges in the US Northern Appalachians including the Adirondack Mountains, Longfellow Mountains, White Mountains, Green Mountains, Taconic Mountains and New England Upland. It is very rare in the Central Appalachians, including the Cumberland Mountains of Kentucky and the Allegheny Mountains of Pennsylvania and West Virginia,



FIGURE 35. Global distribution of Codriophorus aduncoides.

and becoming frequent in the Blue Range Mountains of Virginia, Tennessee and North Carolina in the Southern Appalachians. Its altitudinal range extends from about 300 m to 2013 m on Clingman's Dome in the Great Smoky Mountains in North Carolina, the highest peak in the Appalachians (2020 m). Only once has the species been found at a lower altitude in the Palisades in New Jersey whose highest elevation is 167 m. This last is the specimen distributed by Austin (1870) as Racomitrium aciculare in his Musci Appalachiani as No. 147. Interestingly, in all sets of these exsiccati the material truly represents Codriophorus acicularis and only the specimen in NY has two different species attached to the herbarium sheet. The origin of this specimen is uncertain because Austin often distributed specimens from various localities under the same number (B. Allen, personal communication).

EXSICCATI

SPECIMENS EXAMINED

NORTH AMERICA. USA. CONNECTICUT. Litchfield Co.: Canaan, Great Mountain Forest, Sam Yankee Woodlot, E of Canaan Mountain Road, Allen 25970 (MO). KENTUCKY. Bell Co.: Cumberland Mts, Varilla Quad, Pine Mountain, Shillalah Creek, ca 450 m, Risk & Davison 7494 (DUKE). MAINE. Oxford Co.: Buckfield, Streaked Mountain, headwaters of Bicknell Brook, ca 412 m, Ledlie 1276 (MO); 4 mi SW of Buckfield, 305–516 m, 16 May 2000, Allen 22191 (MO). MASSACHUSETTS. Berkshire Co.: Mt Greylock, 9–10 Oct 1909, Burnham s.n. (CANM, MICH). NEW HAMPSHIRE. Carroll Co.: Crawford Notch, along Webster Cliff, 26 Oct 1975, Judd s.n. (FLAS); Mt Chocorua, Gray 4 (DUKE, TENN); Mt

AUSTIN – Musci Appalachiani No. 147 (as Racomitrium aciculare) (NY).
 CRUM & ANDERSON – Mosses of North America No. 870 (as Racomitrium aciculare) (ALTA, BM, CANM, COLO mixed with R. aciculare, FLAS, H, KRAM, MO, POZG, TENN, UC).

Chocorua, Brook Trail, 20 Oct 1920, Lowe s.n. (MAINE, TENN). Grafton Co.: Wilderness Trail, up Pemigewasset River, N of Kancamagus Hwy, vicinity of Franconia Notch, 457 m, Rolston 81086 (COLO); Town of Ellsworth, Hubbard Brook Upper trail, Cleavitt 503 (NY); same locality, Cushman Brook parking area, Cleavit 504 (FH); base Mt Monadnock, 12 Aug 1934, Thompson s.n. (FH) and 1915, Rathbun & Kite s.n. (US). Hillsborough Co.: Peterborough, 27 Oct 1935, Thompson s.n. (FH). Merrimack Co.: Mt Kearsarge, ca 5 miles SSW of Andover, 635 m, Allen 21154 (MO). New JERSEY. Bergen Co.: Palisades, Austin 147 (NY). NEW YORK. Delavare Co.: Montanville, Beals 1964 (DUKE). Hamilton Co.: Long Lake Village, along Kempshall Mt Trail, 580 m, Hermann 14684 (CANM, MICH, US); Long Lake Village, E of The Gables Cottages, 2 miles SW, 520 m, Hermann 14584 (NY); Lake Pleasant, Levy 1038 (DUKE); same locality, Mt Hamilton, Levy 1039 (DUKE); Blue Mountain Lake, along Routhe 10, 2 miles N, 610 m, Hermann 15701 (DUKE, FH, US). Rockland Co.: E slope of Dunderberg, ca 300 m, Smith & Clum 40133 (MICH, NY). St. Lawrence Co.: Adirondack Region, Cranberry Lake Area Indian Mt, Ketchledge 101 (ALTA); Sucker Brook Syracuse Univ. Forestry Camp Cranberry Lake, Allen 48 (MO). Ulster Co.: Lake Minnewaska vicinity, ca 335-400 m, Smith & Herrick 48921 (hb. J.-P.Frahm, KRAM). NORTH CAROLINA. Jackson Co.: Yellow Face Mountain, S of Blue Ridge Parkway, ca 1677 m, Pittillo & Pittillo 10713 (DUKE); Whiteside Mountain Highlands, Ammons NC84 (DUKE, WVA). Macon Co.: Nantahala Nat. Forest, Blue Valley Scenic Overlook, ca 1150 m, Allen 20155 (MO). McDowell Co.: ca 5 miles S of Mt Mitchell, gorge of Newberry Creek, ca 915 m, Zander 1415 (DUKE). Swain Co.: Great Smoky Mountain National Park, Newfound Gap, ca 1680 m, Whitten 14 (FLAS); same locality, Clingman's Dome, along trail from parking lot to Siler's Bald, 2013 m, Smith 1261 (TENN). Yancey Co.: W slope of Mt Mitchell, ca 1920 m, Anderson 11005 (DUKE). PENN-SYLVANIA. Luzerne Co.: Fairmount Township, Ricketts Glen State Park, along Glen Leigh, Ganoga Glen and Highland trails, ca 3 miles N of Red Rock, Allen 15639 (MO); same locality, ca 2.5 miles NNE of Red Rock, Pursell 9549 (MO). Somerset Co.: Clear Run, Laurel Ridge, 2 mi. W of Miller School, 6 Oct 1935, Boardman s.n. (DUKE, MO) and 17 May 1936, Boardman s.n. (MO); Blue Hole Creek, 27 Apr 1952, Boardman s.n. (DUKE). TENNESSEE. Greene Co.: along road to Cold Spring Knob, Sharp 4536 (F, TENN). Sevier Co.: Great Smoky Mountains, above Gatlinburg, ca 1220 m, Steere 10247 & 10318 (MICH); Greenbrier, Porter's River, top of Ramsey Falls, Voth V462a (COLO, MO); Alum Bluffs Trail, 915 m, 3 May 1972, Griffin s.n. (FLAS); near High Spring Bald, Schofield 10061 (DUKE, KRAM); near Siler's Bald, Schofield 8958 (CANM, CAS, DUKE, POZG); Charlie's Bunion, Schofield 9813 (DUKE); Alum Cave Creek, near Arch Rock, Mt LeConte, Schofield 10585 (ALTA, BM, CANM, COLO, BR, F, FLAS, H, KRAM, MO, O, POZG, TENN, UC - TYPE); Alum Cave trail to Mt LeConte, 1525 m, Clebsch SM22 (TENN); Mt LeConte, along Boulevard Trail, 16 May 1964, Sharp & Worley s.n. (TENN); Mt LeConte trail, Arch Rock, below Alum Cave, ca 1220 m, Steere 10374 (MICH); S side of Mt LeConte, 1830 m, Steere 10398 (MICH); Mt LeConte, Roaring Fork, 15 May 1934. Duncan s.n. (TENN): Mt LeConte, Roaring Fork, 1830 m, Sharp 34500 (TENN); Chimenys Parking Lot, near footbridge, 1100 m, Clebsch 14421 (TENN); near the Chimneys, 915 m, 12 July 1930, Sharp s.n. (WTU); 1/4 mi. below Newfound Gap, 1525 m, Batson 389 (DUKE); Walker Prong of Little Pigeon River, ca 2 km W of Newfound Gap, 1500 m, Crosby 13431(MO); Grassy Patch, ca 1340 m, 16 Nov 1932, Sharp s.n. (TENN); Great Smoky Mountain National Park, Vitez 26 (MO); Great Smoky Mts, Sep 1933, Blanchard s.n. (MICH). VERMONT. Bennington Co.: Manchester, 20 Aug 1920, coll. ? (DUKE). VIRGINIA. Grayson Co.: White Top Mt, ca 1375 m, Ireland 1356 (CANM, US). Lee Co.: without close locality data, on rock in stream, Patterson SW-5 (NY). Smyth Co.: White Top Mt, on rock in stream, Buch-Maple woods below summit, ca 1525 m, Patterson & Schuster 2785 (NY). WEST VIRGINIA. Webster Co.: Straight Creek Mts, Gauley River, 9 & 10 Jun 1934, Roberts s.n. (MO).

Codriophorus mollis (Cardot) Bednarek-Ochyra & Ochyra (Figs 36–39)

Codriophorus mollis (Cardot) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. ≡ *Racomitrium molle* Cardot, Bull. Herb. Boissier Sér. 2, 8: 333. 1908. — TYPE CITATION: Japon: Iwagisan (n. 325 in parte);

Hakkoda, pierres arrosées, à 1300 m. (n. 2951 in parte). [Lectotype (*selected here*): "Herb. J. Cardot. Rhacomitrium molle Card. <u>sp.</u> <u>nova.</u> Japon: Hakkoda, 1300 m, sur pierres arrosées. Leg. Faurie, 1904. n° 2951" – PC-Cardot!; isolectotypes: H-Brotherus!, NY!, s-Roth/Möller!].

Plants medium-sized or moderately large, occasionally small, rather robust or sometimes slender, in dull, fairly soft or, less often, somewhat rigid, dense or loosely coherent tufts or patches, olivaceous, brown, yellow-, golden-, rusty-, olive-, orange- to blackish-brown, sometimes dirty olive-yellow, golden, bright orange to blackishgreen above, brown to blackish-brown below, sometimes brown, blackish-brown to jet throughout. Stems curvedascending to erect, less often procumbent, (1-)2-7(-10)cm tall, often denuded below owing to erosion of the leaf laminae but preservation of the stout costae, giving the stem a bristly appearance, sparsely irregularly dichotomously or fasciculately branched, without tuft-like, horizontal branchlets, often almost unbranched to thread-like, sparsely or densely radiculose at the base or in the lower part with reddish-brown, glossy, smooth, branching rhizoids, in transverse section circular to elliptical, lacking central strand, with a 2-3-layered cortex of small, sclerenchymatous cells with small lumina and brown, incrassate walls and 6-9 layers of large, hyaline medullary cells with moderately thickened walls; axillary hairs filiform, 11-18celled, with 1-2 short, brownish-pigmented basal cells and hyaline, short and barrel-shaped to somewhat elongate upper cells. Leaves usually crowded, closely appressed and imbricate, erect or secund to moderately homomallous, or erect-spreading to patent when dry, erect-spreading to wide-spreading when moist, concave to cochleariform, (1.5-)2.0-2.5(-2.8) mm long, 0.9-1.2 mm wide, broadly ovate, lingulate or elliptical to oblong or oblong-elliptical to oblong-ovate, very broadly rounded-obtuse and usually cucultate or, rarely, subacute at the apex, not or slightly decurrent; margins unistratose, entire throughout to indistinctly, remotely and bluntly eroso-dentate or sinuate at the apex, usually narrowly recurved on one side in the proximal half, rarely on both sides, plane above or plane throughout on both sides; costa single, spurred and commonly forked at the apex, pronounced, olivaceous to yellow-brown, sharply demarcated from the laminal cells, variable in length, usually ceasing at $\frac{1}{2}-\frac{3}{4}$ of the way up the leaf but one slender branch often extending to 5/6 of the leaf length, sometimes vanishing below mid-leaf, 75–100 µm wide at the base, gradually tapering upwards, situated at the bottom of a shallow or, occasionally deeper, wide-angled furrow in the proximal part, in cross-section rectangular and flattened, distinctly convex dorsally, (2-)3(-4)-stratose, with a single ventral layer of 6-8 enlarged cells and a distinct, (1-)2(-3)-layered dorsal stereid band in the proximal portion, bistratose and anatomically undifferentiated above, with 3-6 ventral cells in mid-leaf and 2-4 ventral cells in the upper part; laminal cells unistratose thoughout, transparent, with moderately thickened, sinuose walls, isodiametric, irregularly rounded-quadrate to angular, rhombic or shortly rectangular, $7-10(-15) \mu m$

long, 5-10(-15) µm wide, progressively becoming elongate downwards, 15-25(-30) µm long, 5-10 µm wide in mid-leaf, and 25-50(-75) µm long and 5-10 µm wide in the base; cells at the insertion rectangular, with markedly thickened, nodulose and porose longitudinal walls, (25-)30-55(-70) µm long, 8-13 µm wide, forming a 2-3seriate, olive- or yellow-brown strip across the leaf insertion; alar cells mostly larger than the other basal cells, 30-50 µm long, (12-)15-25 µm wide, moderately thickwalled, forming, hyaline- or yellowish-brownish, somewhat swollen and shortly decurrent auricles, sometimes undifferentiated; supra-alar cells not differentiated. Dioicous. Perigonia gemmiform, ca 2 mm long; outer perigonial bracts broadly ovate to lingulate, 1.8-2.0 mm long, 0.9-1.0 mm wide, similar to the vegetative leaves, with a slender to fairly robust costa, extending 5% of the way up the bract; inner perigonial bracts broadly ovate, 1.0-1.1 mm long, ca 1 mm wide, strongly concave, broadly acute, with a slender costa, the innermost one with about 16 club-shaped, short-stalked, pale brownish antheridia, intermixed with a few filiform, hyaline paraphyses scarcely reaching half the length of the antheridia. Outer perichaetial leaves broadly ovate to oblong-ovate, broadly acute, 2.0-2.8 mm long, 1.0-1.2 mm wide, with a very slender and scarcely visible costa ending in mid-leaf or below; innermost perichaetial leaves oblong-ovate, shortacuminate, narrowly obtuse at the apex, 1.9–2.5 mm long, 0.5-1.0 mm wide, convolute, sheathing the seta, with a very slender costa vanishing in mid-leaf, hyaline throughout or with several thick-walled cells at the extreme apex or chlorophyllous throughout, with an areolation similar to that in the vegetative leaves. Setae single or very rarely geminate, straight, erect, fairly stout, 4-9 mm long, dextrorse, smooth, lustrous, dark brown becoming black with age; vaginula dark brown, about 1 mm long, with elongate, strongly sinuose and thick-walled, epidermal cells. Capsules exserted, erect, straight, symmetric, obloid to shortly cylindrical, 1.2-2.0 mm long, 0.7-0.8 mm wide, light to dark brown, smooth, lustrous, distinctly narrowed at the mouth; operculum conical-rostrate, with a straight rostrum, 1.0-1.3 mm long; annulus deciduous, reddishbrown, about 100 µm tall, 2-3-seriate, composed of cells with strongly thickened walls, large and vesiculose in the outer row; exothecial cells variable, rounded-quadrate to shortly oblong, 12-35 µm long, 12-20 µm wide, with moderately thickened walls, scarcely differentiated at the orifice; stomata at the base of the urn, about 20 disposed in 3-4 rows, superficial, bicellular, rounded, $32-35 \mu m$ wide, with rounded pori; peristome teeth 16, erect whether dry or moist, 400-425 µm long, reddishbrown, densely spiculate-papillose throughout, lanceolate, arising from a fairly tall basal membrane, to 82 µm high, divided nearly to the base into 2, or often imperfectly into 3 terete, rather unequal prongs, often with a long longitudinal slit only; preperistome hyaline, as tall as the basal membrane. Spores globose, lightish brown, finely papillose, (13-)17-20 µm in diameter. Calyptra conical, mitrate-cucullate or mitrate, with 4-5 lobes at the base, dark brown, verrucose at the apex.

Etymology — The name of the species derives from the Latin mollis = soft or pliable, in reference to its leaves which are fairly soft, especially when wet.

Diagnostic characters and differentiation — Despite its ostensible superficial similarity to Codriophorus acicularis, C. mollis is a distinct and unmistakable species that is readily distinguished by the following combination of characters: (1) plants moderately sized to fairly large, fairly pliant, especially on wetting, forming dense or loose tufts or patches, curved-ascending to erect, sparingly irregularly branched to almost unbranched, always without short tuft-like horizontal branchlets; (2) leaves closely appressed to imbricate or erecto-patent to spreading, often secund to homomallous on drying, concave to cochleariform, broadly ovate, lingulate or elliptical to oblong, oblong-elliptical or oblong-ovate; (3) leaf apex very broadly rounded-obtuse, usually cucullate to, seldom, subacute, entire to bluntly distantly eroso-dentate or sinuate; (4) margins unistratose all around, entire to variously indistinctly remotely dentate or sinuate at the apex, narrowly recurved on one or sometimes both sides in the lower half, flat in the distal half or plane throughout; (5) costa spurred and forked at the apex, extending $\frac{1}{2}-\frac{3}{4}$ of the leaf length, often vanishing with one slender branch 5% of the way up the leaf, lying at the bottom of a shallow, wide-angled groove and strongly flattened in the proximal portion, (2-)3(-4)-layered below with 6-8 enlarged ventral cells, bistratose and anatomically not differentiated in the distal portion; (6) laminal cells unistratose across the leaf, pellucid, isodiametric to shortly rectangular in the upper part, becoming elongate below; (7) alar cells most often enlarged, forming hyaline- or yellowish-brownish, somewhat convex short decurrencies; (8) supra-alar cells undifferentiated; (9) innermost perichaetial leaves oblongovate, shortly acuminate, narrowly obtuse at the apex, hyaline throughout or with a small group of chlorophyllous cells at the apex to entirely chlorophyllous throughout; (10) setae rather stout, 4-9 mm long, straight, twisted to the right on drying; (11) capsules ovoid to obloid, 1.2-2.0 mm long; (12) peristome teeth short, 400-425 µm, with a fairly tall basal membrane, divided nearly to the base into 2-3 terete branches, densely spiculate-papillose throughout; (13) spores spherical, finely papillose, 17-20 µm in diameter.

Codriophorus mollis is closely related to *C. acicularis* and actually all collections of this species have been sonamed. It differs in the fairly soft texture of the plants which are often almost unbranched and thread-like with a characteristic 'calliergonoid' appearance owing to the imbricate foliage of broadly elliptical, lingulate or ovate to oblong or oblong-ovate leaves with very broadly rounded-obtuse, entire or faintly eroso-dentate apices. The most characteristic feature of outstanding diagnostic importance for recognition of *C. mollis* is its costa. It is rather slender, commonly spurred and regularly forked at the apex, with one branch much longer and more slender, extending higher up the leaf than the other. The costa usually reaches half or three quarters of the way up the leaf,



FIGURE 36. *Codriophorus mollis.* — 1. Plant with mature sporophyte. 2. Portion of branch, dry. 3. Stem section. 4–7. Axillary hairs. 8–10. Leaf apices. 11. Upper laminal cells at margin. 12. Mid-leaf cells. 13. Basal juxtacostal cells. 14. Alar cells. — [1 from *Deguchi s.n.*, HIRO-12153; 2, 9 from *Grubb & Guymer 226*, BM; 3 from *Deguchi 12153*, KRAM; 4–6 from *Schofield 57874*, KRAM; 7–8, 11–14 from *Faurie 2951 pp.*, s, isolectotype of *Racomitrium molle*; 10 from *Norris & Smith 46334*, UC]. — Scale bars: a – 1 mm (2); b – 1 cm (1); c – 100 µm (3, 8–14) and 200 µm (4–7).

although frequently the longer branch may extend for up to five sixths of the leaf length. In the closely related *C. acicularis* the costa is usually much stouter, subpercurrent, only rarely spurred and although it is quite often forked at the tip, the branches are short, fairly stout, equal and form a V-shape. The leaf apex in *C. acicularis* is very variable, ranging from broadly rounded-obtuse and subentire to acute and distinctly bluntly or sharply dentate but the costa is rather stable and should help in the safe discrimination of the two species. Naturally, in both cases, several leaves should be examined in order to assess correctly the form taken by the costa.

The costa of *Codriophorus mollis* is quite similar to that in *C. aduncoides*, except for being much narrower and more slender, $75-100 \mu m$ wide near the base in the former versus ($80-90-180(-220) \mu m$ wide in the latter. Moreover, the leaf apex in *C. aduncoides* is often subacute and tubular owing to inflexed margins and remotely bluntly or sharply dentate to eroso-dentate. As well, the exothecial cells in *C. aduncoides* have thick to strongly incrassate walls, the peristome teeth are longer, $480-520 \mu m$, and the spores smaller, $14-17 \mu m$ in diameter.

Another western North American endemic species of the type section of *Codriophorus*, *C. norrisii* is distinct at first glance in having distinctly limbate leaves with 2(-4)-stratose and (1-)2-10(-13)-seriate marginal thickenings, generally acute to long acuminate leaves and percurrent and entire costae.

Codriophorus mollis has occasionally been mistaken by Chinese bryologists (Gao 1977; Gao & Chang 1983) for some phenotypes of *Niphotrichum japonicum* that are characterised by having broadly ovate to broadly elliptical leaves, cochleariform and muticous and broadly roundedobtuse at the apex. These plants have been discussed in detail by Bednarek-Ochyra (2004*a*) who showed that they correctly represent *N. japonicum*. They have leaves sharply keeled in the distal part, with a costa which vanishes just below the apex or, on occasion, may be somewhat shorter. Additionally, the laminal cells are papillose throughout with tall conical papillae situated over the lumina, but the papillae of the basal cells are larger and taller than those on the median and upper parts of the lamina. The alar cells form a conspicuous inflated group of hyaline cells.

The habit of *Codriophorus mollis* actually resembles that of *Hydrogrimmia mollis* (Bruch & Schimp.) Loeske, a peculiar hydrophytic member of the Grimmiaceae with the fairly flaccid texture of plants growing in montane streams, as suggested by Cardot (1908*a*) in the original diagnosis. Both species share imbricate and strongly concave leaves with broadly rounded-obtuse and cucullate apices, but they are immediately distinct in leaf areolation. *H. mollis* has irregularly hexagonal to rounded-quadrate, smooth laminal cells with thin and straight, never sinuose walls.

Variability — *Codriophorus mollis* is a species which varies little in its basic diagnostic characters, i.e. in the shape of the leaf apex and the form of the costa, but it shows some phenotypic variation in the plants condi-

tioned environmentally which is typical of all aquatic mosses and depends, among other things, on the degree of submergence, wetness of the habitat and exposure to light. The plants vary rather widely in size although on average they are 2.5-5.5 mm tall. The smallest plants have been found in Alaska (Schofield & Talbot 108263, MO) and on Kamchatka (Czernyadjeva 21 & 22, KRAM, LE) and barely reaching 1. 0 and 1.0-1.5 cm respectively. In contrast, the largest plants have been discovered in British Columbia (Schofield & Schofield 73265, DUKE) and California (Norris 23340, UC), attaining, respectively, 10.0 and 9.5 cm. C. mollis consists usually of plants moderate in size, although sometimes they are exceptionally large and fairly coarse (e.g., Schofield 31175, DUKE) or slender and thread-like (e.g., Schofield & Spence 83694, ALTA, CANM, DUKE; Schofield 87195, CANM, DUKE) in British Columbia. The colour of the plants varies markedly and centres around different combinations and tints of olivaceous, yellow, brown and orange. Worthy of special attention are the entirely black (Vitt 12386, ALTA, BR) and jet (Schofield 41846, DUKE) plants growing submerged on stones in streams in British Columbia and the attractive rusty-brown plants from Vancouver Island (Boas & Halbert 8425, CANM, DUKE).

Leaf length in Codriophorus mollis generally varies from 2.0 to 2.5 mm, but in extreme cases the leaves are as little as 1.5 mm or extend to 2.8 mm. The leaf shape is subject to considerable variation. The Japanese lectotype with its short and broadly ovate leaves is quite unrepresentative of the bulk of specimens and has to be considered as representing the small-leaved extreme form, which appears to be more frequent in Japan (Fig. 37.1-9) and on Kamchatka (Fig. 37.10–13) than elsewhere. The American (Fig. 37.14–22, 28–38) and Aleutian (Fig. 37.23–27) plants have mostly larger and elongate leaves that are lingulate, elliptical, oblong to oblong-ovate or oblong-elliptical. The shape of the leaf apex is a very stable character, showing little variation from broadly rounded-obtuse to broadly subacute. It is always entire to subentire, being only faintly remotely bluntly eroso-dentate to sinuate, and no leaves with sharper and longer teeth have been found. Likewise, costa length is somewhat variable but the general tendency is for the costa to rarely extend beyond three quarters of the way up the leaf with one branch occasionally reaching higher up, to 5% of the leaf length. The costa varies only little in its robustness and its width usually ranges from 75 to 100 µm. Moreover, its anatomical structure is fairly stable, being bistratose in the upper and median parts and tristratose in the basal part, sometimes with incidental 4-layered spots.

The sporophytes are remarkably uniform and only minor variability in the length of the setae and capsule size and shape are recorded. Interestingly, the innermost perichaetial leaves follow the general tendency observed in the type subsection and vary in their form from entirely hyaline to entirely chlorophyllous with the frequent occurrence of intermediates. A very interesting aberration is the excessive number of stomata, to 50 per capsule, found in a population from Moresby Island in the Queen Charlotte



FIGURE 37. *Codriophorus mollis.* — **1–38.** Spectrum of vegetative leaves showing geographical variation of plants from Asia including Japan (1–9) and Kamchatka (10–13), North America including California (14–20), Washington (21–22), Aleutian Islands (23–27) and British Columbia (28–34) and South America (Colombia) (35–38). — [1–9 from *Faurie 2951 pp.*, s, isolectotype of *Racomitrium molle*; 6–7 from *Deguchi s.n.*, 26 Jul 1973, HIRO; 8–9 from *Deguchi s.n.*, 27 Jun 1973, HIRO; 10–11 from *Czernyadjeva 22*, LE; 12–13 from *Czernyadjeva 21*, LE; 14–15 from *Norris 23340*, UC; 16–18 from *Norris 52324*, UC; 19–20 from *Norris & Smith 46334*, UC; 21–22 from *McFarlin A1513*, FLAS; 23–27 from *Schofield et al. 101537*, ALTA; 28–31 from *Schofield 25438*, CANM; 32–34 from *Schofield 24966*, CANM; 35–38 from *Grubb & Guymer 226*, BM]. — Scale bar: 1 mm.



FIGURE 38. Codriophorus mollis. — 1–8. Transverse sections of leaves showing variation in plants from Asia including Japan (4) and Kamchatka (2), North America including Aleutian Islands (8), British Columbia (6–7), Washington (1), and California (5) and South America (Colombia) (3). — [1 from *McFarlin A1513*, FLAS; 2 from *Czernyadjeva 22*, LE; 3 from *Grubb & Guymer 226*, BM; 4 from *Faurie 2951 pp.*, s, isolectotype of *Racomitrium molle*; 5 from *Norris 23340*, UC; 6 from *Schofield 25438*, CANM; 7 from *Schofield 24966*, CANM; 8 from *Schofield et al. 101537*, ALTA]. — Scale bar: 100 µm.



FIGURE 39. *Codriophorus mollis.* — 1. Portion of branch with mature capsule, wet. 2. Perigonium. 3–5. Perigonial bracts, sequentially from outermost to innermost perigonial bract and antheridia. 7–10. Perichaetial leaves, sequentially from outermost to innermost. 11–13. Apices of innermost perichaetial leaves. 14. Transverse section of seta. 15. Epidermal cells of vaginula. 16. Capsule with calyptra, dry. 17. Deoperculate capsule, dry. 18. Same, wet. 19. Same, with destroyed peristome, wet. 20. Operculum. 21. Calyptra. 22. Transverse section of calyptra. 23. Exothecial cells in mid-urn. 24. Exothecial cells at base of urn and stomata. 25. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1–6, 16, 18–19 from *Deguchi s.n.*, HIRO-12153; 7–9 from *Schofield 41233*, CANM; 10, 12, 14–15 from *Grubb & Guymer 226*, BM; 11 from *Schofield 25438*, CANM; 13 from *Persson s.n.*, 1957, KRAM; 17, 20–22 from *Horton 1402*, ALTA; 23–25 from *Vitt 12201*, ALTA]. — Scale bars: a – 1 mm (16–21); b – 100 µm (25); c – 100 µm (14–15, 23–24); d – 100 µm (11–13, 22), 1 mm (7–10) and 2 mm (1); e – 1 mm (2–6).

Islands archipelago (*Vitt 12201*, ALTA, COLO and *Horton 1402*, ALTA).

Reproduction — The species produces sporophytes almost throughout its range, but usually not in great profusion. Only plants from California are sterile.

Taxonomic and nomenclatural notes — Codriophorus mollis has a fairly simple and straightforward taxonomic history. It was described by Cardot (1908a) from two collections from Honshu, Japan. He pointed out the external similarity of the plants to Hydrogrimmia mollis and the affinity of the species to Racomitrium aciculare. It has long remained a poorly known and obscure species which has not been given much attention, most probably owing to its great rarity in Japan. Noguchi (1974) reduced R. molle to synonymy with R. aciculare, although he emphasised its broadly rounded leaf apices with indistinct marginal teeth. Additionally, the drawing of two leaves from the original material shows very short costae, vanishing in mid-leaf. This concept has subsequently been approved in Japanese (e.g., Iwatsuki 1992, 2001, 2005; Noguchi 1988) and Chinese (Redfearn et al. 1996; Cao 2000; Cao et al. 2003) bryology. However, careful assessment of this taxon during the course of the present revisionary study of the genus has led to its resurrection as a distinct and clearly defined species and, accordingly, it was transferred to Codriophorus by Bednarek-Ochyra & Ochyra (in Ochyra et al. 2003).

Plants from Colombia were examined by Edwin B. Bartram who originally intended to describe them as a new species dedicated to Howard A. Crum who dissuaded him from recognition of it (Crum 1966). Indeed, this material has never been published but the herbarium name 'Rhacomitrium Crumii' is visible on the label and is listed in the index to the E. B. Bartram collection of mosses at the Farlow Herbarium (Fralick 1967).

Chromosome number — Not available.

Habitat — Codriophorus mollis is a hydrophytic moss growing on periodically wet cliffs, dripping rocks, splashed or periodically flooded boulders, stones and outcrops in creek and stream beds and on the margins of streamlets, rivers and watercourses, on seepy sloping outcrops on roadsides and thin soil over moist rock ledges. It is found in open and insolated as well as in diffusely lit and shaded sites on both acidic and basic substrates. In North America the species is scattered throughout coastal coniferous forests dominated by *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn, with admixtures of *Picea sitchensis* (Bong.) Carr., *Pseudotsuga menziesii* (Mirb.) Franco and *Chamaecyparis nootkatensis* (D.Don) Spach., and on cliffs and outcrops within subalpine meadows and bogs.

Geographical distribution — *Codriophorus mollis* is a circum-north Pacific moss, ranging from East Asia across the Aleutian arc to north-western North America, and with a highly disjunct locality in the paramo of the Northern Andes of Colombia (Fig. 40). In the Far East of Asia the species is scattered and infrequent on Hokkaido and northern Honshu in Japan where it is recorded at elevations from 450 to 1300 m, with an isolated station on the southernmost tip of Kamchatka. The second and apparently main centre of occurrence of C. mollis is in British Columbia, from the Queen Charlotte Islands to Vancouver Island where it occurs from near sea level to alpine elevations at 1280 m on Vancouver Island, with some isolated stations in the Cascades in northern Washington and northern California, where it attains an elevation of 2000 m. The East Asian and north-western North American centres are connected by scattered localities in the Aleutian arc. This peculiar distribution pattern is exhibited by a number of bryophyte species, for example the mosses Takakia lepidozioides Hattori & H.Inoue, Bartramiopsis lecurii (James) Cardot & Thér., Oligotrichum parallelum (Mitt.) Kindb., O. aligerum Mitt., Pleuroziopsis ruthenica (Weinm.) Kindb., Bryhnia hultenii E.B.Bartram and Hypnum dieckii Renauld & Cardot and the liverworts Treubia nana Hattori & H.Inoue, Plagiochila rhizophora Hattori, P. semidecurrens Lehm. & Lindenb. and Scapania bolanderi Austin (Schofield 1965). In the tropics C. mollis was once recorded at a high-montane elevation of 4100 m in the paramo of the Northern Andes in the Province of Boyacá in Colombia which is a wellknown outpost for many northern bryophytes in the Neotropics (Herzog 1926; Schuster 1983).

SPECIMENS EXAMINED

ASIA. JAPAN. HOKKAIDO. Sôya Pref.: Mt Rishiri, Higashi-Rishiricho, Rishiri-gun, 1230 m, Deguchi s.n. (HIRO-12150), 1280 m, Deguchi sn (HIRO-12153, KRAM) and 1450 m, Deguchi s.n. (HIRO); Rishiri Island, 1450 m, 26 Jul 1973, Deguchi s.n. (ALTA, BR, H, KRAM). Tokachi Pref.: near Tomuraushi spa, Shintoku-cho, Kamikawa-gun, Deguchi sn (HIRO-11723 & 11742), 450 m, Deguchi s.n. (HIRO-11732, 11723 & 11733), 480 m, Deguchi s.n. (HIRO-11738, 11856) and Deguchi 11858 (KRAM). HONSHU. Aomori Pref.: Hakkoda, 1300 m, 1904, Faurie 2951 (H, NY, PC, s – lectotype of Racomitrium molle).

RUSSIA. FAR EAST. Kamchatka Prov.: Yuzhno-Kamchatskiy Zakaznik, Czernadjewa 21 & 22 (KRAM, LE).

NORTH AMERICA. CANADA. BRITISH COLUMBIA. Burnt Bridge Creek near junction with Bella Coola River, Norris 2409 (UC); near docks for village of Bella Coola, Norris 22040 (UC); Wakeman Sound, Kingcome Inlet, Schofield 41233 (CANM, DUKE); Mt McNeil, ca 823-914 m, Schofield 87195 (CANM, DUKE); Pitt Island, Holmes Lake, Schofield, Vitt & Horton 72640 (DUKE); Clavert Island, Long Lake at N base of Mt Buxton, Schofield & Williams 27857 (CANM, DUKE); Sathe Road, ca 26 km from gate, Harrison Mills Logging Road, Schofield 57874 (CANM, DUKE). QUEEN CHARLOTTE ISLANDS. Graham Island: Dawson Inlet., Schofield 15888 (CANM, DUKE); Trounce Inlet, Skidegate Channel, Schofield 14003 (CANM). Louise Island: lakes at head of Skedans Creek, N of Mt Carl, Schofield & Spence 83583 (ALTA, CANM, DUKE); Echo Inlet, 1957, Persson s.n. (KRAM). Moresby Island: NE arm Upper Victoria Lake, 43 m, Vitt 12386 (ALTA, BR) and Horton 1582 (ALTA); Moresby Mt, peaks just E of summit, ca 914 m, Schofield & Spence 83694 (ALTA, CANM, DUKE); Moresby Lake, 95 m, Vitt 12201 (ALTA, COLO) & 12216 (ALTA) and Horton 1402 (ALTA) and 95-610 m, Horton 1432 (ALTA) and Vitt 12250 (ALTA); Takakia Lake, about 15 km S of Moresby Logging Camp, Schofield 24966 (CANM, DUKE); Takakia Lake, about 15 km S of Moresby Logging Camp, 570 m, Schofield 24922 (CANM, DUKE); Anna Inlet, Schofield & Vaarama 24367 (CANM, DUKE); Mosquito Lake, Schofield 25438 (CANM); Mine Mt, above Tasu, Schofield & Schofield 73265 (DUKE); Kootenay Inlet, Schofield 31175 (DUKE); "Alpine lake"



FIGURE 40. Global distribution of Codriophorus mollis.

(unnamed lake at lat. 52°55' N and long. 132°03' W), *ca* 650 m, 28 July–2 Aug 1957, *Persson s.n.* (WTU). *Hecate Strait*: Bonilla Island, *Schofield* 41846 (DUKE). VANCOUVER ISLAND. Zeballos Inlet, near mouth of Hecate Channel, *Halbert* 7431 (CANM, DUKE); Coal Harbor, Quatsino Sound, *Boas & Halbert* 8425 (CANM, DUKE); Strathcona Park, Forbidden Plateau, trail to summit of Mt Becher, 1280 m, *Halbert* 4152 (DUKE, MO); Raza Island, Raza Passage, *Schofield* 64038 (ALTA).

USA. ALASKA Aleutians West Co.: Adak Island, Finger Bay, Schofield, Talbot, Talbot & Schofield 101537 (ALTA, DUKE, TENN); Attu Island, Holtz Bay, Moore Ridge, Bell Howard 712 (US); St Paul Islands, Pribilof Island, Polovina Hill, Schofield & Talbot 108263 (MO). Prince of Wales-Outer Ketchikan Co.: Prince of Wales Island, Sep 1893, Macoun s.n. (CANM). Wrangell-Petersburg Co.: Wrangell Island, about 13 km S of Wrangell, Worley 7608 (BR). CALIFORNIA. Siskiyou Co.: Big Duck Lake, ca 2000 m, Norris 23340 (UC); Granite Creek between Tickner Creek and Blue Garnite Lake, 305–520 m, Norris 52324 (UC); Paines Lake, ca 1830 m, Norris & Smith 46334 (UC). WASHINGTON. Chelan Co.: Washington Pass, North Cascades, stream on S facing slope just N of Hwy line from pass, Spence 3012 (OSC). Chelan/Kititas Co.: Wenatchee National Forest, McFarlin A1513 (FLAS, KRAM).

SOUTH AMERICA. COLOMBIA. **BOYACÁ.** Sierra Nevada de Cocuy, valle de las Playas, Boyacá, 4100 m, *Grubb & Guymer B.226* (BM) & *B.226A* (BM, CANM).

4. *Codriophorus norrisii* (Bednarek-Ochyra & Ochyra) Bednarek-Ochyra & Ochyra (Figs 41–43)

Codriophorus norrisii (Bednarek-Ochyra & Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. \equiv *Racomitrium norrisii* Bednarek-Ochyra & Ochyra Ann. Bot. Fenn. 37: 236, *f. 1–3.* 2000. — TYPE CITATION: U. S. A. California, El Dorado Co.: along South Fork of the American River at Carpenter Creek, 1 300 m, 7 April 1981, *Norris 58449* [Holotype: "El Dorado Co., California 38°46' N X 120°18' W <u>Racomitrium aciculare</u> (Hedw.) Brid. leaves with bistra-

tose streaks! On submerged, moist, diffusely lit boulder in stream in mixed conifer forest along South Fork of the American River at Carpenter Creek. Elev. 1300 m. Coll.: D. H. Norris 58449 7 April 1981" – UC; isotype: KRAM).

Plants small to medium-sized, rather slender, stiff and rigid, forming loose or rarely compact tufts, dull, light to dark olive-green above, blackish-brown below, occasionally dark green above and blackish below or blackish throughout. Stems ascending, (1.5-)2.0-3.0(-3.5) cm long, sparsely to repeatedly irregularly branched, densely foliated, but with leaves often heavily eroded at base, in cross-section circular, without central strand, consisting of 1-3 layers of small, sclerenchymatous cortical cells with moderately incrassate walls and small lumina surrounding a 5-6-layered medulla composed of large, hyaline to yellowish-hyaline cells with thin to slightly thickened walls; rhizoids sparse to abundant, mostly scattered in clusters in the lower parts of stems, smooth, long, branched, reddishbrown; axillary hairs infrequent in the apical parts of stems and branches, filiform, hyaline throughout, consisting of 9-12 relatively short, barrel-shaped cells below, and more elongate above. Stem and branch leaves similar in size and shape, evenly set and crowded, appressed, closely imbricate and erect when dry, erect-spreading when wet, lingulate to oblong-lanceolate, (1.7-)2.0-2.5(-3.0) mm long, 0.7-0.8(-0.9) mm wide, obtusely keeled below, concave above, not plicate, usually distinctly auriculate and decurrent at base, without hair-point, acute to long acuminate, less often rounded-obtuse or subacute at the apex; margins 2(-4)-stratose throughout, broadly recurved on one side and flat to narrowly recurved on the other side from base to mid-leaf or sometimes higher, plane above, entire below, distantly bluntly eroso-dentate at the extreme apex or sometimes down the margin in the upper fourth, sometimes nearly entire, especially on older leaves, bordered from near the base by (1-)2-10(-13) rows of cells in 2(-4) layers; costa single, almost concolorous and weakly demarcated from the laminal cells to dark yellow or brownish on older leaves, almost of the same width throughout or somewhat tapering above, 70-90(-120) µm wide, extending almost to the apex but not sharply delimited above and imperceptibly merging into the laminal cells, in transverse section plano-convex throughout or occasionally somewhat biconvex above, bistratose and crescent-shaped dorsally at the apex with 3-4 larger ventral cells, becoming gradually 3(-4)-stratose below in the upper half, mostly with 3-4 larger cells in the central row and an imperfectly developed row of ventral cells, becoming somewhat wider in mid-leaf, plano-convex and flattened-lunate dorsally, with 6-8 larger cells ventrally, in the lower part lying in a shallow groove, prominent, flattened-reniform dorsally, 4-5-stratose with 6-8 large ventral cells; laminal cells unistratose throughout except for the bistratose marginal limbidia, to variously bistratose in the distal half and with scattered bistratose streaks below, with or without inconspicuous papillae over the cell walls, with moderately to strongly sinuose or nodulose and firm to thick walls; upper cells irregularly rounded-quadrate, oval, short-rectangular to transversely short-rectangular, $6-12(-14) \mu m \log, 6-8(-10) \mu m$ wide, becoming shortly rectangular to irregularly isodiametric in mid-leaf, (8-)12-22(-25) µm long, (7-)8-10(-12) µm wide, and longer rectangular, up to 50 µm long, 8-10 µm wide below; cells at the insertion rectangular, only slightly different from the adjacent laminal cells, weakly sinuose and somewhat porose, moderately thick-walled, forming a distinct yellow to intensively yellow strip of 1-2 rows of cells; alar cells subquadrate to short-rectangular, larger than the other basal cells, 20-30(-60) µm long, 14-25 µm wide, with thin to moderately thick, smooth to sinuose walls, usually forming distinct, yellow-green to brown, flat or swollen, pellucid, shortly decurrent auricles, or sometimes almost undifferentiated and not forming distinct auricles; basal marginal cells quadrate to short-rectangular, 9-11 µm wide, 10-16 µm long, thick-walled, sinuose, not pellucid, not particularly different from the adjacent laminal cells and not forming a distinct border. Dioicous. Perigonia bud-like, 0.8-1.1 mm long, rather infrequent; outer perigonial bracts similar to vegetative leaves, only smaller; inner perigonial bracts yellow-brown, ovate, broadly and shortly acute, 0.9-1.0 mm long, strongly concave, with a rather firm costa ending well below the apex; antheridia 5-7 per perigonium, club-shaped, pale, short-stalked; paraphyses lacking. Outer perichaetial leaves lanceolate to oblong-lanceolate, gradually narrowly acuminate, 2.2–2.5 mm long, 0.7–0.8 mm wide, with narrowly obtuse or acute apex, entire to weakly eroso-dentate, with upper laminal cells thick-walled and sinuose, generally similar to those in the vegetative leaves, and lower cells rectangular, rather thin-walled and weakly sinuose; inner perichaetial leaves oblong-ovate to lingulate, rounded-obtuse to subacute at the apex, 2.8-3.0 mm long, 0.8-0.9 mm wide, entire or indistinctly erose, strongly concave, sheathing, yellowish-brown to hyaline, composed of thin-walled cells below, chlorophyllous in the upper third and composed of cells similar to those in the vegetative leaves, usually with bistratose patches in 1-3 rows at the margin. Setae single in the perichaetium, straight, short, 4.0-4.2 mm long, light brown above, dark brown below, becoming dark brown throughout with age, smooth, dextrorse when dry; vaginula dark brown, 0.7-1.0 mm long, with rectangular, sinuose epidermal cells. Capsules erect, straight, obloid to shortly cylindrical, gradually narrowed towards the seta and the mouth, 1.5-2.0 mm long, 0.9-1.0 mm wide, smooth, dull to somewhat lustrous, light brown becoming dark brown with age, pachydermous; operculum erect, long-rostrate, with a straight rostrum to 1.0 mm long; annulus separating, biseriate, composed of pellucid, orange- to yellow-brown, thick-walled cells with outer row of elongate cells and basal rows of short, isodiametric cells; exothecial cells isodiametric to elongate, irregularly hexagonal, subquadrate to long rectangular, 20-70 µm long, 15-25 µm wide, thin-walled, becoming rounded to oval below the mouth and forming a distinct, 5-7-seriate yellow-brown rim; stomata quite few near the base of the urn in 1-2 rows, superficial, bicellular with rounded pori, variously oriented; peristome single, composed of 16 teeth, 340-420 µm long, orange-brown, irregularly split to the middle or slightly below into 2-3 filiform, terete, not clearly articulated prongs, sometimes irregularly perforated, densely papillose with tall, peg-like papillae; basal membrane short, to 40 µm high, finely papillose; preperistome present as high as the basal membrane. Spores globose, finely papillose, pale yellowish-brown, 15-20 µm in diameter. Calyptra conic-mitrate, dark brown, somewhat roughened at the apex, naked, not plicate, 4-5-lobed at base.

Etymology — The specific epithet honours Dr Daniel H. Norris, Berkeley, and is a tribute to his great collecting activity in California and adjacent territories which yielded many important moss records for the bryoflora of the Pacific coast of North America.

Diagnostic characters and differentiation — Codriophorus norrisii is a prominent species defined by a combination of the following characters: (1) plants mostly small to moderately sized, fairly gracile, stiff and rigid, growing in loose or sometimes dense tufts; (2) leaves appressed and closely imbricate on drying, lingulate to oblong-lanceolate, (1.7-)2.0-2.5(-3.0) mm long, 0.7-0.7(-0.9) mm wide, concave, usually distinctly auriculate; (3) leaf apex epilose, acute to long acuminate, less often rounded-obtuse or subacute; (4) margins variously recurved on both sides in the proximal half, plane in the distal portion, remotely, bluntly eroso-dentate at the apex or in the upper fourth, bordered almost throughout by (1-)2-10(-13) rows of



FIGURE 41. Codriophorus norrisii. — 1. Habit. 2–11. Leaves. 12–27. Transverse sections of leaves from four different plants, sequentially from base to apex. — [1, 9-11, 21-27 from Norris 58449 (isotype); (2–4, 18–20 from Flowers 6507; 5–6, 12–15 from Shevock & York 14499; 7–8, 16–17 from Wagner 810; all in KRAM]. — Scale bars: a – 1 mm (2–11); b – 100 mm (12–27); c – 1 mm (1). (Reproduced from Annales Botanici Fennici, 37: 237, 2000, with permission).



FIGURE 42. *Codriophorus norrisii.* — 1. Axillary hairs. **3–4**. Leaf apices. **5**. Upper leaf cells at margin. **6**. Upper cells. **7**. Mid-leaf cells. **8**. Basal juxtacostal cells. **9–10**. Alar and supra-alar cells. **11**. Portion of stem section. — [1-2, 9-11] from *Norris 58449* (isotype); **3**, 5–8 from *Shevock & York 14499*; **4** from *Flowers 6507*; all in KRAM]. — Scale bars: a – 100 µm (3–10); b – 100 mm (11); c – 100 µm (1–2). (Reproduced from *Annales Botanici Fennici*, **37**: 238, 2000, with permission).


FIGURE 43. *Codriophorus norrisii.* — 1. Habit of plant with sporophyte, wet. 2. Perigonium. 3. Outer perigonial bract. 4–5. Inner perigonial bracts. 6. Innermost perigonial bract with antheridia. 7–9. Innermost perichaetial leaves. 10. Apex of innermost perichaetial leaf. 11–12. Cross-section of apical part of innermost perichaetial leaves. 13–15. Deoperculate capsules. 16. Operculate capsule. 17. Operculum. 18. Calyptra. 19. Transverse section of calyptra. 20. Portion of transverse section of seta. 21. Exothecial cells in middle of urn. 22. Exothecial cells and stomata at urn base. 23. Exothecial cells at orifice, annulus, peristome and spores. — [1, 13–16 from *Norris 58468*; 2–6 from *Wagner 810*; 7–10, 17–23 from *Norris 58449* (isotype); 11–12 from *Shevock & Toren 21511*; all in KRAM]. — Scale bars: a – 0.5 cm (1); b – 100 μ m (10, 19–20); c – 1 mm (6) and 100 μ m (11–12); d – 1 mm (2–5) and 100 mm (7–9, 17–18, 21–22); e – 1 mm (13–16) and 100 μ m (23). (Reproduced from *Annales Botanici Fennici*, 37: 239, 2000, with permission).

cells disposed in 2 or, occasionally, 3-4 layers, forming distinct fleshy limbidia; (5) costa moderately strong, 70-90(-120) µm wide, never spurred or forked, poorly demarcated from the laminal cells above, subpercurrent, bistratose and crescent-shaped above with 3-4 larger ventral cells, becoming 3-4-layered and flattened-lunate in midleaf and 4-5-stratose, flattened-reniform in the basal part with 6-8 large ventral cells; (6) laminal cells unistratose to variously bistratose above and with scattered bistratose strands below, with or without indistinct papillae over the cell walls, isodiametric to short-rectangular in the distal and median parts and longer rectangular below; (7) alar cells usually forming distinct, yellow-green to brown, flat or swollen, shortly decurrent auricles or undifferentiated; (8) basal marginal cells quadrate to short-rectangular, not forming a distinct border; (9) innermost perichaetial leaves strongly concave, sheathing, yellowish-brown to hyaline below, chlorophyllous in the upper third, with an areolation similar to that in the vegetative leaves and frequent bistratose, uni- to triseriate patches at the margins; (10) setae straight, 4.0-4.2 mm long, brown, dextrorse, single in the perichaetium; (11) capsules erect, obloid to shortly cylindrical, 1.5-2.0 mm long; (12) operculum long-rostrate; (13) annulus biseriate, deciduous; (14) exothecial cells isodiametric to elongate, thin-walled; (15) peristome teeth orange-brown, 340-420 µm long, irregularly forked to the middle or somewhat below into 2 or 3 filiform, terete and densely papillose branches, arising from a short (to 40 µm) sparsely papillose basal membrane; (16) spores spherical, finely roughened, globose, $15-20 \mu m$ wide; (17) calyptra conic-mitrate, dark brown.

Codriophorus norrisii shows a close resemblance to C. acicularis and in fact almost all collections of this species were originally so-named. The two species possess lingulate leaves with eroso-dentate margins in the apical part, as well ecological predilections to aquatic habitats. C. norrisii is generally a smaller and fairly slender plant, having the stems mostly 2-3 cm long, and with most leaves long-acuminate to acute and less often roundedobtuse or subacute at the apex. However, the essential differentiating characters are found in the leaf areolation and anatomy as well as in the form of the innermost perichaetial leaves. The leaves of C. norrisii have distinctly fleshy limbate margins extending from base to apex. They are usually bistratose, with occasional 3- or 4-layered patches near the apex, and are mostly 2-10 rows of cells wide, although rarely they are uniseriate in places or broader, to 13 cell rows in width. The limbidia are separated from the costa by unistratose laminae, even at the extreme apex, and only very rarely do they merge imperceptibly with the bistratose laminae. The leaf laminae are essentially unistratose but with various bistratose streaks, especially in the lower part of the leaf. C. acicularis has basically unistratose leaf laminae lacking any differentiated marginal borders but occasionally they are multistratose in some populations, consisting of 2-4 layers of cells. These populations occur predominantly in the Iberian Peninsula in Europe and have been recognised as a separate species, Racomitrium hespericum (Sérgio et al. 1995), whereas in North America only a single population with bistratose leaf laminae has so far been discovered in California (*Shevock & York 18322*, KRAM). Therefore, for geographical reasons, the possibility of confusing *C. norrisii* with *C. acicularis* is minimal. In *C. acicularis* the leaf laminae are entirely bistratose in the distal part, without unistratose patches separating marginal thickenings and the costa. However, the most important character which unequivocally separates *C. norrisii* from the phenotypes of *C. acicularis* with polystratose leaf laminae is the form of the papillosity of the laminal cells. The latter have very large, flat papillae which cover almost the entire lumina of the cells, leaving only a narrow slit over the cell centre, whereas in *C. norrisii* the papillae are lacking on older leaves or narrow and situated strictly over the cell walls.

Codriophorus norrisii is unique in subsect. Codriophorus in the structure of its perichaetial leaves. The innermost perichaetial bracts are strongly concave, sheathing, yellowish-brown to hyaline in the lower two thirds, with a lax areolation of thin-walled cells, whereas in the upper third the cells are chlorophyllous and similar to those in the vegetative leaves, usually with bistratose patches in 1–3 rows at the margins. In contrast, the innermost perichaetial leaves in *C. acicularis* are hyaline throughout, occasionally with some chlorophyllous cells at the extreme apex. Because *C. norrisii* produces sporophytes in great profusion, this character is very valuable and safe for the recognition of this species and its separation from *C. acicularis*.

Variability — *Codriophorus norrisii* shows relatively little variation in its diagnostic characters. Some differences are observable in the leaf shape, especially in the acuteness of the leaf apices, but the leaves are generally subject to remarkable variation in all aquatic mosses, especially those growing in rheophytic habitats. Also, the leaf papillosity is quite variable and in general the older leaves have weakly papillose to nearly smooth laminal cells, whereas the papillae are very prominent on the young leaves. The colour of the plants is usually conditioned by ecological conditions and depends on submergence and insolation.

Reproduction — Codriophorus norrisii is exceptionally prolific in the formation of fully mature sporophytes and all known populations of this species produce capsules abundantly.

Taxonomic and nomenclatural notes — Codriophorus norrisii was described only recently as a new species, *Racomitrium norrisii*, from specimens collected in El Dorado County in California (Bednarek-Ochyra & Ochyra 2000). It was subsequently transferred to the genus *Codriophorus* by Ochyra *et al.* (2003). The species was very infrequently collected in the first half of the twentieth century and the oldest specimen was gathered in Idaho by J. B. Leiberg in July 1902 and named *Racomitrium aciculare*, while the second oldest specimen was found in Tuolumne County in California by Gilford & Ikenberry in March 1935. The majority of collections were made only



FIGURE 44. Global distribution of Codriophorus norrisii.

in the last quarter of the century in California, mostly by Dan H. Norris and Jim R. Shevock.

Chromosome number — Not available.

Habitat — Like other species of the type section of *Codriophorus*, *C. norrisii* is a rheophytic moss growing in swiftly running water. Most collections have come from wet, shaded habitats in streams, brooks and rivers or on their banks. It grows on moist, diffusely lit granite boulders and rockslabs in streams as well as on stones and rocks subject to temporary inundation and often the species has been collected from submerged rocks. Sometimes it grows on boulders exposed when water levels are low in riparian coniferous and mixed woodland. *C. norrisii* grows in monospecific patches and tufts and only once it has been found in a mixed stand with *C. acicularis*.

Geographical distribution — *Codriophorus norrisii* is a montane species, endemic to western North America

and most of its localities are in the Sierra Nevada of California with a few localities known from the Clearwater Mountains of Idaho (Fig. 44). Most stations of *C. norrisii* are at elevations of 1000–1585 m in mixed coniferous forest and only two collections are from lower elevations of 505–630 m.

SPECIMENS EXAMINED

NORTH AMERICA. USA. CALIFORNIA. Amador Co.: E side of Cole Creek, 300 m W of bridge crossing North Fork Mokelumne River and 750 m E of White Azalea Campground, 1045 m, Shevock & Norris 21652 (CAS, KRAM). Calaveras Co.: Central Sierra Nevada, Stanislaus National Forest, ca 1 km E of bridge crossing North Fork Mokelumne River and less than 750 m from Salt Springs Reservoir, 1080 m, Shevock & Norris 21636 (CAS, KRAM). El Dorado Co.: Eldorado National Forest: along South Fork of the American River at Carpenter Creek, 1300 m, Norris 58441, 58448B, 58449, 58468 (KRAM, UC); along South Fork of American River at Bridal Veil Falls Campground, 1000 m, Norris 58364 (KRAM, UC); along South Fork of American River and Hwy 50, 6 km E of Whitehall, 21 Jun 1947, Koch s.n. (MICH); along South Fork American River at Sand Flat Campground, 1325 m, Shevock 24007 (KRAM). Fresno Co.: Sequoia National Forest, off California Hwy 180, just E of Deer Cove Creek, South Fork Kings River, 1325 m, Shevock & York 14499 (CAS, KRAM, MO); Kings Canyon National Park, along Mist Falls trail less than 750 m above trail junction to Bubbs Creek, South Fork Kings River drainage, 1585 m, Shevock & York 14474 (CAS, KRAM, MO). Mariposa Co.: Sierra National Forest, along hwy 140 paralleling the Merced River at Redbud Picnic Area, 505 m, Shevock & Norris 20160 (CAS, KRAM). Yosemite National Park: Yosemite Valley, 1280 m, Flowers 6507 (ALTA, COLO); Yosemite Valley, slopes above the Merced River less than 400 m below the Phono Bridge, 1180 m, Shevock 20411, 20412 & 20423 (CAS, KRAM); same locality, Merced River, along Southside Drive across from El Capitan, 1300 m, Shevock & Toren 21511 (CAS, KRAM); off hwy 140 along the Merced River at El Portal Entrance Station, ca 630 m, Shevock & Norris 20162 (CAS, KRAM). Tuolumne Co.: along Middle Fork Stanislaus River below bridge paralleling Evergreen Road, 1340 m, Shevock & Norris 22240 (CAS, KRAM); on bank of south fork of the Stanislaus River, Gilford & Ikenberry 51 (DUKE). IDAHO. Idaho Co.: Selway Falls, Wagner 810 (CAS, KRAM); near Selway Falls, Young 818 (WTU); by the Lochsa, about 37.5 km W of Lolo Pass, Hunter 24 (WTU); Middle Fork of Clearwater River near Green, Leiberg 442 (US).

A2. Subsection Hydrophilus (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

Codriophorus subsect. *Hydrophilus* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. ≡ *Racomitrium* subsect. *Hydrophilus* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 157. 1995 ['Hydrophilum']. — Type: *Codriophorus aquaticus* (Schrad.) Bednarek-Ochyra & Ochyra (*Trichostomum aquaticum* Schrad).

Plants small or moderately sized to large, slender to robust and coarse, loosely or densely caespitose, stiff and rigid, mostly green, olivaceous or yellow-brown, prostrate, ascending to erect, sparsely or copiously, irregularly dichotomously or fastigiately branched. Leaves crowded, imbricate to loosely appressed, erect, not or only slightly altered when dry, erecto-patent to spreading, often subsecund, when moist, narrowly lanceolate or lanceolate to ovate- or linear-lanceolate, gradually long acuminate, canaliculate-concave or concave throughout, sometimes keeled above, rounded-obtuse to subacute, muticous or shortly hyaline-tipped at the apex; margins recurved on one or both sides to mid-leaf or nearly to the apex, unistratose throughout to variously bistratose in the distal portion, entire throughout to bluntly eroso-dentate or cristate at the apex; costa single, percurrent to subpercurrent, stout, entire, strongly convex on the dorsal side, flat on the ventral side, crescent-shaped, semi-terete to reniform above, lunate or rectangular and distinctly flattened, lying at the bottom of a shallow or deep, narrow- or wide-angled groove in the proximal portion, 2-3-stratose above, 2-3(-4)-layered in the middle and 3-5-stratose near the base, with various numbers of cells on the ventral side; laminal cells unistratose throughout or variously bistratose distally, distinctly papillose, pellucid to opaque, isodiametric, rounded-quadrate, angular, oval to shortly rectangular, thick- and weakly sinuose-walled above, becoming short- to long rectangular, distinctly sinuose-walled in mid-leaf and below; basal cells rectangular, with strongly incrassate, porose and nodulose walls, forming a bright yellow- or orange-brown, 2-3-seriate strip at the leaf insertion; alar cells not differentiated or somewhat larger,

foming \pm distinct, flat or slightly swollen, decurrent auricles; supra-alar cells similar to the adjacent laminal cells or esinuose, forming a pellucid, hyaline or yellowish-hyaline, basal marginal border composed of 5-14(-24) cells. Dioicous. Innermost perichaetial leaves variously ovateoblong, oblong, ovate-lanceolate to lingulate, concave, sheathing the seta, subacute to rounded-obtuse at the apex, hyaline throughout or sometimes with a row of chlorophyllous uppermost cells. Setae single or sometimes 2–3 in the perichaetium, erect, straight, dextrorse. Capsules erect, straight, obloid to cylindrical, symmetric, brown, smooth, pachydermous; operculum conical-rostrate, with a long, straight beak, reaching $\frac{1}{2}-\frac{2}{3}$ of the urn length; peristome teeth split to the middle or nearly to the base into 2-3 terete, regular or irregular prongs, densely finely or spiculate-papillose, with a low basal membrane. Spores spherical, pale brownish, finely papillose, 10-17 µm in diameter. Calyptra conical-mitrate, verrucose or coarsely papillose at the apex.

Codriophorus subsect. *Hydrophilus* is characterised by the following set of characters: (1) plants variously branching but always lacking short, lateral tuft-like branchlets; (2) leaves narrowly lanceolate or lanceolate to ovate-lanceolate, concave below, canaliculate-concave to obtusely keeled distally; (3) leaf apex narrowly roundedobtuse to subacute, entire to bluntly eroso-dentate or cristate, muticous or terminated with a short hyaline tip; (4) costa percurrent or subpercurrent, stout, broad, strongly convex on the dorsal side, 3–5-stratose, often flattened and situated at the bottom of a shallow or deep furrow in the proximal portion, 2–3-layered, reniform, semi-terete to lunate in the distal portion; (5) laminal cells distinctly papillose, isodiametric to shortly rectangular in the upper part, pellucid to opaque; (6) innermost perichaetial leaves hyaline throughout; (7) setae short, dextrorse; (8) peristome teeth fairly short, divided to the middle or nearly to the base into 2-3 terete, densely finely or spiculate-papillose branches, with a low basal membrane.

Codriophorus subsect. Hydrophilus was recognised as a subsection within Racomitrium sect. Stenotrichum (Bednarek-Ochyra 1995) and subsequently transferred to Codriophorus (Ochyra et al. 2003). Originally, this taxon was distinguished to accommodate only a single species, C. aquaticus, but here its concept is expanded and two further species are added, namely C. ryszardii and C. carinatus, which have been misunderstood and consistently merged with C. aquaticus. Bednarek-Ochyra (2000) showed the specific distinctness of the western North American plants commonly named Racomitrium aquaticum and described them as a separate species, C. ryszardii. Likewise, some Japanese populations of C. carinatus with muticous leaves were recognised as a separate species, Racomitrium fauriei, which was considered identical to R. aquaticum (Noguchi 1974). However, the present treatment shows its conspecificity with C. carinatus.

Subsect. *Hydrophilus* shares many characters with the type section of *Codriophorus* but it is given cohesion by the combination of lanceolate leaf shape, narrowly rounded-obtuse to subacute leaf apices and a percurrent or subpercurrent costa which is very stout and broad and strongly convex but often flattened on the dorsal side. In the last character it shows affinity with the monotypic subsect. *Depressi* which, however, differs in having nearly smooth laminal cells and broadly ovate to oblong- or ovate-lanceolate leaves.

Codriophorus aquaticus ([Brid.] ex Schrad.) Bednarek-Ochyra & Ochyra (Figs 45–52)

Codriophorus aquaticus (Schrad.) Bednarek-Ochyra & Ochyra, Cens. Cat. Polish Mosses: 140. 2003. \equiv Trichostomum aquaticum (Brid.) ex Schrad., J. Bot. (Schrader) 1801(1[1]): 196. 1803. \equiv Dicranum aquaticum (Schrad.) Brid., Muscol. Recent. Suppl. 1: 190. 1806, hom. illeg. [non Dicranum aquaticum (Ehrh.) ex P.Beauv., Prodr.: 53. 1805]. \equiv Racomitrium aquaticum (Schrad.) Brid., Muscol. Recent. Suppl. 4: 80. 1819. \equiv Trichostomum aciculare (Hedw.) P.Beauv. var. aquaticum (Schrad.) F.Weber & D.Mohr ex Brid., Bryol. Univ. 1: 222. 1826, nom. inval. in synon. \equiv Grimmia aquatica (Schrad.) Müll.Hal., Syn. Musc. Frond. 1: 800. 1849. — TYPE CITATION: Dill. hist. musc. p. 367 t. 46 f. 26A. [Lectotype (selected here): [icon in] Dillenius (1741): f. 26a on pl. 46; epitype (selected here): The specimen marked 'A₁'on the sheet labelled "26. Bryum hypnoides aquaticum, calyptris nigris acutis. The Hypnumlike Water Bryum, with pointed black Caps." – OXF-Dillenius!).

Dicranum aciculare var. gracile Turner, Musc. Hib.: 67. 1804. \equiv Racomitrium aciculare var. gracile (Turner) Brid., Bryol. Univ. 1: 221. 1826. \equiv Trichostomum aciculare (Hedw.) P.Beauv. var. gracile (Turner) Wilson, London J. Bot. 3: 380. 1841. – TYPE CITATION: [...] in comitatus Wicklow montibus [...] [Lectotype (selected here): "Trichost^m aciculare γ Turn. Musc. Hib. Wicklow Mt^{ns} 1802 (caules 3 (illeg.) hb. D. Turner" – BM-Wilson!]. First synonymised with Racomitrium aquaticum by Wilson (1855: p. 166). Trichostomum protensum A.Braun ex Duby, Bot. Gall. Ed. 2, 2: 573. 1830. = Trichostomum fasciculare Hedw. var. protensum (A.Braun ex Duby) Hartm., Handb. Skand. Fl. Ed. 2: 321. 1832. = Racomitrium protensum (A.Braun ex Duby) Bruch & Schimp. in Bruch, Schimp. & W.Gümbel, Bryol. Eur. 3: 140, pl. 263. 1845 [Fasc. 25–28 Mon.: 6, pl. 2 (Dryptodon)] [Racomitrium protensum (A.Braun ex Duby) Huebener, Musc. Germ.: 211. 1833, nom. inval. in synon.]. = Grimmia protensa (A.Braun ex Duby) Mitt., Phil. Trans. R. Soc. London 168: 30. 1879. — TYPE CITATION: In rupibus humidis sylvarum Vogesorum (cl. Moug. et Nestl.) [Lectotype (vide Bednarek-Ochyra 1999: p. 529): (Mougeot et Nestler, Stirpes Cryptogamae Vogeso-Rhenanae) "215. Trichostomum fasciculare Schrader Spic. Fl. germ. p. 61 Bryum hypnoides b. Linn. Frequens in saxis Vogesorum humidis. Vere" – w!; isotype: COLO!, JE!, KRAM!, M!]. First synonymised with Grimmia aquatica by Müller (1849: p. 800).

Racomitrium cataractarum Brid., Bryol. Univ. 1: 776. 1827. \equiv *R. protensum* var. *cataractarum* (Brid.) Lesq., Mem. Calif. Acad. Sci. 1: 15. 1868, *nom. illeg. prior ut spec.* — TYPE CITATION: In Hercynia Suevica superiore ad cataractas rivulosque in saxis perpetuo roridis caespitose habitat. Diligentissimus Braun detexit et communicavit. [Holotype: "Racomitrium cataractarum cum fructu In rupibus aqua semper rorantibus ad cataractas rivulos Hercynia Suevica superioris (Braun) D. Bauer 1825" – B-Bridel!; isotype: PR!]. First synonymised with *Grimmia aquatica* by Müller (1849: p. 800).

R. protensum fo. *robustum* Loeske, Moosfl. Harz.: 194. 1903 ['robusta']. — TYPE CITATION: Hbg.: Riefenbachth. bei 300 m. [Holotype: "Rhacomitrium protensum Braun Harzberg, Riefenbachthal bei 300 m, an schattig-feuchten Felsplatten 12.VIII.1902 L. Loeske" – M!], *syn. nov.*

Plants medium-sized to large, robust and coarse, rarely fairly slender, forming large, dense or loose tufts or intricate patches, stiff and rigid, dull, olivaceous, olivegreen, olive- or greenish-brown, rusty-golden or blackishbrown above, blackish-brown or black below. Stems prostrate, decumbent or erect, (0.5-)2.5-10.0(-16.5) cm long, tough, irregularly, sparingly dichotomously or fastigiately branched, sometimes with short, mostly decumbent branches, rarely almost unbranched, sparsely radiculose at base with branched, lustrous, dark brown, smooth rhizoids, in transverse section lacking a central strand, with a 3-4(-5)-stratose cortex of small cells with brown, strongly incrassate walls and small lumina, surrounding a 4-6-stratose medulla composed of large, thick-walled, yellow-brown cells; axillary hairs filiform, hyaline throughout, composed of 13-14 short, barrel-shaped cells. Leaves crowded, evenly arranged, usually eroded in the older parts of the stem, rigid and stiff, imbricate to loosely appressed, erect, with incurved apices when dry, erecto-patent to patent and often subsecund when wet, straight to somewhat curved, (1.9-)2.1-3.0 mm long, 0.7-1.0 mm wide, not or slightly decurrent, lanceolate, narrowly lanceolate to oblong-lanceolate, gradually tapering to a narrowly rounded-obtuse or subacute, muticous apex, narrowly to broadly canaliculate to obtusely carinate above, broadly canaliculate-concave or concave below; margin broadly recurved to $\frac{1}{2}-\frac{2}{3}$ of the leaf length on one side and more narrowly recurved to about the same length on the other side, deflexed to nearly plane above, entire, unistratose thoroughout or variously bistratose in 1-3 rows of cells in the distal part; costa single, sharply demarcated from the laminal cells, though sometimes imperceptibly merging with the bistratose laminal cells near the apex, very robust (80-)100-180 µm wide at base, yellow-brown to brown below, becoming dark yellow above, ceasing a few cells below the leaf apex, gradually tapering upwards, entire or sometimes uneven distally with some hints of spurs, shallowly or deeply grooved in a wide- or narrow-angled furrow in the proximal part, strongly convex dorsally over its whole length, in transverse section often somewhat asymmetric, lunate to reniform or rectangular above, often distinctly flattened below, in the distal part 2-3-stratose, with (3-)4-7 ventral epidermal cells, usually equal in size to the median and dorsal cells, 3(-4)-stratose in the middle, with (3-)5-8 ventral cells, 3-5-stratose below, consisting of a row of (4-)7-14 large, circular or elliptical ventral cells and small, substereid or stereid central and dorsal cells; laminal cells densely covered on both surfaces with large, flat papillae covering the longitudinal walls and most of the lumina and leaving only a narrow slit in the middle on both the dorsal and ventral surfaces of the leaf, transparent; upper cells isodiametric to shortly elongate, irregularly rounded-quadrate to angular, shortrectangular or often oblate at the margins, thick- and weakly sinuose-walled, (8-)10-15(-20) µm long, 8-10(-12) µm wide, becoming elongate towards mid-leaf, (10-)15-25(-35) µm long, 5-8 µm wide, and somewhat longer above the base, (20-)25-45 µm long; basal cells rectangular, (20-)25-35(-45) µm long, 8-12 µm wide, with incrassate, porose and nodulose longitudinal walls, intensely yellow or yellow-brownish pigmented in 2-3 rows, forming a distinct colourful strip at the leaf insertion; alar cells not differentiated from the adjacent basal cells or short-rectangular, 25-35 µm long, 13-15 µm wide, with strongly incrassate, porose or sinuose walls, forming slightly swollen, brown auricles; supra-alar cells not differentiated or quadrate to short-rectangular, 10-25(-30) μ m long, 4–8(–10) μ m wide, with moderately thickened, straight walls, pellucid, hyaline to yellowish-hyaline, forming a distinct, uniseriate marginal border consisting of 7-15 cells, occasionally biseriate with a second short row of 2-4 cells. Dioicous. Perigonia bud-like, pale brown, about 2 mm long; outer perigonial bracts lanceolate, 2.0-2.1 mm long, 0.9-1.0 mm wide, with a single, percurrent costa; inner perigonial bracts ovate, broadly acute, pale brownish, 1.0-1.1 mm long, 0.9-1.0 mm wide, deeply concave, distinctly costate, the innermost one with about 20 club-shaped, brownish, antheridia, intermixed with few filiform, pale hyaline-brownish paraphyses reaching half of the length of the antheridia. Outer perichaetial leaves lanceolate, 2.5-3.0 mm long, 1.0-1.1 mm wide, similar to the vegetative leaves; inner perichaetial leaves ovate-lanceolate to lingulate, 1.5-1.9 mm long, 0.5-0.9 mm wide, obtuse or subacute to broadly rounded at the apex, strongly concave and sheathing the seta, the 2-3 innermost ones yellowish-hyaline throughout, with a lax areolation of thin-walled cells. Setae single per perichaetium, rarely geminate or triple, 5-10 or, very rarely, 18 mm long, reddish-to blackish-brown, erect, straight, smooth, dextrorse; vaginula brown to reddish-brown, ca 1 mm long, with rectangular, thick- and sinuose-walled epidermal cells.

Capsules exserted, erect, straight, symmetric, obloid to cylindrical, 2.0-3.1 mm long, 0.8-1.0 mm wide, smooth, dull or slightly glistening, pale brown or olive-brown, becoming dark brown with age, pachydermous; operculum conical-rostrate, 1.1-1.5 mm long, long-beaked, with a straight rostrum up to ²/₃ of the urn length; annulus separating, 2-3-seriate, composed of large, vesiculose cells with incrassate walls; exothecial cells isodiametric to oblong, oval, subquadrate to rectangular, 20-50 µm long, 10-20 µm wide, thick-walled with distinct corner thickenings; stomata 11-15 at the extreme base of the urn in 2-3 rows, superficial, 30-35 µm long, 30-40 µm wide, bicellular with rounded pori; peristome single, consisting of 16, dark yellow-, brown- or orange-reddish, densely finely papillose teeth, to 400-480(-530) µm long, split to near the middle or almost to the base into 2(-3) terete, weakly barred prongs, with a short basal membrane, 15-30 µm tall and with a distinct hyaline preperistome. Spores globose, (10-)13-17 µm in diameter, pale brownish, nearly smooth to finely roughened. Calyptra conic-mitrate, 4-5lobate at the base, pale brown below, dark brown and verrucose at the apex.

Etymology — The name of this species is of Latin origin – *aquaticus* means growing in or associated with water – and clearly indicates its ecological predilections.

Diagnostic characters and differentiation — Externally Codriophorus aquaticus is not a particularly attractive or handsome moss and does not possess characters which could rivet immediate attention upon it. However, closer examination of the species reveals a number of features which, tout ensemble, make it distinct and readily identifiable from all other grimmialean mosses. Thus, C. aquaticus is diagnosed by the following combination of characters: (1) plants fairly large to robust, coarse, stiff and rigid, loosely or densely caespitose, olivaceous, olive-green, olive- or green-brown; (2) stems usually sparsely, irregularly and dichotomously branched; (3) leaves straight, imbricate and erect on drying, erect-spreading to spreading on wetting, lanceolate, rounded-obtuse and muticous at the apex, broadly canaliculate and carinate in the distal part, concave below; (4) margins entire throughout, recurved on both sides to $\frac{1}{2}-\frac{2}{3}$ of the way up the leaf, unistratose to variously bistratose in 1-3 rows of cells in the upper part; (5) costa robust, (80-)100-180 µm wide at the base, subpercurrent, strongly convex dorsally, lying at the bottom of a shallow or deep, wide- or narrow-angled groove, reniform or crescent-shaped, 2-3-stratose and homogeneous in transverse section in the upper part, with (3–)4–7 ventral cells, 3(-4)-stratose, mostly with 5–8 ventral cells in the middle, lunate or distinctly flattened, and 3-5-stratose in the proximal part, consisting usually of a row of 7-14 large, rounded or elliptical cells and 2-4 layers of stereid cells; (6) laminal cells transparent, isodiametric to short-rectangular, thick- and weakly sinuose-walled in the upper and median parts, long-rectangular at the base, unistratose to variously bistratose at the apex; (7) alar cells not or scarcely differentiated; (8) basal marginal border



FIGURE 45. Codriophorus aquaticus. — 1. Plant with mature sporophyte. 2. Portion of branch, dry. 3–20. Leaves. 21–35. Transverse sections of leaves. — [1 from *Medelius s.n.*, 21 Mar 1918 (s); 2 from *Hakelier s.n.*, 23 Apr 1961 (s); 3–5 from *Nordenstrom s.n.*, 7 Jul 1886, s; 6–8 from *Viera s.n.*, 7 Feb 1982, MA; 9–11 from *Glowacki s.n.*, 3 Aug 1904, GJO; 12–14 from *Kola s.n.*, 22 Sep 1968, KRAM; 15–17 from *Bauer s.n.*, 25 Aug 1896, OP; 18–20 from *Kaalaas s.n.*, 27 Jul 1896, s; 21–22 from *Stenholm s.n.*, 5 Jul 1922 (s); 23–26 from *Stenholm s.n.*, 18 Mar 1920 (s); 27–28 from *Adlerz s.n.*, 7 Jul 1886, s; 29–31 from *Lindberg s.n.*, May 1853, s; 32–35 from *Holmgren s.n.*, 4 Jul 1868, s]. — Scale bars: a – 1 cm (1); b – 200 μ m (21–35); c – 1 mm (3–20); d – 1 mm (2).



FIGURE 46. Codriophorus aquaticus. — 1–4. Leaves. 5. Leaf apex. 6. Upper cells at margin. 7. Mid-leaf cells. 8. Basal cells. 9–10. Angular cells. 11–19. Transverse sections of leaves, sequencially from base to apex. — [All from *Braun s.n.*, 1825, holotype of *Racomitrium cataractarum*, B]. — Scale bars: a - 1 mm (1-4); b - 100 µm (11-19); c - 100 µm (5-10).



FIGURE 47. Codriophorus aquaticus. — 1–2. Transverse sections of leaves, showing sequences from base to apex and gradual transition from the plants with very strong and thick to very narrow and thin costae. — [1 from *Nordenstrom s.n.*, 7 Jul 1886, s; 2 from *Viera s.n.*, 7 Feb 1982, MA]. — Scale bar: 100 μ m.

present or absent, composed of 7–15 pellucid, straightwalled, hyaline to yellowish-hyaline cells; (9) innermost perichaetial leaves lingulate, obtuse to broadly rounded at the apex, *hyaline throughout*; (10) setae short, dextrorse; (11) capsules obloid to cylindrical, straight and erect; (12) peristome teeth short, 400–480(–530) μ m, divided to the middle or to the base into 2(–3) terete, densely low papillose prongs.

The principal characters that ensure quick and safe recognition of *Codriophorus aquaticus* are its lanceolate leaves with entire, obtuse and narrowly rounded apices lacking any hair-point coupled with a very pronounced broad costa that is prominently convex on the dorsal side, as is clearly visible on dry plants even with a hand lens. Outside Europe, the species has been confused with the other two species of subsect. *Hydrophilus*, namely *C. carinatus* and *C. ryszardii* and the differences separating them are discussed in detail under these species.

In Asia, *Codriophorus aquaticus* has been recorded in Japan (Noguchi 1974, 1988), China (Zhang 1978), Siberia (Abramova & Abramov 1966; Bardunov 1969) and the Russian Far East (Blagodatskikh 1984). The Japanese records were based upon the taxonomic interpretation of the type material of *Racomitrium fauriei* Cardot which, on the basis of its lanceolate leaves with narrowly roundedobtuse and muticous apices, was considered conspecific with R. aquaticum (Noguchi 1974). The identity of this species is discussed in greater detail under Codriophorus carinatus to which it is now considered identical. Of several differentiating characters, the anatomy of the costa is crucial for separating muticous ecads of C. carinatus and C. aquaticus. The costa in C. carinatus is bistratose in the central part, with two very large, transversely elliptical cells on the ventral side which are distinctly larger from the dorsal cells, and in the basal part it is narrow, 85-105 µm wide, 2-3-stratose, with 3-4(-5) enlarged ventral cells and much smaller dorsal stereid cells. In contrast, the costa in C. aquaticus is usually tristratose and with 4-7 ventral epidermal cells in the central part that do not differ in size and shape from other cells and at the base it is very broad and thick, 100-180 µm wide, 3-6-stratose, with 7-15 ventral epidermal cells that are transversely elliptical and much larger than those forming the dorsal stereid band.

The continental collections of *Codriophorus aquaticus* from Asiatic Russia proved to be misdeterminations of muticous ecads of *Bucklandiella sudetica* (Funck) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra 2004b). These plants have entirely smooth laminal cells and this character is sufficient to preclude their alliance with the genus *Codriophorus* because the presence of broad and flat papillae over the cell walls and major parts of the lumina is the basic generic character of the latter. Also, the internal structure of the costa which is (2–)3-stratose in the basal part and has only 3–4 enlarged ventral epidermal cells clearly indicates that these plants are *Bucklandiella sudetica*. This difference applies equally to European populations of the two species since they are likely to be confused there as well.

In western North America *Codriophorus aquaticus* has consistently been mistaken for *C. ryszardii* (Bednarek-Ochyra 2000). The differences between these species are discussed with full particulars under the latter and here it is necessary to emphasize that *C. ryszardii* is very readily distinguishable by its bluntly eroso-dentate leaf apices giving them a cristate appearance. This shape of the leaf apex sharply contrasts with the entire and rounded-obtuse apex in *C. aquaticus*.

The possibility of confusion of *Codriophorus aquaticus* with other congeners is minimal or simply improbable. It shares short and isodiametric upper laminal cells with *C. acicularis*, *C. aduncoides*, *C. mollis* and *C. norrisii* but typical expressions of these species have broadly lingulate, ovate, elliptical to ovate-lanceolate leaves that are broadly rounded, broadly rounded-obtuse to acute and usually toothed at the apex. An aberrant specimen of *C. acicularis* from Spain, resembling very much *C. aquaticus*, is discussed under the former. *C. aquaticus* has a costa of similar width to that in *C. depressus* from California but the latter has laminal cells smooth or nearly so and the costa is strongly flattened throughout its whole length, not reniform to lunate in the upper and median parts and often also in the basal part on the dorsal side.

The lanceolate and muticous leaves with a strong, subpercurrent costa make *Codriophorus aquaticus* sim-

ilar to Bucklandiella elliptica (Turner) Bednarek-Ochyra & Ochyra and small stunted forms of B. obtusa, two European endemics, of which the former occurs in the north-western part of the continent in the British Isles, the Faeroes and Norway (Størmer 1969) and the latter extends additionally to the Iberian Peninsula and Central Europe (Bednarek-Ochyra et al. 1990). Putting aside the basic difference between the genera Bucklandiella and Codriophorus, i.e. entirely smooth laminal cells versus papillose ones, B. elliptica has narrowly lanceolate leaves, consisting of an ovate or ovate-lanceolate base gradually or fairly abruptly narrowed to a narrow subula mostly filled with a costa and entirely bistratose and opaque upper laminal cells. Additionally, the capsules are short and ovoid and the spores larger, 18-21 µm in diameter, and coarsely papillose. B. obtusa has been particularly often mistaken for C. aquaticus but it is distinct at the first glance by its leaf margins which are revolute to broadly recurved on both sides from the base almost up to the apex.

Codriophorus aquaticus bears also a superficial resemblance to Bucklandiella lamprocarpa, a rheophytic moss species characterised by having lanceolate leaves with a robust and percurrent costa, and in Europe they have been considered to be closely related by some authors (Loeske 1913, 1930; Podpěra 1954). B. lamprocarpa is a Southern Hemisphere moss, having an amphiatlantic temperate range. It is widespread along the western coast of southern South America from the Juan Fernandez Islands and Central Chile to Cape Horn, with some stations on the Falkland Islands and in Sierra de la Ventana on the eastern coast of the continent (Ochyra 1993; Bednarek-Ochyra & Ochyra 1994b; Bednarek-Ochyra et al. 1996) and in the northern Andes (Churchill et al. 2000). On the other hand, it occurs frequently in South and East Africa and in the Tristan da Cunha group (Ochyra et al. 1988) and extends to Iles Kerguelen in the Subantarctic in the southern Indian Ocean (Bednarek-Ochyra & Ochyra 1998). In addition, it has also been discovered in widely disjunct stations on the Iberian Peninsula in western Europe (Ochyra et al. 1988; Casas et al. 1992).

The European populations have twice been described as separate species, namely Racomitrium levieri Kindb. (Kindberg 1898) and R. dixonii Guim. (Machado 1915), and once as a variety, Racomitrium aciculare var. radiculosum Guim. (Machado 1916). The first of these was described from material collected by E. Levier in 1878 in Serra d'Estrella in Portugal during his well-known Iter Ibericum he had made together with E. Boissier and L. Leresche (Leresche & Levier 1880). This species was shortly discussed by Loeske (1913) and reduced to a form of Racomitrium protensum and later to a variety of this species, R. protensum var. levieri (Loeske 1930). It should be noted that in *Index muscorum* (Wijk et al. 1967) the combination Racomitrium aquaticum var. levieri is erroneously attributed to Loeske (1913) but it was actually made by Podpěra (1954).

Racomitrium dixonii was described from two sterile collections from Serra de Arga in Minho Province in north-western Portugal (Machado 1915, 1918a, 1930).



FIGURE 48. Codriophorus aquaticus. — 1–2. Transverse sections of leaves, showing sequences from base to apex and gradual transition from the plants with very strong and thick to very narrow and thin costae. — [1 from Kaalaas s.n., 27 Jul 1896, s; 2 from Bauer s.n., 25 Aug 1896, OP]. — Scale bar: 100 μ m.

Loeske (1930) considered it to be a distinct species, though closely related to *R. levieri*, and Podpěra (1954) reduced it to a veriety of *R. aquaticum*. Both *R. levieri* and *R. dixonii* are actually conspecific with *Bucklandiella lamprocarpa* (Ochyra *et al.* 1988) which has nothing to do with *Codriophorus aquaticus*, except for external similarities of the plants resulting from their convergent evolution on account of their identical ecological requirements. *B. lamprocarpa* has perfectly smooth laminal cells which are only occasionally pseudopapillose owing to the presence of longitudinal cuticular lamellae giving the leaves a papillose appearance in transverse section, for example in the type material of *Racomitrium looseri* Thér. from Chile (Bednarek-Ochyra & Ochyra 1994*b*). The smooth laminal cells in this species distinctly contrast with the strongly papillose laminal cells in *C. aquaticus*. Moreover, its laminal cells are entirely 2–4-stratose in the distal portion or at the margins which take the form of strong, swollen, (1-)4-15(-20)-seriate limbidia that extend from the leaf base to the apex where they eventually diffuse with the multistratose laminal cells. In *C. aquaticus*, the bistratosity of the upper cells and margins is restricted to the distal portion of the leaves and is very irregular. *B. lamprocarpa* always lacks a differentiated basal marginal border of pellucid and esinuose cells and has very large coarsely papillose spores 18–32 µm in diameter.

Conversely, in *C. aquaticus* the basal marginal border is usually present and is composed of 7–15 pellucid, straight-walled, hyaline to yellowish-hyaline cells and the spores are smaller, 14–17 μ m in diameter and are only delicately papillose.

Codriophorus aquaticus may be mistaken for epilose ecads of Bucklandiella lusitanica (Ochyra & Sérgio) Bednarek-Ochyra & Ochyra, a hydrophytic moss endemic to Portugal on the Iberian Peninsula (Ochyra & Sérgio 1992). Typically, the latter species has piliferous leaves with hyaline hair-points that are 0.1-0.5 mm long and this character coupled with the presence of 2-3(-4)-stratose swollen limbidia and variously bistratose upper laminal cells makes it easily recognisable and unmistakable. It is the epilose plants of *B. lusitanica* that are likely to be confused with C. aquaticus as both species possess relatively small, finely papillose spores that are 14–16 µm in diameter. However, the narrowly lanceolate leaves with distinct polystratose limbidia extending from base to apex and the bistratose upper laminal cells, as well as the narrowly cylindrical capsules of B. lusitanica, should safely distinguish the two species.

Codriophorus aquaticus is superficially very similar to *Dryptodon patens* (Hedw.) Brid. but the latter has costae distinctly winged on the abaxial side. Moreover, these are much narrower with only four enlarged epidermal cells on the adaxial side. Furthermore, the capsule in *D. patens* is ribbed, the seta is curved on wetting, twisted to the left on drying and the laminal cells are entirely smooth.

Variability — The complex and intricate taxonomic and nomenclatural history may suggest that *Codriophorus aquaticus* is a very variable species which poses serious identification problems. However, nothing of the kind is observed in this species, indeed quite the opposite as *C. aquaticus* is a distinct and easily distinguished taxon whose variability is on a par with that recorded in other species of the genus showing similar ecological predilections.

The plants growing in relatively dry habitats are usually more delicate and fairly slender and the smallest ones, reaching only 0.5 cm, were collected on dry erratic blocks in Western Pomerania in northern Poland (*Hintze s.n.*, 26 Oct 1928, KRAM). The plants that thrive in wet sites are usually large and robust and in favourable environmetal conditions they may reach a dozen or so centimetres and the tallest ones, to 16.5 cm, were found in Sweden. Very robust and coarse plants collected in the Harz, Germany, were designated by Loeske (1903) as *Racomitrium protensum* fo. *robustum*. It is the only infraspecific taxon recognised within *Codriophorus aquaticus* which is quite unusual because various habitat modifications, especially of aquatic mosses, were often given taxonomic recognition by the older taxonomists.

Robustness of the plants is strictly correlated with the stoutness of the costa in *Codriophorus aquaticus*. Generally, the width of the costa in this species varies from 100 to 180 μ m and in some plants it is as narrow as 80 μ m in the basal part. Plants with a fairly narrow costa,

80-110 µm, are less frequent and are relatively gracile (e.g., Koła s.n., 22 Sep 1968, KRAM) and were described as a separate species, Racomitrium cataractarum (Bridel 1827). In cross-section the costae in these phenotypes are bistratose almost throughout, except for the extreme base where they are tristratose. Also, they have only four or five larger ventral epidermal cells near the base and three or four ventral cells in the median and/or upper parts (Fig. 46, 50.2). The opposite extreme is represented by the type of C. aquaticus itself (Bednarek-Ochyra & Ochyra 2004, Figs 15–17); robust phenotypes of the species are decidedly more frequent than slender ones. The costae in these plants are very pronounced, often 120–150 µm wide, but in extreme cases to 180 µm wide, for example in the plants from Sweden (e.g., Hakelier s.n., 19 May 1956, s). In transverse section they are 4–5-layered with 7–14 large ventral epidermal cells and a 3-4-stratose dorsal stereid band. These extremes are connected by a full series of intermediates (Fig. 47-50) and therefore the differences in the structure of the costa have no taxonomic importance in C. aquaticus so that Racomitrium cataractarum was quickly reduced to synonymy with R. aquaticum (Müller 1849).

The stratosity of the laminal cells is very variable in Codriophorus aquaticus, although this character has been entirely misinterpreted by bryologists. Except for Chałubiński (1882), all bryologists have stated that the laminal cells in this species are unistratose (e.g., Limpricht 1890; Roth 1904; Warnstorf 1906; Loeske 1913, 1930; Mönkemeyer 1927; Jones 1933; Jensen 1939; Nyholm 1956, 1998; Savicz-Lyubitskaya & Smirnova 1970; Smith 1978, 2005). However, cross-sections of the leaf laminae from all parts of its range, with particular reference to the Iberian Peninsula, show that the cells in the distal part of the leaf are very often variously bistratose. The bistratosity takes the form of streaks of one to a few cell rows wide, or sometimes the lamina is entirely bistratose on one or both sides of the costa. Finally, only the leaf margins are bistratose in one to three cell rows. A tendency for multiplication of the layers of laminal cells is frequently observed in aquatic mosses and it is evidently an adaptation and reaction of the species against the destructive action of fast flowing water and presumably the genetic determination of this character can be easily modified (Ochyra 1987a). The bistratosity of the laminal cells is not correlated with other structural characters of the gametophyte and therefore it has no diagnostic value.

The coloration of the plants varies much in *Codriophorus aquaticus* but generally within the limits typical of other aquatic members of the genus, depending primarily on inundation and exposure of the plants to light. The submerged parts of the plants are usually blackish-brown to blackish, whereas the emerged shoot tips are mostly yellow- or olive-brown.

The sporophyte in *Codriophorus aquaticus* varies little. The only remarkable aberration is observed in the seta length in the specimen collected in Śnieżne Kotły (*germ.* Schneegrube) in the Karkonosze range in the Sudetes (*Schoepke s.n., sine dato*, WRSL). The setae are up

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FIGURE 49. Codriophorus aquaticus. — 1–2. Transverse sections of leaves, showing sequences from base to apex and gradual transition from the plants with very strong and thick to very narrow and thin costae. — [1 from Schmidt s.n, Aug 1895, OP; 2 from Glowacki s.n., 3 Aug 1904, GJO]. — Scale bar: 100 μ m.

to 18 mm long and are at least twice as long as is usual in this species. Loeske (1930) mentioned setae reaching 13 mm and plants with setae of this length are occasionally observed throughout the range of *C. aquaticus*. Such aberrations are not exceptional in the Racomitrioideae. For example, the plants originally described as *Racomitrium levieri* Kindb. from Portugal (Kindberg 1898) has setae to 18 mm long, whereas *Bucklandiella lamprocarpa* with which this species is conspecific normally has setae up to 9 mm long (Ochyra *et al.* 1988). The setae are typically single in the perichaetium and only occasionally are two or three setae found in one perichetium. The peristome teeth are fairly short in *C. aquaticus*, 400–480 µm, and only sometimes are they somewhat longer, 500–530 µm (e.g., *Medelius s.n.*, 21 Mar 1918, s). **Reproduction** — Codriophorus aquaticus is rather infrequently found with sporophytes and they are not produced in abundance.

Taxonomic and nomenclatural notes—Although Codriophorus aquaticus is a distinct and easily distinguished species, it has a relatively complex early taxonomic and nomenclatural history. In the genus *Racomitrium* as traditionally understood it was, after *R. canescens* (Hedw.) Brid. [=*Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra] and *R. lanuginosum* (Hedw.) Brid., the third earliest species to be recognised. It is generally assumed that *C. aquaticus* was described and illustrated by Dillenius (1741) in his *Historia muscorum* who designated it by the phrase-name *Bryum hypnoides aqua*- ticum, calyptris nigris acutis. However, this author cited as synonyms two earlier phrase-names, namely Muscus aquaticus pileis acutis of Petiver (1695) and Bryum hypnoides repens, aquaticum, erectis capsulis acutis of Ray (1724). Additionally, he cited the description of the species by Ray (1696, 1704), Morison (1699) and Vaillant (1727) who used Petiver's name for it. However, the interpretation of the species in Vaillant's Botanicon parisiense varies depending on the author. Bridel (1798) considered Vaillant's plants as Codriophorus aquaticus, whereas Lindberg (1863) believed that the drawing of the fertile plant represented C. acicularis while the sterile plant was Philonotis fontana (Hedw.) Brid. (see also De Sloover 1997). Prior to the Dillenian description, C. aquaticus was also recognised by Haller (1738) as Hypnum caulibus teretibus, foliis lanceolatis, imbricatis, capsulis erectis, ovatis, aristatis and this name was also used in the subsequent works of this author (Haller 1768, 1769) as well as by Grimm (1773).

Although Linnaeus (1753) gave binomial names for most Dillenian moss species, Codriophorus aquaticus is missing from his Species plantarum. The taxon appeared only in Hudson's (1762) Flora anglica as an unnamed unranked infraspecific taxon $[\eta]$ of 'Bryum hypnoides' (=Racomitrium lanuginosum). Weber (1778) was the first to introduce a formal binomial designation for C. aquaticus when describing it as 'Hypnum aciculare' Scop. [unranked] ß aquaticum'. Hoffmann (1796) raised this unranked taxon to species, giving direct references to Weber's (1778) variety and to figure 26 in table 46 in Dillenius (1741). In order to avoid homonymy with his 'Bryum aquaticum' (=Dichodontium pellucidum (Hedw.) Schimp.) he named this species 'B. rivulare'. Bridel (1798) also approved this species as a taxon of its own and named it 'Trichostomum aquaticum'. He provided a brief diagnosis of the species, accompanied by an extensive list of synonyms, full description and distributional data. Finally, two years later, C. aquaticus was once more renamed by Röhling (1800) as 'Dicranum subulatum' who included in synonymy all of the above-mentioned earlier names of C. aquaticus. Bridel (1826) placed the 'Bryum nigrescens' of Villars (1789) in synonymy with Racomitrium aquaticum but Limpricht (1889) interpreted this invalidly published pre-Hedwigian taxon as Codriophorus acicularis.

All the above-cited binomials are obviously invalid since they date from the pre-starting point for moss nomenclature (1801). There has been some confusion regarding the validation of the pre-1801 name of *Codriophorus aquaticus*. The name is missing from Hedwig's (1801) *Species muscorum frondosorum* which is accepted as the starting point for moss nomenclature (*Sphagnum* excepted). Initially, Wijk *et al.* (1967) ascribed the validation of *Trichostomum aquaticum* to Palisot de Beauvois (1805) but later the compilers of the *Index muscorum* stated that actually this name was legitimised by Schrader (1803) in his review of Bridel's (1797–1801) *Muscologia recentiorum* (Wijk *et al.* 1969). Bridel (1819) transferred *Trichostomum aquaticum* to *Racomitrium*, although earlier he (Bridel 1806) placed it in *Dicranum* Hedw. as *D. aquaticum* (Schrad.) Brid. but this name is an illegitimate homonym. Müller (1849) transferred *R. aquaticum* to his catch-all genus *Grimmia* Hedw. but this concept has largely been ignored.

The authorship of *Trichostomum aquaticum* is problematical. It is usually ascribed to H. A. Schrader and, consequently, the type material of this name should be looked for in his herbarium. However, all evidence seems to indicate that this species was completely unknown to Schrader since it is missing from his major work on German mosses (Schrader 1794) and he quite simply mechanically validated *T. aquaticum* when mentioning this name in a review of Bridel's (1797–1801) *Muscologia recentiorum* ["... *T. obtusum (Br. aciculariforme* H. Dillen. 47. 30 und *aquaticum* (Dill. 46. 26) sind ziemlich ausführlich beschrieben ..."].

The authorship of the review in which validation of *Trichostomum aquaticum* was effected by a reference to a pre-1801 description is uncertain. It is generally ascribed to H. A. Schrader but in fact this review is anonymous because its author is nowhere indicated, as is the case with all reviews published in *Journal für Botanik*. Schrader served only as editor of this journal and, as an experienced bryologist, he most probably could have completed the review but that he did so is not explicitly stated (Sayre 1959). Thus, to be entirely correct, *Trichostomum aquaticum* should be ascribed to '(Brid.) *ex* Anonymo' rather, than to '(Brid.) *ex* Schrad.', unless this is considered as a reference to the editor of the journal.

Bridel (1798) did not quote any definite specimen(s) in the protologue of his '*Trichostomum aquaticum*' and he simply summarised in a separate entry all the distributional data for this species taken from the literature cited for synonymous names. His entry is as follows: "In uliginosis et aquaticis Norwegiae, Hercyniae, Helvetiae, Galliae habitat. In rupibus riguis Thuringiae prope Isenacam Grimmius etiam illud invenit. Tempus florescentiae ignotum; vere autem capsulae vigent. Vita longa". In the personal Bridel herbarium in Berlin (B) there are several specimens of *Codriophorus aquaticus* but all were collected in the post-1798 period so they are not suitable for lectotypification and, additionally, some of them are *C. fascicularis*.

Bednarek-Ochyra & Ochyra (2004) presented a detailed taxonomic and nomenclatural history of *Codriophorus aquaticus* and lectotypified this name with a specimen from the Dillenian herbarium at OXF. Unfortunately, they misinterpreted some elements in the protologue as syntypes and this is a common error committed by bryologists in typification of early moss names when considering the specimens cited indirectly through the literature as syntypes (Koponen 1967, 1979, 1980; Frisvoll 1983*a*, 1984; Pursell 1986; Hedenäs & Geissler 1999). If there are no specimens that could be accepted as original material for such species names, quite often the only elements eligible as lectotypes are illustrations cited in the protologue. Bednarek-Ochyra & Ochyra (2004) selected the specimen in the Dille-



FIGURE 50. *Codriophorus aquaticus.* — 1–2. Transverse sections of leaves, showing sequences from base to apex and gradual transition from the plants with very strong and thick to very narrow and thin costae. — [1 from *Kola s.n.*, 22 Sep 1968, KRAM; 2 from *Lisowski 58391*, KRAM]. — Scale bar: 100 μm.

nian herbarium corresponding to figure 26 on plate 46 in *Historia muscorum* of Dillenius (1741) as the lectotype of *Trichostomum aquaticum*. Schrader (1803) cited this illustration in the protologue, but there is no evidence that he studied the Dillenian specimen preserved in his herbarium prior to publication of *Trichostomum aquaticum*. Because there is other original material including the Dillenian plate (t. 46, f. 26A), this lectotypification cannot be accepted. In order to maintain the current usage of *Codriophorus aquaticus* and accommodate Bednarek-Ochyra & Ochyra's (2004) action, but in accordance with the rules, the illustration in the Dillenian *Historia muscorum* (t. 46, f. 26a) is selected here as lectotype and the corresponding specimen in the Dillenian herbarium as epitype.

A year after the recognition of *Trichostomum aquaticum*, this species was again described as a separate taxon by Turner (1804). He distinguished it as a variety within the broadly conceived *Codriophorus acicularis*, namely as *Dicranum aciculare* var. *gracile*. Later, this variety was given a name under *Trichostomum aciculare* (Wilson 1841) and finally reduced to synonymy with *Racomitrium aquaticum* (Wilson 1855).

Despite the clear priority of *Trichostomum aquaticum* of 1803, this specific epithet had remained almost totally neglected in the bryological literature in the nineteenth and in the first half of the twentieth centuries in favour of the much younger *Trichostomum protensum* A.Braun *ex* Duby of 1830 which was almost universally used as *Racomitrium protensum* (Duby) Bruch & Schimp.

(Bednarek-Ochyra 1999b). This was because Bruch *et al.* (1845) ignored the principle of priority and accepted *R. protensum* as the proper name for this species. Moreover, their *Bryologia europaea* was the oracle as far as taxonomic and nomenclatural questions in European mosses were concerned. This name also has a complex history which has been detailed by Bednarek-Ochyra (1994).

The compilers of Index muscorum (Wijk et al. 1967, 1969) ascribed the name Racomitrium protensum to "(Braun) Hueb." and, more precisely, referred its basionym, Trichostomum protensum, to "Braun in Schultz". The epithet protensum first appeared in the literature in association with this species in the work of Schultz (1828) who used it in the combination Trichostomum protensum. Although Wijk et al. (1967, 1969) ascribed this name to Alexander Braun, his name had not been mentioned in Schultz's (1828) work at all. The appearance of the epithet protensum in this paper has generally been overlooked and the usual practice has been to ascribe the authorship of this name to A. Braun and to attribute its first publication to Hübener (1833). Thus the name was frequently cited as Racomitrium protensum A.Braun in Huebener. It is necessary to add that this name is invalidly published because Hübener (1833) used it as a synonym of R. cataractarum Brid. which is in accordance with the rule of priority because the latter name is six year older (Bridel 1827).

Schultz (1828) mentioned the name in his discussion of *Trichostomum obtusum* Brid. and the interpretation of his statement is crucial for acceptance or rejection of *T. protensum* in the present paper. His comment reads: *"Tandem memorandum adhuc habeo muscum,* Trichostomi protensi *nomine ex Helvetia absque specialioribus allatum, quem quomodo a* T. aciculari *distinguam, non perspicio; unice foliis laxioribus minusque secundis ab illo recedit."* This sentence may be translated as follows: *"Finally, it is worth mentioning that I have a moss from Switzerland called Trichostomum protensum* and I do not see in what manner how to distinguish it from *T. aciculare;* it differs from the latter solely by the leaves being more lax and smaller".

Trichostomum protensum was evidently not accepted by C. F. Schultz and therefore was not validly published under Art. 34(1) of the current Code (Greuter et al. 2000). He merely reported the existence of the name Trichostomum protensum on a specimen which he considered belonged to T. aciculare because it differed only in minor vegetative characters. However, a careful search through the old bryological literature revealed a very helpful was discussion on *Racomitrium aquaticum* in the important, though forgotten, work on moss nomenclature by Le Jolis (1895) in which he stated that R. protensum had been validly published by Duby (1830) as Trichostomum protensum. That author had provided a brief description, in Latin, and cited the specimen named as Trichostomum fasciculare from the Vosges, which was distributed by Mougeot and Nestler in 1812 in their exsiccati Stirpes cryptogamae vogeso-rhenanae as No. 215 (Mougeot 1843). The name was ascribed to A. Braun who presented it in a letter to J. B. Mougeot. Two years after the valid description of *T. protensum*, Hartman (1832) reduced this name to a variety of *Trichostomum fasciculare* Hedw. and the fact that A. Braun was referred to in a short discussion of this name is a clear link to Duby's (1830) *T. protensum*.

It is also necessary to explain why the epithet *protensum* has so frequently been ascribed to A. Braun. Indeed, he actually was the first to discover this moss in a waterfall at Geroldsau in the Black Forest in south-western Germany and specimens have been located in several herbaria (BM, G, PC, W) bearing the name *Racomitrium protensum* 'mihi' or 'A. Braun' which had been collected in 1823. Because duplicates were widely distributed, this herbarium name became widely known well before its valid and effective publication.

The gracile phenotypes of Codriophorus aquaticus with narrow costae were described by Bridel (1827) as Racomitrium cataractarum. It was based upon a specimen collected by A. Braun "in Hercynia Suevica" and the information on the type locality is very misleading. Actually, Bridel (1827) refers to remote regions in Germany, namely to the Harz (Hercynia) in mid-Germany and Swebia in south-western Germany. This species name was reduced to synonymy with Grimmia aquatica by Müller (1849). It is worth noting that Lesquereux (1868) reduced Racomitrium cataractarum to a variety of R. protensum but the name R. protensum var. cataractarum is illegitimate since R. cataractarum had been described earlier as a species in its own right distinct from R. protensum. Nonetheless, this varietal name was overlooked by the compilers of Index muscorum (Wijk et al. 1967, 1969).

Chromosome number — Codriophorus aquaticus has been twice studied cytologically in the British Isles and the chromosome number n = 12 has consistently been found in four populations (Smith & Newton 1967; Ramsay 1969).

Habitat — *Codriophorus aquaticus* is a hydrophytic moss which, however, contrary to its name, does not grow in permanently submerged or inundated sites. It seems to be restricted to non-calcareous rocks, including sandstone, granite, basalt, gneiss, but sometimes, in Sweden, it has been found on quartziferous cliffs with calcareous intrusions, and in the Polish Carpathians it often grows on sandstone rocks which are generally enriched with lime (Stebel & Bednarek-Ochyra 2004). It is usually associated with sheltered, steeply sloping or vertical rocks that are moistened or flushed (at least periodically), on cliff faces in damp places, mostly in forest and woodland but also in open, treeless areas and on wet soil in areas of late snow lie. The species most often grows on wet or dripping bare rock faces or on thin soil over stones, boulders, ledges and rock outcrops, on the banks of streams and brooks and in the spray zone near waterfalls and rapids, rarely on the beds of intermittent streams. According to Størmer (1969) when not growing on stream beds C. aquaticus prefers specially positioned rocks, namely steep faces that are periodically moistened by water filtering through



FIGURE 51. *Codriophorus aquaticus.* — 1–3. Leaf apices. 4. Upper laminal cells at margin. 5–6. Mid-leaf cells. 7. Basal juxtacostal cells. 8–12. Angular cells. 13. Transverse section of stem. 14–17. Axillary hairs. — [1, 4–5 from *Nordenstrom s.n.*, 7 Jul 1886, s; 2, 7 from *Viera s.n.*, 19 Mar 1983, MA; 3, 6 from *Glowacki s.n.*, 3 Aug 1904, GJO; 8–9 from *Breidler s.n.*, 6 May 1890, GJO; 10–11 from *Kaalaas s.n.*, 27 Jul 1896, s; 12 from *Hintze 1100*, KRAM; 13 from *Kola s.n.*, 22 Sep 1968, KRAM; 14–17 from *Lisowski 58391*, KRAM]. — Scale bars: a – 100 µm (14–17); b – 100 µm (1–13).

vegetation-covered soil accumulations on ledges or gently sloping ground just above the steep rock face upon which the moss is growing. The vegetation on these ledges usually consists of *Vaccinium* species, *Calluna vulgaris*, herbs and grasses and carpets of such mosses as *Hylocomium splendens* and *Pleurozium* schreberi. Such vegetation mats secure the water and nutrient supply for a prolonged period.

As an acidophilous saxicolous moss, Codriophorus aquaticus is considered by phytosociologists to be a characteristic species of the class Grimmio-Racomitrietea heterostichi, the order Racomitrietalia heterostichi and the alliance Grimmion hartmanii (Hübschmann 1986; Marstaller 1993). However, it is not closely related to any associations of these syntaxa and as a rule it shows a low degree of constancy and phytosociological fidelity. It is a relatively frequent component of the association Diplophylletum albicantis (Herzog 1943; Magnée 1968; Nörr 1969) together with such species as Diplophyllum albicans (L.) Dumort., Scapania nemorea (L.) Grolle, Cynodontium polycarpon (Hedw.) Schimp., Heterocladium heteropterum (Brid.) Schimp., Bartramia pomiformis Hedw. and Tritomaria quinquedentata (Huds.) Buch. In other associations C. aquaticus is found only sporadically, for example in Racomitrio-Andreaetum rupestris (Philippi 1956), Andreaeetum nivalis (Krajina 1933), Frullanietum tamarisci (Strømer 1938; Philippi 1956) and Diplophyllo-Scapanietum nemorosae (Koła 1986) in which it grows together with Marsupella emarginata (Ehrh.) Dumort.

Geographical distribution — Owing to different taxonomic interpretations, the phytogeographical status of Codriophorus aquaticus varies markedly in the bryological literature. In most Floras and geographical treatments (e.g., Jones 1933; Podpěra 1954; Smith 1978, 2005; Nyholm 1998; Dierßen 2001), it is considered to be a bipolar species, occurring in Tierra del Fuego (Hermite Island), on the Falkland Islands, Îles Kerguelen and in New Zealand, although it is not mentioned in separate accounts of Du Rietz (1940), Schofield & Crum (1972), Schofield (1974) and Ochyra (1992) in which bipolar mosses were considered in detail. The southern South American and Kerguelen materials were originally reported as unnamed varieties of Racomitrium protensum (Wilson & Hooker 1847) but it is generally overlooked that soon afterwards Müller (1849) described var. 1 from Hermite Island as a new species, Grimmia nigrita Müll.Hal., and var. 3 from the Falkland Islands as G. lamprocarpa Müll.Hal. The former is now known to be conspecific with Bucklandiella didyma (Mont.) Bednarek-Ochyra & Ochyra (Deguchi 1984) and the latter is a distinct species, B. lamprocarpa (see "Diagnostic characters and differentiation" section, p. 116). Finally, the material from Iles Kerguelen recorded by Wilson & Hooker (1847) as vars 2 and 3 represents B. membranacea (Mitt.) Bednarek-Ochyra & Ochyra (Ochyra et al. 1988) and the plants reported from the North Island of New Zealand as Racomitrium protensum (Mitten 1867) represent a species of the Racomitrium crispulum complex (Dixon 1926). Thus, Codriophorus aquaticus definitely has to be excluded from the moss flora of the Southern Hemisphere, as pointed out by Ochyra *et al.* (1990b).

With the exclusion of the austral records, Codriophorus aquaticus was considered a boreal-montane species having a strongly dissected pan-Holarctic range and showing a clear affinity to areas with an oceanic climate (Ochyra et al. 1990b). However, this species was subsequently excluded from the moss flora of North America (Bednarek-Ochyra 2000) and continental Asia (Bednarek-Ochyra 2004b) and in the present treatment also from the bryophyte flora of Japan when Racomitrium fauriei was reduced to synonymy with Codriophorus carinatus (see p. 144). C. aquaticus was also once recorded from East Greenland (Lange & Jensen 1887) but the voucher material (Ingiteifjord, 23-27 Aug 1884, Eberlin s.n., C) actually represents C. fascicularis. Accordingly, C. aquaticus has become restricted in its distribution to Europe with extensions to Macaronesia (the Azores, the Canaries and Madeira) (Fig. 53).

Codriophorus aquaticus is chiefly distributed in areas strongly affected by an Atlantic climate, especially the British Isles (Ratcliffe 1968; Proctor 1992b) and Norway (Størmer 1969) (Fig. 54). It is widely distributed in Ireland (Holyoak 2003) and in western and northern Britain where it extends from Cornwall through to Wales and northern England to Scotland and the Shetlands (Proctor 1992b). In Scandinavia, the species is common in southern Sweden to lat. ca 60° N (Möller 1931) and in the coastal areas of south-western Norway, extending northwards to Sør-Trøndelag, becaming rare and scattered northwards (Størmer 1969) and reaching its northernmost station in Finmark at lat. ca 71° N. The record of the species from Jan Mayen (Lid 1941) correctly belongs within Bucklandiella sudetica (Funck) Bednarek-Ochyra & Ochyra (Watson 1964). In eastern Fennoscandia it is very rare and restricted to southern Finland along the costal areas of the Gulf of Finland. In mainland Europe C. aquaticus is widely distributed, especially in the mountains and highlands, extending from Portugal and north-western Spain in the Iberian Peninsula, the Massif Central and Brittany of France through to the Ardennes, Vosges, Black Forest, Alps and Sudetes eastwards to the Eastern and Southern Carpathians of Poland, the Ukraine and Romania and the Stara Planina of Bulgaria. In addition, it is known from relictual stations on erratic blocks in the Central European Plain of northern Gemany and Western Pomerania of northern Poland. In the Mediterranean region the species is rare and scattered in the Apennines Peninsula in Italy extending southwards to Lazio, although in the literature it is also recorded from Calabria (Cortini Pedrotti 2001), and Croatia and Bosnia-Herzegovina in the Balkan Peninsula. Moreover, the bryological literature provides information on the occurrence of this species in Sardinia (Fleischer 1893) and Corsica (Camus 1901) but no voucher specimens have been located. A highly isolated centre of occurrence of Codriophorus aquaticus is on the eastern coast of the Black Sea in the Caucasus of Russia and Georgia and in the Pontic Mountains of north-eastern



FIGURE 52. Codriophorus aquaticus. — 1. Portion of branch with mature capsule, wet. 2. Perigonium. 3–7. Perigonial bracts, sequentially from outermost to innermost. 8. Innermost perigonial bract and antheridia. 9. Epidermal cells of vaginula. 10. Transverse section of seta. 11–16. Perichaetial leaves, sequentially from outermost to innermost. 17. Apex of innermost perichaetial leaf. 18. Calyptra. 19. Transverse section of calyptra. 20–24. Operculate capsules, wet. 25–27. Deoperculate capsule, wet. 28–29. Deoperculate capsules with destroyed peristomes. 30. Exothecial cells in mid-urn. 31. Exothecial cells at base of urn and stomata. 32. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 9–10, 19 from *Lisowski* 58391, KRAM; 2–8, 28–29 from *Bauer 121*, KRAM; 11–17, 30–32 from *Medelius s.n.*, 21 Mar 1918, S; 18, 22–22 from *Perry 56/3*, NMW; 23 from *Schoepke s.n, s. dato* (Schneegrube), KRAM; 24–25 from *Persson s.n., s. dato* (Nyckleviken), S; 26–27 from *Bauer 223*, KRAM]. — Scale bars: a – 1 mm (1, 18, 20–29) and 100 μm (17, 39–32); b – 1 mm (11–16); c – 100 μm (9–10, 19); d – 1 mm (2–8).





FIGURE 53. Global distribution map for Codriophorus aquaticus.

Turkey. The easternmost disjunct station of the species is in the Southern Urals.

The altitudinal range of *Codriophorus aquaticus* extends from sea level to 2600 m in the Alps of the Tirol and Carinthia (Limpricht 1889). On the continent the species occurs chiefly in montane and altimontane regions, whereas in western and northern Europe the great majority of occurrences are in the lowlands, for example in Norway (Størmer 1969).

EXSICCATI

- Allorge V. S. & Allorge P. *Bryophyta Azorica* No. **81** (Canm, Colo, F, MO).
- ALLORGE V. S. & ALLORGE P. Bryotheca Iberica No. 177 (COLO, G).
- ARDISSONE Erbario Crittogamico Italiano No. 819 (G, M, UC).
- BARTLING & HAMPE Vegetabilia Cellularia in Germania Septentrionali Praesertim in Hercynia et in Agro Gottingensi No. 17 (M, UC, W).
- BAUER Bryotheca Bohemica No. 121 (BRNM, JE, KRAM, M, OP, PRC, PRC, S, W, WTU).
- BAUER *Musci Europaei Exsiccati* No. **222** & **223** (BR, BRNM, COLO, FH, G, GZU, JE, KRAM, M, PRC, S, UC, W).
- BILLOT Flora Exsiccata de C. Billot (cont. par Bavoux, Guichard, Guichard & Paillot) No. **3964** (JE, M, US).
- BREUTEL *Flora Germanica Exsiccata* Cent III No. **274** (BR, GJO, JE, M, POZG, UC, S, W).
- BROTHERUS Bryotheca Fennica No. 124 (M, S, US); No. 327 (JE, M, S, US).
- DELOGNE & GRAVET Les Mousses de L'Ardenne No. 122 (W).
- DISMIER Bryotheca Gallica No. 85 (BR, FH, BCB, WTU).
- FAMILLER Flora Exsiccata Bavarica: Bryophyta No. 727 (GZU, M, S).

- FLEISCHER & WARNSTORF Bryotheca Europaea Meridionalis No. 149 (JE, M, POZG, W).
- FRAHM *Bryophyta Vogesiaca Exsiccata* No. **62** (ALTA, BR, BRNM, CANM, G, H, herb. Frahm, KRAM, S).
- GRAVET Bryotheca Belgica No. 171 (BR, S).
- HARTMAN Bryaceae Scandinaviae Exsiccatae No. 38 (COLO, W).
- HOLMEN Bryophyta Danica Exsiccata No. 192 (Alta, Br, Cas, Colo, H, O, POZG, PR, S, TNS, UC, W).
- HUSNOT Musci Galliae No. 222 (BR, M, S); No. 222a (BR, G, M, S).
- JACK, LEINER & STIZENBERGER *Kryptogamen Badens* No. **384** (M, POZG, W).
- JĘDRZEJKO, ŻARNOWIEC & KLAMA Musci Macroregioni Meridionali Poloniae Exsiccati No. 209 (ALTA, BR, JE, KRAM, M, POZG, PR, S).
- KERNER Flora Exsiccata Austro Hungarica No. **725** (G, GJO, GZU, KRAM, M, PRC, PRC, S, US, W).
- KOPSCH Bryotheca Saxonica No. 132 & 417 (JE, KRAM).
- *Kryptogamae Exsiccatae* No. **672** (BR, G, GJO, KRAM, M, O, PRC, PRC, S, US, W).
- LIMPRICHT Bryotheca Silesiaca No. 314 (GJO, JE, KRAM, M, S, W).
- LISOWSKI *Bryotheca Polonica* No. **260** (BR, BRNM, CANM, KRAM, M, O, S); No. **1160** (Alta, CANM, KRAM, M, O, S).
- MOUGEOT & NESTLER *Stirpes Cryptogamae Vogeso-Rhenanae* No. 215 (COLO, JE, KRAM, M, W).
- MÜLLER Westfalens Laubmoose No. 99 (CANM, M, POZG, S, W).
- Ochyra *Musci Poloniae Exsiccati* No. **738** (Alta, Canm, Br, Je, Kram).
- PILOUS *Musci Čechoslovenici Exsiccati* No. **90** (BRNM, US, W); No. **291** (BRNM); No. **494** (BRNM, W); No. **775** (BRNM, OP, W).
- POECH Musci Bohemici No. 34 (G, W).
- RABENHORST *Bryotheca Europaea* No. **220** (KRAM, W); No. **221** (BR, CANM, G, JE, KRAM, M, S, W).
- SILLÉN Musci Frondosi Scandinaviae Exsiccati No. 226 (W).
- SPRUCE *Musci Pyrenaici* No. 289 (G, s); No. 290 (W).



FIGURE 54. Distribution map for Codriophorus aquaticus in Europe.

WILSON – Musci Britannici No. 163 (BR); No. 164 (CANM, W). ZETTERSTEDT – Grimmiae et Andreaeae Exsiccatae No. 27a & 27b

(M, O, S); No. **27c** (DUKE, G, M, S).

SELECTED SPECIMENS EXAMINED

EUROPE. ANDORRA. Llorts, 15 Jul 1978, *Casas s.n.* (BCB, KRAM); Vall d'Inclés, 1800 m, 13 July 1979, *Casas s.n.* (ALTA, BCB, herb. Frahm).

AUSTRIA. *Carinthia*: Hohe Taüern, Taüerntal-Gütenbrünn, Mallnitz, 1300 m, 10 Jul 1966, *Thyssen s.n.* (M); Ragabachschlucht by Ober-Vellach, *ca* 800 m, 30 Jul 1881, *Breidler s.n.* (GJO); Koralpe, Nordseitige Hänge am Koglerck over Lavamünd, *ca* 1300 m, 12 May 1974, *Poelt s.n.* (GZU); Hochalmfall im Maltathale, 31 Jul 1902, *Glowacki s.n.* (GJO); Untere Drautal bei Vellach a.d. Drau, 2 Sep 1905, *Glowacki s.n.* (GJO). *Niederösterreich*: Burgsteinmauer by Isper, *ca* 970 m, 29 May 1891, *Baumgartner s.n.* (W); Ispertale, Kl. Isper, 17 Aug 1875, *Juratzka s.n.* (W). *Oberösterreich*: Mühlviertel, Durchbruch des Naarn-Flusses oberh. Perg, *ca* 350 m, 23 May 1922, *Baumgartner s.n.* (W); Haugstein by Engelhartszell, 870 m, 30 May 1922, *Baumgartner s.n.* (W); Grein, Sep 1862, Heufler s.n. (W). Salzburg: in Gerlos et Kriml, 1100-1525 m, Sep 1863, Molendo s.n. (G, JE, M, UC, S, W); Kriml, 4 Aug 1858, Schwartz s.n. (GJO). Steiermark: Schieferfelsen im Sulmtal by Schwanberg, 14 May 1875, Breidler s.n. (GJO); Sulmthal by Schwanberg, 14 Apr 1875, Breidler s.n. (GZU, W); Schladnitzgraben by Leoben, 12 May 1970, Breidler s.n. (W) and 2 Jul 1869 (GJO); Gleinalpe by Leoben, 27 Jul 1868, Breidler s.n. (GJO, W); Waltenbachgraben by Leoben, 1000-1100 m, 19 May 1877, Breidler s.n. (GJO, GZU, W); Gössgraben by Leoben, May 1870, Breidler s.n. (GJO,W); Mugel by Leoben, 3 Sep 1868, Breidler s.n. (GJO); Strechengraben by Rottenmann, Thonschiefer, 900 m, 16 Jul 1887, Breidler s.n. (GJO); Klaüse by Deutsch Landsberg, 15 May 1875, Breidler s.n. (GZU, W) & 25 May 1932, Baumgartner s.n. (GZU); Koralpe, Klause by Deutschlandberg, in Lassnitz, 30 Mar 1959, Hachtmann s.n. (GZU), 7 Sep 1892, Glowacki s.n. (GJO) and 10 Aug 1883, Breidler s.n. (GJO); Lassnitzschlucht by Deutschlandsberg, 1 Oct 1941, Huber s.n. (W); Grazer Bergland, Raabklamm by Weiz, by Grünbichl, 500-600 m, 18 Jun 1977, Poelt s.n. (GZU); Raabklamm by Weiz, 500 m, 6 May 1890, Breidler s.n. (GJO); Feistritzgraben near Salzstiegel of Stubalpe, 1200-1500 m, 30 Jul 1883, Breidler s.n. (GJO); Winkelalm by St. Nikolai in Sölk, 1800 m, 21 Aug 1886, Breidler s.n. (GJO); Rantenspitz in Sölk-Kraggauer Alpen, 2300-2400 m, 12 Jul 1881, Breidler s.n. (GJO); Wartenstein by Gaisfeld, 600-800 m, 19 Sep 1897, Breidler s.n. (GJO); "Herkulessteine" in Klause by Deutschlandsberg, 13 Aug 1883, Breidler s.n. (GJO); Stubenbergklamm, 450 m, 16 May 1890, Breidler s.n. (GJO); Kohlrissgraben by St. Michael, 26 May 1892, Glowacki s.n. (GJO); Lainsbach by St. Michael over Leoben, 10 May 1870, Breidler s.n. (GJO); Rennfeld by Bruck, 1 Nov 1893, Glowacki s.n. (GJO); Gamsgraben by Frohnleiten, 800-900 m, 9 Sep 1884, Breidler s.n. (GJO). Tirol: Kematner Wasserfall near Innsbruck, 750 m, 31 Jul 1903, Handel-Mazzetti s.n. (BR, BRNM, COLO, FH, GZU, JE, KRAM, M, PRC, S, UC, W) [Musci Eur. Exs No. 222]; near Innsbruck, ca 640 m, 18 Jul 1899, Handel-Mazzetti s.n. (w); Riffelsees im Pitztal, 2220 m, 25 Aug 1961, Poelt s.n. (GZU); Arlberg, 2600 m, 9 Sep 1914, Molendo s.n. (M); Senderstal near Oenipontem, ca 1200 m, 23 Jul 1903, Handel-Mazzetti s.n. (W); near Rotenbrunn in the Sellrain valley, Laigesfall, 100 m, 26 Jul 1903, Handel-Mazzetti s.n. (w); Lienz, Schlossberg, Garcke 251 (w). Voralberg: Gampadelthal by Schruns, 1900 m. 19 Jul 1882, Breidler s.n. (GJO).

BELGIUM. Hainaut Prov .: vallée de l'Eau Noire, St Nicolas, Aug 1949, Duvigneaud s.n. (BR). Liége Prov.: Statte, affl. Hoegne, Delvosalle 40 (BR); vallée de la Statte, Sladden 947 H.F. (BR) & 5 Oct 1902, Sladden 954 H.F. & 956 H.F. & 957 H. F. (BR); Amblève, Sladden 140 (W); Bois Roslin, Parfondbois, Sladden 949 H. F. (BR) & 1057 (W); Monceveux valée du Minglinspo, near the "Cascade Bain de Diane", 300 m, Arts 5/25 (ALTA, BRNM, G, KRAM, UC); Spa (Liége), 14 Jun 1887, Vandenbroeck, Cardot, Dens & Pietquin s.n. (WTU); Ardennen, Hohes Venn, Francorchamps, Eau Rouge E of Hockai-Baches, 400-420 m, Heinrichs, Müller & Reiner-Drehwald JH 3834 (KRAM); Spa, de la promenade des Artistes, Dec 1908, Cornet s.n. (BR); Membach, vallée de la Soor, De Sloover 8835 (BR); Baraque Michel, vallée de la Helle, Demaret 1699 (BR); Nivelles, Promenade Meyerbeer Spa, 14 Jun 1887, Pietquin s.n. (BR); Francorchamps, Vallée de l'Eau-Rouge, S of Hez Fagnou, De Sloover 5152 (BR, TNS). Luxembourg Prov.: Chassepierre, N of Froid-Vent, De Sloover 24624 (KRAM); Chiny, De Zuttere 66/2817 (BR); Salme, 11 May 1899, Sladden s.n. (w): Muno, Roche à l'Appel, De Sloover 9671 & 70/6219 (BR). Namur Prov.: Grand-Halleux, Salm, Rochers de Hourt, De Sloover 4325 (BR, PR); Willerzie, Jul 1869, Gravet s.n. (BR); Stavelot, Bois Lafreuster, De Sloover 4462 (BR); Namur, Stavelot, Bois de la Ville, De Sloover 4475 (BR).

BOSNIA-HERZEGOVINA. Zeyernica over Fojnica, 3 Aug 1904, *Glowacki s.n.* (GJO).

BULGARIA. *Stara Planina Mountains (Balkan Range)*: from Karlovo to Botev, 1200 m, 30 Aug 1960, *Kuc s.n.* (KRAM); Botev, Levski river, 31 Aug 1960, *Kuc s.n.* (KRAM); Chaidushkite waterfall near Berkovica, *Natcheva & Ganeva 8107-B* (SOM); Kom, 1750 m, *Petrov 3859-B* (SOM); near Hubavec, 1000 m, *Petrov 3862-B* (SOM).

CROATIA. Kom. Lika-Krbava, Poljana od Sv. Ivana am Füsse und Velebit bei Medak (= Metka), 650 m, 21 Jun 1912, *Baumgartner s.n.* (W).

CZECH REPUBLIC. BOHEMIA. Brdy Mountains: Pilský rybník, near Březové Hory, Pilous 283 (CANM, DUKE). Chotěboř: Doubravka, 27 May 1944, Šmarda s.n. (BRNM). Domažlice: Žulové skály, ca 900 m, Ortmann s.n. (PRC). Jizerské hory: Hejnice, sine dato, Poech s.n. (G, w, w) [Musci Boh. No. 34]; Bukovec, 990 m, 13 Aug 1898, Schiffner s.n. (OP); Hájený potok near Bílý Potok, 670-800 m, 21 Aug 1898, Schiffner s.n. (OP); Štolpich, 610 m, 7 Aug 1898, Schiffner s.n. (OP); waterfall Desné, ca 600 m, 19 Aug 1898, Schiffner s.n. (BRNM, M, OP). Krkonoše: Důl Bílého Labe, 1000 m, 3 Sep 1980, Váňa s.n. (BR, DUKE, KRAM, PRC, TNS); Bílé Labe, near Luční bouda, ca 1420 m, 6 Jul 1980, Váňa s.n. (PR); Dolní Malá Úpa, ca 610 m, May 1948, Pilous s.n. (BRNM, W) [Musci Čech. Exs. No. 494] and Oct 1948, Pilous s.n. (BRNM, OP, w) [Musci Čech. Exs. No. 775]; Obří důl, Úpský vodopád, Traxler 430 (PRC); Krausovy Boudy, Pilous 208 (BISH, CANM, DUKE, TENN); Mumlávka, ca 1250 m, 5 Jun 1966, Váňa s.n. (PRC); Špindlerův Mlýn, Jun 1914, Winkelmann s.n. (POZG) and Sept 1896, Velenovský s.n. (PRC); Labský důl - Strmá stráň, 850 m, 28 Aug 1983, Šašková s.n. (PRC) and ca 950 m, 25 Jul 1986, Váňa s.n. (PRC-Váňa), Krušné horv: Okres Chomutov, Hora sv. Šebestiána, pod Ottersteinem, 800 m, 3 Sep 1960, Váňa s.n. (PRC). Šumava: Smrkový potok, SE of Mt Ždanidla, 1130-1160 m, Kučera 114/2 (PRC); Prášilské jezero, 1080-1110 m, Kučera 110/3 (PRC); Plešné jezero, 1200 m, Kučera 140/11 (PRC); Plešné jezero, below the Stifter-monument, 1150 m, Kučera 135/11 (PRC); Mt Laka above Laka lake, 1090-1130 m, Kučera 107/2 (PRC); Malá Řezná, 1070-1130 m, Kučera 169/3 (PRC); Švarcenberský kanál below Mt Třístoličník, 925 m, Kučera 110/3 & 172/9 (PRC); Jezerní Stěna u Železné Rudy, 1000 m, Bauer 338 (PRC); Čertovo jezero, 1080–1180 m, 27 Aug 1994, Kučera s.n. (PRC); Chalupská slať near Borová Lada, ca 900 m, 11 Jul 1998, Váňa s.n. (PRC); Černé jezero, 1170 m, 26 Aug 1994, Kučera s.n. (PRC); Plechý Mt, 1320 m, Kučera 198 (PRC); Nature Reserve Povydří, near Turnerova chata, 810 m, Kučera 125/4 (PRC); Černé jezero, 20 Jul 1956, Kůrka s.n. (BRNM). MORAVIA. Bystřice n. Pernštejnem: u Víru, 25 Mar 1941, Šmarda s.n. (BRNM, PR). Hrubý Jeseník: Kamenné rokle below Praděd, 900 m, 5 Jul 1946, Šmarda s.n. (BRNM, oP); Branné, ca 800 m, 21 May 1954, Šmarda s.n. (BRNM); "Vidly" opposite H. Domášov, 1000 m, 9 May 1951, Duda s.n. (OP).

DENMARK. BORNHOLM. Bornholms Amt: Hammeren, 14 Jul 1901, Möller s.n. (H, KRAM, S); Hammershuus, Aug 1866, Jensen s.n. (CANM); Almidingen, 6 Jul 1854, Jensen s.n. (S); Eihotak by Almindingen, Jul 1910, Mönkemeyer s.n. (JE); Ekkodal in Almindingen, 7 Jul 1908, Hesselbo s.n. (ALTA, BR, CAS, COLO, H, O, POZG, PR, S, TNS, UC, W) [Bry. Dan. Exs. No. 192]; Ekkodal, 16 Jul 1901, Porsild s.n. (CANM, S); Ekkodalens Klippevag, 20 Jul 1919, Lünd s.n. (O); Dybdal i Paradisbakkerne, 7 Apr 1882, Jensen s.n. (CANM). ZEALAND. Roskilde Amt: Storskoven, Hvalsö, 25 Oct 1901, Jensen s.n. (CANM).

FINLAND. Alandia: par. Hammarland, Frebbensby, 15 Jul 1910, Brotherus s.n. (M, S, US) [Bryoth. Fenn. No. 124]; Hammarlund, Marsum, 16 Jul 1928, Möller s.n. (BR, POZG, S); Saltvik, Ersberg, 17 Jun 1865, Bomansson s.n. (s); Saltvik, 10 May 1886, Bomansson s.n. (G); Saltvik, Kuggböle, 21 Apr 1961, Roivainen s.n. (H, PR); Gesterby, Aug 1871, Brotherus s.n. (JE, S,W); par. Sund, Nara Kyrkan, 25 Jun 1910, Brotherus s.n. (NMW); Ahvenanmaa, Sund, Brändbolstad, Jul 1925, Buch s.n. (BR); Ahvenanmaa/Aland Islands, Geta, Västergeta, Getabergen hills, Djupviksgrottan, 30 May 1976, Laine s.n. (COLO, H, M). Karelia Australis: Miehikkälä, Suur-Miehikkälä?, branter Kuivakankaanmäki, 22 Jul 1968, Fagerström s.n. (H). Nylandia: par. Esbo, Kasberget, Jun 1928, Buch s.n. (G, S); Vihti, 18 Aug 1871, Brotherus s.n. (G); Kerava, Alikerava, Jokimies, 7 Jun 1958, Laila & Roivainen s.n. (COLO, PR, US); Vantaa City, Sotunkylä, Väinölä, 21 May 1934, Roivainen s.n. (PR); Uusimaa, Siuntio, Övitsby, Kimpari, Koponen 2439 (ALTA, KRAM); Espoo, 3 May 1914, Kari s.n. (POZG). Ostrobotnia Australis: par. Öfvermark, Valsbärget, Skuggig, 4 Jul 1904, Hällström s.n. (H). Regio aboënsis (Äbo): Ekenäs, Bromarv, Norvstrand, 4 Aug 1903, Sundvik s.n. (s) and Jul 1904, Sundvik s.n. (JE, M, S) [Bryoth. Fenn. No. 327]; Pargas, 25 Jun 1872, Elfving s.n. (O, S); Varsinais-Suomi, Nauvo, Pensar, 22 May 1940, Auer s.n. (CANM); Lohia City, Kuulukainen Island, 10 Aug 1891, Lindberg s.n. (s).

FRANCE. ALSACE. Haut-Rhin: Le Hohneck, Jun, Boulay s.n. (BR, M); Hohneck, NE of Rainkopf, 1180 m, Heinrichs 1276 (KRAM); Masevaux Seewen, E Tremontkopf, Grande Roda roches, 700 m, 1 Sept 1983, Geissler s.n. (G); Ballon d'Alsace, Onraedt 68.F.13084 (BR); Ballon de St Maurice, Aug 1867, Pierrot s.n. (DUKE). AUVERGNE. Puy-de Dôme: Monts du Forez, W of Lyon, Pierre-sur-Haute, 1200 m, 3 Jul 1949, Cuynet s.n. (PC) and 1500 m, Cuynet 376 (BR, PC) & 384 (PC). BASSE NORMANDIE. Manche: Cherbourg, 14 Apr 1885, Le Jolis s.n. (M) and 25 May 1884, Le Jolis s.n. (CANM, GJO, H, S, W); Gréville, à Landemer, 1 Mar 1901, Martin s.n. (BR); Gréville near Cherbourg, 27 Nov 1884, Corbière s.n. (H). BRETAGNE. Finistère: Brèche de Toul au Dioul by St. Rivoal, 29 Aug 1878, Camus s.n. (BR); Huelgoat, Pierrot 2104 (BCB, BR, PC) &4012 (BR); Saint-Rivoal, Toul-au-Dieull rochers, Pierrot 54,064 (PC). CHAMPAGNE-ARDENNE. Ardennes: entre Hauts-Buttés et Linchamps, ravin du Ruisseau de l'Ours, Lawalrée 12458 (BR) and De Sloover 5576 (BR); entre Revin et Fumay, bois de Fumay, De Sloover 7196 (BR); Fumay, bord de la Meuse, Onraedt 68.F.7770, 68.F.13080 & 68.F.13083 (BR); La Neuville-aux-Haies, 6 Apr 1869, Gravet s.n. (BR); Laifour, 15 Jun 1885, Vandenbroeck s.n. (BR) and 1895, Dismier s.n. (COLO). FRANCHE-COMTÉ. Haute-Saône: Corravillers, ca 460 m, 6 Oct 1986, Frahm s.n. (ALTA, BR, BRNM, CANM, G, H, hb. Frahm, KRAM, S) [Bryo. Vog. Exs. No. 62]. LIMOUSIN. Haute-Vienne: St. Sylvestre, 22 Feb 1902, Lachenaud s.n. (WTU). Lorraine: Vosges, Gerbamont, 700 m, May/Jun 1867, Pierrot s.n. (JE, M, US); Gerbamont, Jun 1882, Pierrot s.n. (BR), MIDI-PYRÉNÉES, Haute-Garonne: Luchon, Sep 1856, Zetterstedt s.n. (o, s); Montauban near Luchon, 10 Jul 1851, Lange s.n. (M); Vallée de Luchon, lake Espingo, Aug 1851, Jordan s.n. (CANM). Hautes-Pyrénées: Gorge de Labassère, Spruce s.n. (G, W) [Musci Pyren. No. 289]; Vallée de Castelloubon, Spruce s.n. (W) [Musci Pyren. No. 290]. POITOU-CHARENTES. Deux-Sèvres: Parthenay, vallée du Thouet, Bluteau, Rallet 377 (BR, PC). RHÔNE-ALPES. Haute Savoie: Servoz, la Diosaz, Jul 1982, Duvivier s.n. (G); Servoz, Chatelad, 850 m, Geissler 15745 (G, S); Mont Blanc, 25 Aug 1856, Müller s.n. (G); ContaminesMontjoie, S Notre Dame de la Gorge, 1250 m, *Geissler 14177* (G); Notre-Dame de la Gorge, *Puget s.n.* (BR, G, M, S) [*Musci Gall.* No. 222a]; St Gervais, May 1854, *Kaitel s.n.* (G); Gorges de la Diosaz, *De Sloover 1984* (BR) and *Guinet 7R* (G); Aiguilles Rouges lac Corwe, 2275 m, 4 Aug 1907, *Guinet s.n.* (G). *Loire:* Planfoy, gorges du Furan barrage du Pas-du-Riot, 850 m, 26 Jun 1949, *Cuynet s.n.* (PC); Massif du Pilat, sous-bois résineux rive dr. du Gier, 1200 m, 22 Oct 1950, *Cuynet s.n.* (PC); Monts du Forez, pentes est de Pierre-sur-Haute, *ca* 1500 m, 24 July 1950, *Cuynet 376* (BR); Massif du Pilat, pentes du Crêt de la Perdrix, 1200 m, 7 Nov 1948, *Cuynet s.n.* (PC); Massif du Pilat Planfoy, gorges du Furan, 850 m, 26 Jun 1948, *Cuynet s.n.* (s).

GEORGIA. Imeretia, Oprtsheti on the Rioni river, 3 Jul 1877, Brotherus s.n. (H); Botanical Garden in Batumi, 29 Jun 1961, A. & I. Abramov s.n. (KRAM, LE); Republic of Abkhazia, Riza Lake, 2300 m, 3 Aug 1933, Petayev s.n. (KRAM, LE).

GERMANY. Baden-Württemberg: Geroldsauer Wasserfall near Baden, 20 Sep 1857, Bausch s.n. (M, POZG, W) [Krypt. Bad. No. 384] and Sep 1859, Bausch s.n. (BR, CANM, G, JE, KRAM, M, S, W) [Bryo. Eur. No. 221]; Wiedenbachsthal near Baden, 1884, Röll s.n. (POZG); Freiburg, am Kandel, ca 1100 m, Sep 1899, Herzog s.n. (JE); Freiburg, Hoh-Kelch (Belchen), ca 1250 m, May 1898, Herzog s.n. (JE); Gottschläg, 15 Jul 1933, Dietzow s.n. (BRNM); Baden, Hornberg, ca 435 m, Keller 653 (G); between Todmoos and Mambach, Lawalrée 21250 & 21249 (G); Henbronn (Gem. Neuenberg.) and Münsterhalden, NW of Haldenhof, Lawalrée 21333 (G); Zastlertal, 660 m, Lüth 833 (hb. Lüth, KRAM); Feldberg, 1200 m, Lambinon 64/D/918 (BR); Feldberg, Bärental, Fürsatz Wald, 1110 m, 3/7 Oct 1962, Grützmann s.n. (M); Feldberg, Felsenweg, 1400 m, 16/14 Oct 1961, Grützmann s.n. (M); Schwarzwald, Schiltachtal, 380 m, Lüth 1516 (hb. Lüth, KRAM); Schwarzwald, Schönwald, Farnberg, 930 m, Lüth 1016 (hb. Lüth, KRAM); Neuglashütten, 1100 m, Hegewald 1481 (ALTA); Rüttnergrund near Wieden, ca 900 m, Sep 1955, Herzog s.n. (JE); bei Schönau, ca 650 m, Jan 1918, Herzog s.n. (JE); Schwarzwald, Baldenweger Buck, 31 Jul 1904, Janzen s.n. (JE); Kinzigtale near Röthenbach-Alpirsbach, Apr 1902, Wälde s.n. (BR, BRNM, BRNM, COLO, FH, G, GZU, JE, KRAM, M, PRC, S, UC, W) [Musci Eur. Exs. No. 223]; Notschrei, 1000 m, De Sloover 11352 (BR). Bayern: Waldmünchen, 937 m, May 1887, Progel s.n. (M); Böhmerwald, Arbersee, Aug 1896, Krieger s.n. (JE); Oberpfalz, Schneeberger Felsen over Alsenschneeberg, Sept 1883, Progel s.n. (M); Böhmerwald, Teufelsee, 1100 m, 25 Aug 1896, Bauer s.n. (OP); Bayerische Wald, Kaitersberg, 956 m, Schwab 727 (KRAM); Krs. Grafenau, Waldhäuser, road to Lusen, 1100 m, 26 Sep 1960, Grützmann s.n. (M); Bayerischer Wald, Markungsgraben, 3.5 km SE of Mt Rachel, 1005 m, Kučera L13/1 (PRC); Kulmbach, 1901, Harz s.n. (M); SW Ostefalberg, 9 Sep 1973, Geissler s.n. (G); Krs. Cham, Kaitersberg, Meinunger & Schröder 20763 (JE); Krs. Traunstein, Weissenbach,, Meinunger & Schröder 21357 (JE); Allgaü, Guzesrieder Tal, 1350 m, De Sloover 17027 (BR, UC); Oberallgäu, Obermeiselstein, 1620 m, Lübenau 8 (M); Oberallgäu, Wertach, 1140 m, Lübenau 7 (M); Oberallgäu, Wertach, 1140 m, Lübenau 3173 (KRAM). Hessen: Rhöngebirge, Bubenbader Stein, 1872, Geheeb s.n. (BR, M) and 1897, Brückner s.n. (M). Niedersachsen: Harz, St. Andreasberg, 26 Apr 1994, Piszczek s.n. (KRAM); Lehnstedt, Heesener Holz, 18 Mar 1995, Koperski s.n. (hb. Koperski); Hamburg Süd, Fischbeker Heide, 18 Jan 1998, Baur s.n. (hb. Koperski). Rheinland-Pfalz: Krs. Birkenfeld, Oberes Nahebergland, Unnerbachtal, S Heimbach, 400 m, Caspari & Heinrichs JH 2836 (KRAM). Sachsen: Muldetal near Rochsburg, Meinunger 12410 (JE); Erzgebirge, Natschungtal, 620 m, Aug 1930, Flößner s.n. (KRAM) [Bryo. Sax. No. 417]; Tellerhäuser, Jun 1919, Kopsch s.n. (JE, KRAM) [Bryo. Sax. No. 132]. Sachsen Anhalt: Harzberg, Riefenbaufthal, 12 Aug 1902, Loeske s.n. (M); Harz, Bodethal, Nov 1862, Lorentz s.n. (GJO, M). Thüringen: Krs. Suhl, Adlersberg, 9 Apr 1974, Meinunger s.n. (M); Markthal near Ilmenau, 18 Jul 1882, Röll s.n. (GJO); Eisenach, Annatal, 280 m, 30 Dec 1920, Krüger s.n. (BRNM, JE); Eisenach, Töpfchenborn, 2 Dec 1894, Wuth s.n. (JE); Eisenach, Hochwaldgrotte, 380 m, 8 April (JE); Eisenach, Luisengrotte, 375 m, 31 May 1902, Wuth s.n. (JE); Eisenach, Wolfslöcher, 360 m, 27 Jul 1918, Krüger s.n. (JE); Eisenach, Breitengescheid, 310 m, 12 May 1925, Krüger s.n. (JE); Eisenach, Ludwigsklamm, 310 m, 30 Nov 1905, Krüger s.n. (JE); Inselsberg, Venetianerstein, 800 m, 17 Jul 1919, Krüger s.n. (JE); Krs. Hildburghansen, Eselgrund S Masserberg, 5 Sep 1971, Meinunger s.n. (JE); Krs. Hildburghausen, N Fehrenbach, Meinunger 4452 (JE); Krs. Suhl, Mittlerer Dillesgrund W of Frauen wald, 25 Sep 1971, Meinunger s.n. (JE); Krs. Gotha, S of Tabarz, Meinunger 1126 (JE); Krs. Gotha, Kanzel in Schmalwassergrund S of Dietharz, Meinunger 10778 (JE); Mittelwassergrund S Dietharz, 18 Sept 1974, Meinunger 1092 (JE); Krs. Ilmenau, Loch by Stützerboch, 8 Aug 1969, Meinunger s.n. (JE); Krs. Ilmenau, Marktal E of Stützerbach, 31 Aug 1974, Meinunger s.n. (JE); Krs. Sonneberg, Leierlochfelsen W of Steinach, Meinunger 4434 (JE); Krs. Schmalkalden, NE of Rotterode, Meinunger 6197 (JE); Krs. Schmalkalden, Gr. Schmiebach N of Schnellbach, 24 Jun 1968, Meinunger s.n. (JE); Krs. Schmalkalden, Hohe Möst SE of Oberschönau, Meinunger 1103 (JE); Krs. Hildburghausen, N of Giessübel, Meinunger 15502 (JE); Krs. Hildburghausen, Dachsbach S of Giessübel, Meinunger 4454 (JE).

GREAT BRITAIN. ENGLAND & WALES. Brecon (VC 42): river Hepste, near Penderyn, Apr 1927, Richards s.n. (NMW). Caernarvon (VC 49): Nant Ffrancon Pass, Jul 1952, Turner s.n. (NMW); Llyn Glas, Snowdon, 28 Mar 1963, Perry s.n. (NMW, US); Caernarvon, 11 Apr 1963, Størmer s.n. (0); Snowdon, Glaslyn, 610-910 m, Lawton 5337 (WTU); Aber Waterfall, 13 Apr 1855, Wilson s.n. (BR); Llanberis, May 1883, Stabler s.n. (E). Cardigan (VC 46): Cwm Einion, Aberystwyth, May 1940, Armitage s.n. (NMW). Carmarthen (VC 44): Ystrand-ffin, 13 May 1909, hb. Knight s.n. (NMW). Cheshire (VC 58): Crowden Great Brook, Longdendale, Blockeel 16/108a (NMW). E. Cornwall (VC 2): Stelmentor, Aug 1889, Yellam s.n. (E); near Golitha Falls, Holyoak 96-167 (hb. Holyoak). W. Cornwall (VC 1): Carn Galva, 12 Apr 1958, Laflin s.n. (NMW); Trengwainton Carn, Holyoak 97-348 (hb. Holyoak). Cumberland (VC 70): Buttermere, Fleetwith Pike, 13 Jan 1946, Muirhead s.n. (NMW); near Rosthwaite, Borrowdale, Jun 1937, Duncan s.n. (E); opposite Grange, Borrowdale, Aug 1870, Baker s.n. (US); N of Millom, Lawton 5432 (WTU); Braithwaite, near Keswick, 5 Aug 1919, Beesley s.n. (E); Scale Hill, Baker 102 (US); Wigton, Apr 1951, Fairley s.n. (E). Denbigh (VC 50): near Betws-y-Coed, Coed Hafod, 21 Mar 1968, Wanstall s.n. (NMW). Derby (VC 57), Nether Tor, Grinds Brook, Edale, ca 540 m, June 1994, Blockeel 23/126 (NMW). S. Devon (VC 3): by the River Teign, Fingle Bridge, near Moretonhampstead, 15 Jun 1962, Townsend s.n. (COLO, US, WTU); Dartmoor, Crockern Tor, 410 m, Goffinet 1750 (ALTA); Drewsteignton, above Fingle Bridge, 14 Feb 1957, Appleyard s.n. (NMW); Holne, 20 May 1918, Sherrin s.n. (NMW). Durham (VC 66): Widdy Bank, 5 Jun 1897, Ingham s.n. (NMW); Falcon Clints, Aug 1851, Baker s.n. (US). Glamorgan (VC 41): Craig-y-Llyn, Knight 181 (S) and Fitzgerald 56/3 (hb. Holyoak). S. Lancashire (VC 59): Todmorden, sine dato, Nowell s.n. (E). W. Lancashire (VC 60): Damas Gill, May 1900, Wheldon s.n. (NMW), Merioneth (VC 48): Rivers Llavbeds. Sep 1904, Duncan s.n. (E); Rhaiadr Du, Tyn-y-Graes (near Dolgelly), 150-190 m, 25 Jun 1954, Evans et al. s.n. (s); Betws-y-Coed, Aug 1882, Barker s.n. (UC); Harlech, 10 Jun 1915, Rhodes s.n. (WTU); below Harlech Castle, Sep 1903, Thompson s.n. (NMW); Geu Graig, Cader Idris, ca 580 m, Jul 1949, Watson (PC, hb. Holyoak); Maentwrog valley, Dec 1900, Jones s.n. (NMW). Montgomery (VC 47): near Machynlleth, 12 Sep 1941, Webb s.n. (NMW). N. Northumberland (VC 68): Cheviot, Sept 1925, Duncan & Millar s.n. (NMW). Pembroke (VC 45): Treffgarne, 4 Apr 1958, Pettifer s.n. (NMW), Radnor (VC 43): near Carreg Ddu Reservoir, Elan Valley, 21 Apr 1951, Webb s.n. (NMW); Elan Valley, 9 Apr 1965, Harrison s.n. (H); Craig Ddu, Radnorshire, 7 Apr 1965, Harrison s.n. (UC); road from Rhayader to Aberystwyth, ca 5 km NW of Rhayader, Townsend 87/379 (ALTA, COLO). S. Somerset (VC 5): River Barle below Simonsbath, 4 Jun 1961, Paton s.n. (NMW); Tarr Steps, 22 Mar 1963, Applevard s.n. (NMW). Westmorland (VC 69): Coniston, 18 Mar 1963, Lowne s.n. (NMW); Wetherlam, near Coniston, Aug 1921, Tetley s.n. (NMW); Kertmere, Jun 1886, Iraddell s.n. (E); Naddle Forest, Hawes Water, Jun 1901, Wilson s.n. (E); Great Langdale, Wilson 181 (WTU); Stickle Gill, Langdale, 26 Aug 1940, Catchside s.n. (E). Mid-West Yorkshire (VC 64): Ingleton, May 1926, Armitage s.n. (NMW) and 14 Aug 1934, Wallace s.n. (KRAM); near Pecca Falls, Swilla Glen. Ingleton, 1 Sep 1958, Perry s.n. (NMW). N.W. Yorkshire (VC 65): Teesdale, White Force, Mar 1853, Baker s.n. (BR); Bronkley Fell, Teesdale, Jun 1851, Baker s.n. (E, US); Cronkley Scars, upper Teesdale, Oct 1884, Barnes s.n. (GJO). S.W. Yorkshire (VC 63): Marsden Clough, Holmfirth, Blockeel 18/398 (NMW). SCOTLAND. S. Aberdeen (VC 92): Corrie Ceamsemor, Aug 1886, Ewing s.n. (E); Glen Callater, Braemar, Jul 1856, A.C. s.n. (E). Angus (VC 90): Strone dhu, Jul 1845, Gardiner s.n. (NMW); Clova, Forfarstine, Nov 1868, Fergusson s.n. (E), above Loch Brandy, Angus, Sep 1945, Duncan s.n. (E); Carrie Farchel, Clova, 20 Jul 1923, Robertson s. n. (E), Strome Dhu. Glen Callatu Forfar, Jan 1846, Gardnier s.n. (US); Caenlochan, July 1888, Smith s.n. (E). Argyll (VC 98): Ben Narnain,

29 Oct 1960, Clear s.n. (NMW); W Lochgilphean, June 1911, McAndrew s.n. (E); Ben More, Sep 1899, Murray s.n. (E); Loch Goil, 1866, Hunt s.n. (H); upper source of Allt Coire Gabhail, 350-450 m, Schofield & Schuster 69560 (DUKE). Ayr (VC 75): Knockdolian Hill, Sep 1915, Armitage s.n. (NMW). Banff (VC 94): Caingorms, above Loch Avon, by Feithe Budhe (Bridhe), 9 Aug 1984, Yeo s.n. (NMW). Clyde Islands (VC 100): Rothesay, Barone Hill, Jun 1908, McAndrew s.n. (E); Arran, Lamlash, Jun 1909, McAndrew s.n. (E); Arran, above Lochranga, Long 287 (E); Arran, Monamore Glen, May 1947, Appleyard s.n. (NMW); Ben Lester Burn, Arran, 30 Jul 1928, Mackesch s.n. (NMW). Dumfries (VC 72): Whitecoomb, Moffatt, Jul 1901, Duncan s.n. (E, NMW). Dunbarton (VC 99): Ben Vorlich, 19 Feb 1961, Clear s.n. (NMW); Loch Lomond, Yarbet, 23 May 1905, Andrew s.n. (E); Allander Burn, near Milngavie, 19 Mar 1955, Crundwell s.n. (CANM, PR). Mid Ebudes (VC 103): Iona, 14 Jul 1938, Trotter s.n. (NMW). N. Ebudes (VC 104): Portree area, Isle of Skye, 50 m, Janssens 594 (ALTA). W. Inverness (VC 97): N of Onich, Newton 1021 (NMW); Fort William, 7 May 1939, Størmer s.n. (0); Glen Nevis, 10 May 1939, Størmer s.n. (O); Ardtornish, Morvern-Fossil Burn, Schofield 68847 (ALTA, CANM, DUKE); near Ardtornish at head of Loch Aline, Norris 51435 (UC): below Loch Morar, 4 Apr 1966, Grierson s.n. (E): Gleann Dubh above intersection with Gleann Geal. ca 76 m. Norris 51507 (UC); Craig Phadrick, Jun 1914, Smith s.n. (E); Torr na Moine, Camas Salach, Loch Sunart, Long 13634 (E).. Kirkcudbright (VC 73): Kells, Kirkcudbright, 7 Sep 1961, Pettifer s.n. (NMW); Loch Trool, 26 Apr 1937, Wallace s.n. (E); Minnigaff, Craignaw, near Glen Trool, Jun 1951, Ratcliffe s.n. (E); New Galloway, N of Black Craig, Jun 1898, McAndrew s.n. (E); Ben-y-guinea, Oct 1897, McAndrew s.n. (E); Airie Hill, Mar 1897, McAndrew s.n. (E); Bennan Hill, Sep 1897, McAndrew s.n. (E). E. Lothian (VC 82): Traprain Law, ca 120 m, Long 25041 (E); Traprain Law, East Linton, 3 Oct 1908, McAndrew s.n. (E). Moray (VC 95): Huntly's Cave, Grantown, 3 Jun 1973, Richter s.n. (NMW). Orkney (VC 111): Ward Hill, Hoy, Johnston 2890 (E). Outer Hebrides (VC 110): Isle of Harris, Moorland rock near Tarbert, 19 Apr 1938, Trotter s.n. (NMW); St. Kilda, Hirta, Mullach Bi, May 1959, Ratcliffe s.n. (E); Barra, Heva, above Castlebay, Sinclair 337 (E); Barra, Jul 1936, Watson s.n. (E); Barra, Heaval, Jul 1936, Watson s.n. (E). E. Perth (VC 89): Rhodorach, Glen Beag, Jul 1885, Ferguson s.n. (E); Kindrogan Crag near Enochdu, Sep 1967, Duncan s.n. (E), Loch Ordie, 14 Apr 1902, M'Intosh s.n. (E). Mid Perth (VC 88): Ben Lawers, Jul 1929, Millar s.n. (NMW); Morvern, river Atina, near Acharn, 16 Jun 1992, Coppins, James & Poelt s.n. (GZU); Craig Chailleach, Aug 1916, Adam s.n. (E); St. Hillans, 24 May 1910, McAndrew s.n. (E); Crnach Ardran, Jul 1901, Smith s.n. (E); Stob Garth, 7 Jul 1906, Meldrum s.n. (E); Tarmachans, Coire Fionn Lairige, 16 May 1909, Evans s.n. (E); Inver Wood, 24 Dec 1902, M'Intosh s.n. (E); Craig Mohr, 3 Aug 1886, Mann s.n. (BR); Gleneagles, near Auchterarder, 22 Sep 1880, Martin s.n. (E). W. Perth (VC 87): Oakwood N of Callander, Aug 1950, Fairley s.n. (E); hills behind Dollar, 18 Apr 1897, Evans s.n. (E); Aberfogle, Loch Ard, Apr 1896, Evans s.n. (E); Inverarnan, Mar 1960, Clear s.n. (NMW); Callander, Kelty Glen, Apr 1900, Evans s.n. (E). E. Ross (VC 106): 750 m E of Loch Garve, 2 Jun 1959, Crundwell s.n. (NMW); Murdochy Bay, Black Isle, May 1966, Duncan s.n. (E). W. Ross (VC 105): Five Sisters Range, Sgurr na Moraich, SE end of Loch Duich, Schofield & Schuster 69693 (CANM, DUKE). Sheltand (VC 112): Mainland, Dumossness parish, Hoo field, 9 Sep 1960, Warburg s.n. (NMW). Stirling (VC 86): Strathblane, 21 Apr 1895, Murray s.n. (E); Trossachs, 26 May 1913, Hall s.n. (NMW); Inchcailloch, 8 Oct 1960, Clear s.n. (NMW); Loch Lomond, 2 Aug 1953, Wallace s.n. (NMW) and Hermann 19514 (CAS). W. Sutherland (VC 108): Quinag, 20 Jul 1899, Dixon et al. s.n. (NMW).

HUNGARY. *Comit. Nógrád*: Börzsöny Mountains, Sasfészek near Királyháza, *ca* 700 m, 3 May 1958, *Boros s.n.* (BP, POZG) and 22 May 1958, *Vajda s.n.* (BP); Vikibic near Királyháza, 1 Jul 1957, *Vajda s.n.* (BP); Magosfa near Diósjenö, 30 Jun 1957, *Vajda s.n.* (ALTA, BRNM, POZG); Magosfa near Kemence, 850 m, 30 Jun 1957, *Boros s.n.* (BP, CANM); Bacsó-patak near Királyháza, *ca* 700 m, 17 Jun 1958, *Boros s.n.* (BP, BR, CANM, POZG) and 23 May 1958, *Vajda s.n.* (BP, BR); Dosnyapatak near Királyháza, 17 Jun 1958, *Vajda s.n.* (ALTA, BP, BR).

ITALY. *Emilia Romagna*: Distr. Boscolungo in Apennino Mutinensi Aemiliae, "Valle belle Pozze" above Finmalbo, 1200 m, 12 Sept 1883, *Levier 352a* (TENN). *Lazio*: Frascati, Agro romano, *De Notaris* 32 (BR). *Lombardia*: Prov. Como, Monte Legnone on Como Lake, *ca* 1200 m, 30 Sep 1897, *Artaria s.n.* (JE, M, POZG, W) [*Bryoth. Eur. Mer.* No. 149]; Bellano on Como Lake, *ca* 500, 8 Sep 1898, *Artaria s.n.* (BR, BRNM, GJO); in Valle Intrasca, Lago Maggiore, Apr 1862, *De Notaris s.n.* (G, M, UC) [*Erbar. Crittog. Ital.* No. 819]; Alpe Darengo, Aug 1898, *Artaria s.n.* (WTU). *Piemonte:* Campello-Monti, 1200 m, *Levier 150 & 804* (s) and 1400 m, *Levier 539* (TENN); Caprezzo over Intra Langensee, 500 m, 6 Jun 1897, *Artaria s.n.* (GJO, JE); Cambiasca above Intra, *ca* 400 m, 8 Jun 1899, *Artaria s.n.* (BR). *Toscana:* agro Versiliensi, ad pedem Alpium Apuanarum, Etnnia, Jun 1880, *Bottini s.n.* (o). *Trentino-Alto Adige:* Val Nambron in Presanellastocke, *ca* 1800 m, 17 Sep 1903, *Baumgartner s.n.* (W); Monte Sello, Val di Sole, 11 Aug 1864, *Holler s.n.* (GJO); Roveda near Trente, *Hampe 338* (G); Val Daone, 18 Aug 1864, *Lorentz s.n.* (M).

IRELAND. Antrim (VC H39): Antrim, Fair Head, 29 Jul 1963, Perry s.n. (NMW). Armagh (VC H37): Camlough Mt, Jul 1916, Houston s.n. (NMW). Carlow (VC H13): Mt stream near Kilbrannish south, 28 July 1911, Tetley s.n. (NMW). Mid Cork (VC H4): Musherabeg, 29 Aug 1967, Fitzgerald s.n. (NMW); Glengarriff, Aug 1905, Duncan s.n. (E); Coomshingaun, Waterford, 23 Jul 1933, Armitage s.n. (NMW); Coomshingaun, Comeragh Mountains, Armitage 101 (NMW). Down (VC H38): Slieve Donard, Armitage H38 (NMW); Mourne Mountains, Slievenabrock, 1 Jul 1915, Lett s.n. (w). Dublin (VC H21): near Dublin, 1854, sine collector (CANM). Fermanagh (VC H33): Belcoo, Cuilcagh, 19 May 1965, Fitzgerald s.n. (NMW). W. Galway (VC H16): E side of NE corrie of Muckanaght Twelve Bens, ca 400 m, Long 26253 (E); Twelve Bens, NW corrie of Muckanaght, ca 500 m, Long 25546 (E). Leitrim (VC H29): SE of Bronagh, ca 360 m, 14 Sep 1970, Perry s.n. (NMW); Cloonaquin Mt, 16 Apr 1909, Tesley s.n. (NMW). Londonderry (VC H40): Dungiven, Mullaghmore, ca 490 m, 2 Jun 1965, Fitzgerald s.n. (NMW); Mullaghmore, Holyoak 99-685 (hb. Holyoak); Binevenagh Lake, Holyoak 99-263 (hb. Holyoak). Louth (VC H31): Carlingford Mt, 21 Aug 1963, Synnott s.n. (CANM). W. Mayo (VC H27): Achill Is., Slievemore, Aug 1933, Richards s.n. (NMW). N. Kerry (VC H2): Cromaglan Valley), Killarney, Aug 1936, Richards s.n. (NMW). S. Kerry (VC H1): near Cloonaghlin Lough, 8 Aug 1975, Scotter s.n. (NMW). Roscommon (VC H25): Sheegorey, 6 April 1910, Tetley s.n. (NMW). Sligo (VC H28): S of Knockachree, Slieve Gamph., ca 305 m, 27 Jul 1963, Perry s.n. (NMW, US); Ox Mountains, Lake Minnaun, Hegewald 2521 (ALTA). Tyrone (VC H36): Beleevanmore Mt, Eagle Rocks, 290 m, 18 Jun 1958, Fitzgerald s.n. (NMW). Wicklow (VC H20): Glendalough, ca 24 km S of Dublin, upper Lake, 134 m, Jury & Rumsey 4932 (BCB, BR).

NORWAY. AKERSHUS. Asker: Skaugumsåsen), 28 May 1889, Fridtz s.n. (0). Aurskog: Tavsjö, 27 Jun 1948, Størmer s.n. (0); Skaadalen, 28 May 1887, Fridtz s.n. (o, s). Bærum: Osternvannet, 23 May 1964, Størmer s.n. (0); Kveåsen, 12 Jun 1887, Fridtz s.n. (0); Kolsås, 12 Jun 1887, Fridtz s.n. (s); Kolsaastoppen, 3 May 1940, Störmer s.n. (o). Frogn: Håøya, 12 Jul 1937, Størmer s.n. (s); Håøya, 29 May 1949, Størmer s.n. (0); Håøya, ved Brudesteinen, 12 Jul 1934, Størmer s.n. (0); Håøya paa Nordspissen, 23 Jul 1935, Størmer s.n. (0); Grogn, Håøya, 12 Jul 1937, Størmer s.n. (DUKE). Nannestad: Bratt, W of Kringlervagen, 505 m, 2 Sep 1971, Homble s.n. (0). Nittedal: Eriksknarten S of Hakadal, 10 Jul 1943, Størmer s.n. (0). Oppegaard: Linnebukta, 22 May 1955, Størmer s.n. (0). Oslo: Skådalen, 2 Oct 1938, Størmer s.n. (0); Hakkloa i Nordmarka, 8 Jul 1941, Størmer s.n. (0); Tryvasshytta, 18 Sep 1936, Størmer s.n. (0); Trekørningen i Nordmarka, 24 Jul 1942, Størmer s.n. (0); Nordmarken, Björnsaasen, 10 May 1866, Blytt s.n. (0); Melemkollen, 9 Sep 1868, Blytt s.n. (o, s); Oslo, Grafsenaas, sine dato, Scheutz s.n. (s); Oslo, Rynbergen, 16 Jun 1858, Zetterstedt s.n. (s); Grafsenaas, 10 Jun 1868, Blytt s.n. (s); Oslo, Sandefjord, Apr 1895, Hoffstad s.n. (s). Raelingen: Vesledammen W of Narvestad, 25 Jul 1953, Størmer s.n. (0); Fjerdingbydammen, 4 Jul 1952, Størmer s.n. (0); Barlindaasen, 8 Aug 1952, Størmer s.n. (0); between Breimaasen and Brenndammen, 21 Jul 1954, Størmer s.n. (0). AUST-AGDER. Aamli: Haugelandsfjell, 10 Aug 1950, Størmer s.n. (o). Birkenes: Fisktjorn i Urddalen, 5 Aug 1968, Størmer s.n. (0); Urddalen, 5 Aug 1968, Størmer s.n. (0). Bygland: Arda Isnuten, 19 May 1918, Sørensen s.n. (0). Evje: Syrtveit, 28 May 1916, Sørensen s.n. (o). Grimstad: Homedal, Gurebø, 25 Jul 1891, Hagen s.n. (M, O). Hornnes: Birkelands fossen, Jun 1914, Sørensen s.n. (COLO, O); Jortveit, 6 Jun 1918, Sørensen s.n. (0). Landvik: Auesoya, 30 Jul 1968, Størmer s.n. (0). Lillesand: Nord for Yttre Eikeland, 7 Aug 1968, Størmer s.n. (0); Skogeroya, 31 Jul 1968, Størmer s.n. (0); Meboheia paa Justoya, 2 Aug 1968, Størmer s.n. (o). Tromøy: Hefte S of Lofstad, 18 Jun 1960, Størmer s.n. (o). Tromsö: NW Arendal, 17 Jun 1885, Kiær s. n. (0); Arendal, 19 Jun 1885, Kiær s.n. (0). Tvedestrand: Tvedestrand, 27 Jun 1976, Størmer s.n. (0); ved Myre paa Askeroya, 26 Jun 1976, Størmer s.n. (0); ved Sandvika paa Sandoya, 3 Jul 1976, Størmer s.n. (0); Furoya, 29 Jun 1976, Størmer s.n. (0); Dypvaag, Borøen, 1 Aug 1891, Hagen s.n. (0). Vegaarshei: Nordtjern N of Selaas, 20 Jun 1960, Størmer s.n. (0). V. Moland: Honsviga, Justoya, 10 m, 1 Aug 1954, Jørstad s.n. (0). Vegusdal Hovlandsdalen: Kvikjern, 7 Jul 1918, Sørensen s.n. (0). BUSKERUD. Eggedal: vest for Engar, ca 250 m, 27 Jul 1965, Størmer s.n. (0). Hurum: Holm, 21 Jun 1957, Størmer s.n. (0); mellom Myren og Knatvold, 13 Aug 1962, Størmer s.n. (0); Striglevand og Roskestadvand, 27 Jun 1945, Størmer s.n. (0). Krødsherad: Olberg, ca 150 m, 3 Aug 1941, Størmer s.n. (0); Surtebergseter, 500 m, 8 Aug 1941, Størmer s.n. (0). Lier: Storsteinsfjellets, 6 Aug 1944, Størmer s.n. (o). Modum: Austad, 28 Jul 1947, Størmer s.n. (o). Sigdal: SW of Halsteinrud, 300 m, 2 Aug 1965, Størmer s.n. (0). HEDMARK. Aamot: Blikkberget, ca 450 m, 14 May 1972, Hogholen s.n. (o). Aasnes: NE of Komperud, ca 300 m, 7 Sep 1975, Hogholen s.n. (0). Loten: ved elva Oksna sor for Nordhue, 3 Jun 1968, Hogholen s.n. (0). Stange: Svartaasen, lia mot Rasensjoen, 19 Jul 1970, Hogholen s.n. (0). Stor-Elvdal: ca 2 km N of Ophus st., ca 400 m, 9 May 1971, Hogholen s.n. (0). FINMARK. Hammerfest, Jul 1922, Söderberg s.n. (S). HORDALAND. Asane: Astveit, 19 Feb 1961, Bödtker s.n. (0). Bergen: Brennhogda N of Sandviken, 1 May 1965, Størmer s.n. (0); Bjørnedalen, 25 Mar 1977, Balle s.n. (CANM, COLO, G, M, US); Bergen, 31 Dec 1897, Greve s.n. (S); Sandviken ved Bergen, 12 Aug 1906, Schellenberg s.n. (H, KRAM, S); Damsgaaredfjeld ved Bergen, 5 May 1871, Wulfsberg s.n. (o). Bomlo: Kalavag, 20 Aug 1967, Størmer s.n. (0). Bremnes: Melingsvagen, 20 Aug 1967, Størmer s.n. (0): Grutle, 18 Aug 1967, Størmer s.n. (0). Eidfjord: paa Gjeld ved Vøringen, 3 Aug 1901, Möller s.n. (0). Evanger: Björgo, 300 m, 26 Jun 1951, Lid s.n. (0). Fana: Espeland, 29 Apr 1956, Størmer s.n. (0); Mörkvatnet ved Store Milde, 29 Jun 1946, Størmer s.n. (0). Fitjar: Levaag, 21 Jun 1946, Størmer s.n. (0); Kalvanes, 18 & 20 Jun 1946, Størmer s.n. (0); Sörfonno, 17 Jun 1946, Størmer s.n. (0); Tveitafiell, Vik, 19 Jun 1946, Størmer s.n. (0); SE of Gloppavatnet, 21 Jun 1946, Størmer s.n. (o). Fjell: Apalvag ved Selskingstod, 4 May 1965, Størmer s.n. (0); Algeröy, 24 Apr 1961, Bödtker s.n. (0). Fusa: Kirkebygda, 11 Jun 1962, Bödtker s.n. (o). Granvin: Eide, 4 Aug 1943, Størmer s.n. (0); Röynstrand, 21 Aug 1943, Størmer s.n. (0); Eide i Graven, Apr 1885, Kiær s.n. (0). Herdla: Misje ost for Turoy, 24 May 1964, Bödtker s.n. (0). Jondal: östenfor Berge, 20 Aug 1943, Størmer s.n. (0). Kinsarvik: Rauberg, 25 May 1954, Gjaerum s.n. (0); Indre Kvalvik - Alsaker, 22 Apr 1954, Gjaerum s.n. (0). Kvam: Aksnes, 20 Aug 1943, Størmer s.n. (0). Kvinnherad: Beinaviki, 11 Aug 1943, Størmer s.n. (0); Haaland, 7 Aug 1943, Størmer s.n. (0). Lindås: Bögeskoven, 21 Sep 1876, Wulfsberg s.n. (s); Bögevalden, 2 Sep 1876, Wulfsberg s.n. (0, s). Moster: Siggjarvag, ved Stokka, 18 Aug 1967, Størmer s.n. (0); Mosterhamn, 18 Jun 1936, Størmer s.n. (0). Odda: Odda, Jul 1883, Möller s.n. (o). Os: Lii, 29 Apr 1956, Størmer s.n. (o); between Tveit and Lii, 29 Apr 1956, Størmer s.n. (0); Mosunken, 31 Aug 1930, Kotilainen s.n. (H). S. Bergenhus: Sunde i Kvinhered, 19 Aug 1873, Wulfsberg s.n. (0, s); Haus, 17 Jul 1885, Kiær s.n. (0, s). Stord Island: Jekteviki, 11 Aug 1967, Størmer s.n. (0); Bardveitdalen, Nyholm 67/130 (ALTA, CANM, KRAM, PRC, S); Borgtveit, Holmen 177 (DUKE). Sund: Bukken, 29 Apr 1956, Størmer s.n. (0); Telavaag, 24 Jun 1950, Størmer s.n. (0); Leröy, 23 Jun 1950, Størmer s.n. (0); Store Brattholmen, 26 Jun 1946, Størmer s.n. (0). Sveio: Byrkjeland, 3 Aug 1969, Størmer s.n. (0). Tysnes: Tysnäs, 1873, Hartman s.n. (S). Ullensvang: Gamleheimen, 9 Apr 1954, Gjaerum s.n. (o). Valestrand: Einstapavoll, 21 Aug 1967, Størmer s.n. (0); Valevag, 21 Aug 1967, Størmer s.n. (0). Varaldsöy: Mundheim, 15 Aug 1943, Størmer s.n. (0). MÖRE OG ROMSDAL. Averøy: Nordmøre, Averö, Jun 1867, Kiær s.n. (o, s). Fræna: Talstadhesten, ca 110 m, 11 Apr 1965, Malme s.n. (0); Lindset, 21 Jul 1966, Malme s.n. (0); Ersholmen naer Bud, 8 Aug 1971, Størmer s.n. (o). Midsund: Dryna paa Midøya, 12 Aug 1872, Blytt s.n. (s). Molde: ved Torhus paa Bolsoya, 3 Aug 1971, Størmer s.n. (0); Vestnes, Frosta ved Tomra, 9 Aug 1971, Størmer s.n. (0); Kvam vestenfor Molde, 27 Jul 1869, Kiær s.n. (0). Nordmøre: Averö, Jun 1867, Kiær s.n. (s). Rauma: Grytten, nära Aandalsnäs, Aug 1907, Buch s.n. (H); Veblungsnæes, 30 Jul 1869, Kiær s.n. (O); Romsdalen nära Aandalsnaes, Aug 1907, Buch s.n. (H). Söndmöre: Sunelven, 24 Jul 1869, Kiær s.n. (0). Stangvik: Kvanne, 12 Apr 1960, Mehl s.n. (0). NORD-TRÖNDELAG. Aasen, 200 m, 9 Aug 1910, Hagen s.n. (0); Otteröya, 1824, Blytt s.n. (0). NORDLAND. Lofoten, Austvågřy, 18 Aug 1953, Arnell 21 (s); Meloy, Ornes, 6 Jul 1952, Kierulf s.n. (o); Ballangen, 29 July 1925, Kotilainen s.n. (H). OPPLAND. Gjøvik: Skonhovdhøgdas nordhelling, 29 Jul 1978, Størmer s.n. (0). ÖSTFOLD. Idd: Boltjern ved Holmen, 4 Jul 1953, Størmer s.n. (0); Holmen vest for Prestebakke, 3 Jul 1953, Størmer s.n. (0); Klo N of Berby, 14 Jul 1953, Størmer s.n. (0); Glenne SW of Holmen, 7 Jul 1953, Størmer s.n. (0). Krageröen: Trolldalen, 30 May 1887, Hagen s.n. (ALTA, CANM, M, S). Onso: Tasse, 29 Apr 1886, Ryan s.n. (0); Saster, 10 May 1895, Ryan s. n. (0); Åle, 26 Apr 1888, Ryan s.n. (0). Råde: Aaven, 20 Jun 1963, Størmer s.n. (0); N Smålanene, Ovenoen i Raade, 2 Jul 1886, Hagen s.n. (O, S). Rodenes: ved Svarttjern, 12 Aug 1963, Størmer s.n. (O). Varteig: Grytedalen, E of Glaama, ca 300 m, 22 Aug 1982, Størmer s.n. (0); Dalen, 20 Jun 1977, Størmer s.n. (0). ROGALAND. Avaldsnis: Vaaga, Fosnaoy, 21 Jun 1939, Størmer s.n. (o). Bjerkreim: Vikesaa, 7 Jun 1951, Størmer s.n. (O, POZG); Baerland, 6 Jun 1951, Størmer s.n. (O); Store Svele, 8 Jun 1951, Størmer s.n. (0); Odlandsto, 28 Jul 1972, Størmer s.n. (0). Egersund: Varberg, 5 Jun 1951, Størmer s.n. (0); Egersund, 13 Sep 1939, Hadač s.n. (BRNM, O); ved Fajansefabrikken, 26 Jul 1972, Størmer s.n. (0). Eigersund: Rotveit, 1 Aug 1972, Størmer s.n. (0); Loyning paa Sore Eigeroy, 31 Jul 1972, Størmer s.n. (0). Hå: Nordre Ogna, 28 Jul 1972, Størmer s.n. (0). Heskestad: Gya, 11 Aug 1938, Størmer s.n. (0). Hetland: Ullenhang, 10 Mar 1952, Størmer s.n. (0). Hjelmeland: Vadla i Jösenfjorden, 9 Aug 1886, Kaalaas s.n. (o). Höle: Ims, 30 May 1948, Størmer s.n. (0). Hoyland: Gramstad - Stranden, 28 Apr 1958, Størmer s.n. (0); ved Stranden, 28 Apr 1958, Størmer s.n. (0). Randaberg: Vistnes, 11 Mar 1952, Størmer s.n. (0); Sande, 11 Mar 1952, Størmer s.n. (0). Sandnes: Höle, Trodal, ca 30 m, 14 Jun 1971, Hegewald 3426 (ALTA). Skåre: Solvang, 21 Jun 1939, Dahl & Hadač (0); Horingstad, 6 Aug 1912, Hagen s.n. (o). Skudenes: Langaker – Rulleviki, 4 Aug 1969, Størmer s.n. (0). Sokndal: Knubedal, 13 Jun 1951, Størmer s.n. (O, W); Eia, Ryvarden 7383 & 7385 (O); Skaraas, 10 Jun 1951, Størmer s.n. (0); between Nesvaag and Vatland, 12 Jun 1971, Størmer s.n. (0); Ymerstein, 10 Jun 1951, Størmer s.n. (0). Stavanger: Lyse, 22 Jul 1885, Kaalaas s.n. (o, s); Lyse, Ryfylke, 10 Jul 1893, Nyman s.n. (s); Lutsi, 4 Jun 1948, Størmer s.n. (0); Risfjell, 11 Jun 1948, Størmer s.n. (0); Udburfjeld, Fossan, 12 Jul 1885, Kaalaas s.n. (s); Öie i Lande, 18 Jul 1914, Kaalaas s.n. (s); Lande, 24 Jul 1914, Kaalaas s.n. (s); Skudenes, Lyse, 13 Aug 1912, Hagen s.n. (0); Skudenes, Kuviken, 10 Aug 1912, Hagen s.n. (0); Boku, Gdegaarden, 24 Aug 1912, Hagen s.n. (0); Boku, Bokufjeldet, 160 m, 25 Aug 1912, Hagen s.n. (0); Skjold, Skjoldeviken, 24 Jul 1912, Hagen s.n. (0); Skjold, Hvalaasen, 120 m, 23 Jul 1912, Hagen s.n. (0); Sande, i line ovenfor Söndenaa, 24 Jul 1914, Kaalaas s.n. (o, s). Suldal: Roaldkvam, 7 Apr 1960, Myren s.n. (o); Kvilldal, Aug 1945, Bakka s.n. (0). Strand: Idse, 31 May 1948, Størmer s.n. (0); Strand, NW of Nordvatn, Hedenäs B11958 (s). Torvastad: Bjorgjene, 6 Aug 1969, Størmer s.n. (0). SÖR-TRÖNDELAG. Hitra: Kvenvær, Hitra, 10 Oct 1936, Høeg s.n. (o). Namsos: Namsos, 3 Aug 1868, Holmgren s.n. (s). Trondheim: Ilsviken, 14 May 1888, Hagen s.n. (s); Ilsvikbergen, 14 May 1888, Hagen s.n. (o, s). SOGN OG FJORDANE. Askvoll: Værlandet, 15 Aug 1948, Moss s.n. (0). Davik: Förde, 24 Aug 1949, Størmer s.n. (0). Fjaler: Fjaler, Eikerolsheia, 3 Oct 1907, Landmark s.n. (0). Flora: Sørsiden av Svardalsvatnet, SE of Osen, 9 Jul 1973, Størmer s.n. (BR, O); Kinn, 5 Jul 1973, Størmer s.n. (O); Florø, Storåsen, 29 Jul 1871, Kiær s.n. (0); Svanö i Storaasen, 9 Aug 1871, Kiær s.n. (0). Førde: Førde, Sunde, 27 Aug 1948, Moss s.n. (0); Havstad i Førde, 28 Jul 1871, Kiær s.n. (0). Gloppen: Sandane, 26 Aug 1948, Moss s.n. (0). Høyanger: Laviksaata, 16 Jul 1867, N.W. s.n. (0). Kyrkjebö: Kyrkjeböneset-Ramsli-Haland, 27 Jul 1960, Kvamme & Wendelbo s.n. (0). Sogndal: Skredstol NE of Aroy, ca 250 m, 5 Aug 1970, Størmer s.n. (0); Barsnes, 4 Aug 1970, Størmer s.n. (0); Sogndal, 9 Jun 1951, Størmer s.n. (0). Sør Vågsøy: Seljenes, 19 Aug 1949, Størmer s.n. (0); Setenes, 18 Aug 1949, Størmer s.n. (0); Halsör, 22 Aug 1949, Størmer s.n. (0); Vage, 23 Aug 1949, Størmer s.n. (0); Oppedal, 19 Aug 1949, Størmer s.n. (0). Stryn: Visnes, 26 Aug 1949, Størmer s.n. (0). Vik: Vik i Sogn, 6 Aug 1898, Kaalaas s.n. (0). TELEMARK. Bamble: between Ese and Vinterdalen, 10 Jul 1955, Størmer s.n. (0). Drangedal: Skultrevannsaasens sydostre del mot Skultrevannet, 30 Aug 1977, Størmer s.n. (0). Eidanger: Håřya, 8 Jul 1955, Størmer s.n. (BCB, O). Gransherad: Nordstol, ca 750 m, 20 Aug 1942, Størmer s.n. (0). Kragerø: Kalstad kirkegaard i Kragero by, 9 Jun 1979, Størmer s.n. (0); between Levang and Vedalen near Portorhalvoya, 10 Jun 1979, Størmer s.n. (o); Berg gard NW of Kragero by, 9 Jun 1979, Størmer s.n. (0); Skaato, Krajso, 9 Jul 1894, Jørgensen s.n. (0). Kviteseid: Ulgedalsfjern, 20 Aug 1937, Størmer s.n. (0); Napper ved Vsaanum, 26 Jul 1936, Størmer s.n. (0). Mo: Nevestveit ved Bortevann, 450 m, 10 Jul 1956, Størmer s.n. (0). Sannidal: Tassdal, 27 Dec 1942, Johannes

s.n. (0). Seljord: Djuvlandsdjuvet, 22 Jul 1885, Esmark s.n. (0); Seljord, 15-16 Aug 1937, Størmer s.n. (0); Glosemo, 22 Jul 1936, Størmer s.n. (0). Skåtøy: Finsbudalen, 20 Jun 1937, Størmer s.n. (0); Kjelso paa Gomoya, 19 Jun 1958, Størmer s.n. (0). Solum: Rugla, 22 Jun 1949, Størmer s.n. (0); Spiredalen, 22 Jun 1949, Størmer s.n. (0). VEST-AGDER. Audnedal: Sør-Audnedal, Fossvatnet, 12 Jun 1954, Jørstad s.n. (0). Bakke: Strandeli, 9 Aug 1938, Størmer s.n. (0); nar Kirken, 11 Aug 1939, Størmer s.n. (0); Lindeli ved Sirdalsvann, 6 Aug 1938, Størmer s.n. (0). Feda: Feda, 18 July 1977, Størmer s.n. (0). Fjotland: Kvinlaug, 7 Aug 1939, Størmer s.n. (o). Flekkefjord: Gronsund ved Langevatnet, 20 Jul 1977, Størmer s.n. (0); between Ovstefjellsa and Langevatnet, 20 Jul 1977, Størmer s.n. (0); Hidra, between Veisdal and Langeland, 25 Jul 1977, Størmer s.n. (0); Ved Storedranga, 19 Jul 1977, Størmer s.n. (0); Flekkefjord, 26 Jul 1881, Kaalaas s.n. (o, s). Greipstad: Bertelsödegaard-Trobbevann, 11 Aug 1959, Størmer s.n. (COLO, O). Hagebostad: Tiugvatn, 15 Aug 1939, Størmer s.n. (o). Halse og Harkmark: Ikebuk, 26 Aug 1939, Størmer s.n. (0); Skjernoya, 24 Jun 1947, Størmer s.n. (0). Herad: Sande, 9 Aug 1954, Størmer s.n. (0); lia S. for Briseid, 9 Aug 1954, Størmer s.n. (O, TENN). Hidra: Abilsnes, 5 Aug 1939, Størmer s.n. (0); Ystebö, 15 Apr 1916, Thele s.n. (0); Ysteböbekken, 11 Jun 1951, Størmer s.n. (0). Holum: Grös vest for kirken, 22 Aug 1939, Størmer s.n. (0); Sodeland, 22 Aug 1939, Størmer s.n. (0). Kvinesdal: Liknes, 7 Aug 1939, Størmer s.n. (o). Laudal: Aaksad nar Manflavd, 24 Aug 1939, Størmer s.n. (0). Lista: Minde, 11 Aug 1954, Størmer s.n. (0); Straumsland, 3 Aug 1954, Størmer s.n. (O, PR); Udal, 12 Aug 1954, Størmer s.n. (0); Sigersvoll, 6 Aug 1954, Størmer s.n. (0); Helvig, 3 Aug 1954, Størmer s.n. (0). Lyngdal: Berge, 15 Aug 1939, Størmer s.n. (0); Mandal, 18 Aug 1939, Størmer s.n. (o). Nes: Fjellsaa, 5 Aug 1939, Størmer s.n. (0); Grönnes v. Flikkefjord, 13 Aug 1939, Størmer s.n. (0); Store Drange, 13 Aug 1939, Størmer s.n. (0). Oddernes: between Mosby and Mestad, 8 Aug 1959, Størmer s.n. (0); Gilsvannets, 12 Aug 1959, Størmer s.n. (0); Andoya, 15 Aug 1959, Størmer s.n. (0). Øvre Sirdal: Rauaa ved Tjorhom, 12 Aug 1938, Størmer s.n. (0). Øyslebø: Breland, 16 Aug 1959, Størmer s.n. (o). Sirdal: Tonstad, 5 Aug 1938, Størmer s. n. (0). Sögne: Ospedalen, 28 Jun 1947, Størmer s.n. (0); Try, Hegewald 3324 (ALTA, KRAM, O); Kapelloya, 23 Jun 1947, Størmer s.n. (O); Monsoya, 29 Jun 1947, Størmer s.n. (0); Strandstova v. Sondre Eig, 10 Aug 1959, Størmer s.n. (O); Lastad-Ålo, 14 Aug 1959, Størmer s.n. (O, WTU); Ålo-Dvalås, 14 Aug 1959, Størmer s.n. (O, US); Vige, 14 Aug 1959, Størmer s.n. (0); Höllen, 11 Jun 1918, Sørensen s.n. (0); Folkehogskulen, 22 Jun 1947, Størmer s.n. (o). Vennesla: Grovane, 23 May 1916, Størmer s.n. (0). TROMS. Tromsö: Kvalöy, Straumhella, 16 Aug 1967, Fagerstén s.n. (H). VESTFOLD. Barkevik: Torpvand, 6 Aug 1884, Kiær s.n. (S). Hedrum: ved Lågen nær veien fra Sandefiord, 18 May 1889, Jorgensen s. n. (0). Holmestrand: 1826, Blytt s.n. (0). Larvik: Larvik, 24 Jul 1884, Kiær s.n. (0); Farrisvand, 2 Jul 1884, Kiær s.n. (0). Sande: Mefjorden, 4 Oct 1891, Jorgensen s.n. (0); Dunsaasen E of Galleberg, 8 Sep 1949, Størmer s.n. (0); Mokollen nar Sandefjord, 5 Oct 1889, Jorgensen s.n. (0); Tangen ved Sandefjord, 12 Apr 1891, Jorgensen s.n. (0); bak Hjertuesparken, 2 Mar 1891, Jorgensen s.n. (0). Sandefjord: Sandar, Tønsberg Tønde, 19 Jun 1958, Størmer s.n. (0); Årøy, 26 & 28 Jun 1962, Størmer s.n. (0). Sem: Undrumsåsen, 22 Jun 1962, Størmer s.n. (0). Stokke: S of Brekke W of Melsom, 20 Jun 1962, Størmer s.n. (0); Gjennestadvan, 27 Jun 1962, Størmer s.n. (0). Svelvik: Berger, Jørstad 89 (0). Tjøme: Rød, 2 Jul 1977, Størmer s.n. (0); ved Nes gård på Hvasser, 3 Jul 1977, Størmer s.n. (0). Tjömö: Tjomo, Jun 1886, Kaurni s.n. (0).

POLAND. Beskid Mały: Ślemień, Przysłopek, 720 m, 7 Aug 1995, A.M. Stebel & A. Stebel 718/95 (KRAM). Beskid Śląski: Wisła, Czarna Wisełka, 30 Jun 1985, Jedrzeiko, Żarnowiec & Klama s.n. (ALTA, BR, JE, KRAM, M, POZG, PR, S) [Musci Mac. Mer. Pol. No. 209]; Potok Wolny, 900 m, Sep 1985, Uziębło s.n. (KRAM). Bieszczady Zachodnie: Wielka Rawka, Lisowski 92905 (KRAM) and 1280 m, 7 Aug 1956, Lisowski s.n. (BR, BRNM, CANM, KRAM, M, O, S) [Bryo. Pol. No. 260]; Kińczyk Bukowski, Lisowski 58391 (BR, KRAM); Wetlina, 24 Jun 1955, Lisowski s.n. (s); Terebowiec Valley, 1000-1025 m, 13 Jun 1993, Żarnowiec & Szymocha s.n. (KRAM). Góry Bialskie: Bielice, 780 m, 18 May 1959, Lisowski s.n. (ALTA, CANM, KRAM, M, O, S) [Bryo. Pol. No. 1160]. Góry Złote: Brusek, ca 900 m, 28 Aug 1988, Piszczek s.n. (KRAM). Góry Izerskie: Mt Łużec above Świeradów Zdrój, 800 m, 26 Sep 1981, Ochyra s.n. (ALTA, BR, CANM, JE, KRAM) [Musci Pol. Exs. No. 738]; Polana Izerska, sine dato, Limpricht s.n. (GJO, JE, KRAM, M, S, W) [Bryo. Siles. No. 314]. Karkonosze: Kamienna River, 490 m, 20 Sep 1968, Kola s.n. (KRAM); Wielki Śnieżny Kocioł, Lisowski 91103 (KRAM) and Fudali 249/2001

& 63/2001 (KRAM); Mały Staw, 1950, Czubiński s.n. (KRAM, POZG); Kamienica River above Szklarska Poręba, 800 m, 22 Sep 1968, Kola s.n. (KRAM); Wielki Staw, 2 Aug 1906, Krieger s.n. (JE); Gorzów, 1859, Unger s.n. (W). Masyw Ślęży: Sobótka, 27 Mar 1880, Schulze s.n. (GJO). Pogórze Śląskie: Bielsko-Biała, ca 700 m, Jul 1935, Graw s.n. (KRAM). Pojezierze Bytowskie: Bobolice, Nowosiółki, 2 Aug 1913, Hintze s.n. (KRAM); Kępno, Hintze 1103 (KRAM). Pojezierze Kartuskie: Mirachowo, 20 May 1937, Krawiec s.n. (KRAM) and Lisowski 512 (KRAM, S); Bukowo Paczeskie, Rusińska 1473 (KRAM). Tatry Wysokie: Roztoka, 28 Aug 1879, Chałubiński s.n. (KRAM) & 18 Aug 1880, Chałubiński s.n. (KRAM); Miedziane, 10 Sep 1880, Chałubiński s.n. (KRAM); Miedziane - slope from Dolina Pięciu Stawów, 10 Sep 1880, Chałubiński s.n. (KRAM); Rybie, 21 Aug 1879, Chałubiński s.n. (KRAM); Rybie - Roztoka, 18 Aug 1879, Chałubiński s.n. (KRAM); Morskie Oko, 22 Aug 1879, Chałubiński s.n. (KRAM); Rybie - Morskie, 21 Aug 1879, Chałubiński s.n. (KRAM); Roztoka Valley, Świstówka, 1600 m, Lisowski 92904 (KRAM). Wyżyna Krakowsko-Częstochowska: Olsztyn near Częstochowa, Jun 1861, Karo s.n. (KRAM).

PORTUGAL. Alto Alentejo: Portalegre, S. Mamede, 820-840 m, 3 Jun 1987, Sérgio, Brugués, Cros & Sim-Sim s.n. (LISU). Beira Alta: Serra da Estrela, 30 July 1878, sine collector (G) [Musci Lusit. No. 91]; Covăo da Ametade, 1500 m, 26 May 1993, Greven s.n. (BRNM, hb. Frahm, KRAM); supra S. Romao, 31 Jul 1878, sine collector (G) [Musci Lusit. No 113]; Ponte da Caniça e Buraco da Moura, 700-800 m, 25 Jan 1995, Sérgio, Brugués, & Cros s.n. (KRAM); Vale entre Cântaro Gordo e Cântaro Magro, ca 1850 m, Sérgio, Sim-Sim & Jansen 9859 (LISU); 6 km de Cedrim, estrada florestal de Arcas, St Adrião, Sérgio 1953 (LISU); pr. Arcozelo das Maias, zona florestal do Ladário, Sérgio 1182 (LISU). Beira Litoral: Mata de Bussaco, 420 m, 29 May 1930, Allorge s.n. (COLO, G) [Bryo. Iber. No 177]. Douro Litoral: Serra do Marão, S. Gonçalo, proximo da Pousada, Sérgio 9398 (LISU). Minho: entre Monção e Melgaço, Ponte de Mouro, Sérgio 3092 (LISU); Serra da Penêda-Gerês, Arcos de Valdevez, Mesio, 640 m. Sérgio & Schumacker 5149 (LISU): Serra da Gerêes, 1 km de Alles gario, estrada pase a Geisa Romana, 650 m, Sérgio & Schumacker 9381 (LISU); Gerês, entre Malhadoura e Sobreiral da Ermida, ca 700 m, Sérgio 4003 (LISU); Arcos de Valdevez, Soajo, Mata do Ramiscal, junto á nascente do Vez, 1200 m, Sérgio 4175 (LISU); Moledo do Minho, Azevedo, 200 m, Séneca & Sérgio 296 (KRAM) & 302 (LISU); Serra de Góis, Lanhelas, 300 m, Séneca & Sérgio 309 (LISU). Trás-os-Montes e Alto Douro: Pitőes das Junias, próximo do Convento, ca 1100 m, Sérgio 11062 (LISU); Vila Real, Quedas d'água do Poio, Sep 1923, Ervid s.n. (G); Vila Real, Santuario de Nta. Señora de Gracia, pr. Mondim do Basto, ca 600 m, 21 Aug 1990, Muñoz s.n. (hb. Frahm).

ROMANIA. Județ Brașov: Fagărăş Mountains, Cârtișoara towards Bilea, 1200 m, Boros 2870 (BCB, BP, BR, S), 1250 m, 19 Jul 1963, Boros s.n. (PC) and 1400–1550 m, 20 Jul 1963, Boros s.n. (BP); Podragul, 13 Aug 1966, Vajda s.n. (BP, BR, S). Județ Cibin: Paltiniş, ca 1400 m, 2 Jul 1968, Vajda s.n. (BP) and 1600 m, 2 Jul 1968, Boros s.n. (BP). Județ Cluj: Bihor Mountains, Răcătău, Someşul-Rece, ca 700 m, 27 Sep 1962, Boros s.n. (BP); Tranişu, 600 m, 5 Jul 1963, Boros s.n. (BP); V. Drăganului and Vişagu, ca 600 m, 6 Oct 1941, Boros s.n. (BP); Drăgan valley near Poieni, 5 Jul 1963, Vajda s.n. (BP). Județ Huedin: Retezat Mountains, Râu Marevalley near Gura-Râului, 900 m, 10 Jul 1963, Boros s.n. (BP). Județ Maramures: Marmaros Mountains, Nieguiescu valley near Borşa, 900–1500 m, 26 Jul 1963, Boros s.n. (BP).

RUSSIA. *Caucasus*: Krasnodar Territory, Adler Region, 6 km of Krasnaja Poliana, Aibga Mt, 25 km E of Sochi, *Rasmonov 29* (LE, KRAM). *Gulf of Finland*: Gogland Island, 19 Jun 1867, *Lindberg s.n.* (s). *Karachaevo-Cherkessia*: Teberda State Reserve, Buulgen Gorge, 28 Aug 1997, *Onipchenko s.n.* (KRAM, MW); Northern Klukhor Gorge, Buulgen Ridge, 11 Sep 1994, *Onipchenko s.n.* (KRAM, MW); Kłuchori, Dombaj, *Tumadjanov 18* (LE). *Urals*: Bashkortostan, Beloretzk Distr., 7 km E of Zuyakovo, 22 Jul 1995, *Baisheva s.n.* (KRAM, MW).

SERBIA-MONTENEGRO. *Serbia*: Golija Biosphera Reserve, at Orlov kamen between Bele Vode and Kumanica, 950 m, 10 Jul 2003, *Papp s.n.* (BP).

SLOVAKIA. Bielské Tatry: Votrubova chata, ca 1700 m, 17 Jul 1937, Šmarda s.n. (BRNM). Kralovany, Jul 1936, Šmarda s.n. (BRNM). Kremnické Pohorie: Biely stream, S of Ihráč, ca 625 m, 23 Jun 1976, Doležal s.n. (BRNM). Liptovské Hole: Ráčkova dolina near Pribilina, 1000–1100 m, 16 Sep 1962, Boros s.n. (BP). Malá Fatra: Starhrad near Strečno, ca 450 m, Apr 1936, Pilous s.n. (BRNM) [Crypt. Čech. Exs. No. 291] and ca 500 m, Jul 1935, Pilous s.n. (BRNM, US, W) [Musci Čech. Exs. No. 90]; Nezbudská Lúčka near Starhrad, ca 400 m, Aug 1947, Pilous s.n. (ALTA, CANM, DUKE, UC); Bystričky valley, ca 600 m, 10 Jul 1951, Šmarda s.n. (BRNM). **Roháče**: between the Chochołowska and Pod Zubercom Valleys, 11 Jul 1880, Chalubiński s.n. (KRAM). **Slovenské Rudohorie**: Detva, Poľana, 1450 m, 28 Sep 1954, Šmarda s.n. (BRNM). Vihorlat: Mt. Sninský Kameň, 1000 m, Kučerová CS 109 (PRC), 21 Jun 1978, Váňa s.n. (PRC) and 17 Jun 1959, Kuc s.n. (KRAM). Vysoké Tatry: Velká Studená dolina, ca 1600 m, 10 Sep 1955, Šmarda s.n. (BRNM); Velická dolina, ca 1680 m, 9 Aug 1954, Šmarda s.n. (BRNM); Kriváň, Bystrica, Nyárády & Gyüla 62 (BP).

SLOVENIA. Lobnica near Maribor, 17 Sep 1910, *Glowacki s.n.* (GZU) and 29 Apr 1876, *Breidler s.n.* (GJO); St. Lorenzen near Maribor, *Salzmann 3014B & 3014C* (GZU); Oplotnica, 21 Nov 1897, *Glowacki s.n.* (GJO); Gornji Grad, 13 Aug 1898, *Glowacki s.n.* (GJO) and 450 m, 27 Apr 1888, *Breidler s.n.* (GJO); "Schokatgraben" near Gornji Grad, 550 m, 5 May 1882, *Breidler s.n.* (GJO); Ruše, Sep 1900 and 14 & 17 Sep 1910, *Glowacki s.n.* (GJO); Praprotno, 2 Nov 1907, *Glowacki s.n.* (GJO).

SPAIN. Álava: Sarria, rio Larreakorta, ca 730 m, Heras 84/85 (VIT), ca 738 m, 29 Mar 1986, Heras s.n. (hb. Frahm), Heras 471/86 (VIT) and 780 m, Heras 1415/85 (VIT); Larreakorta, 900 m, Heras 1735/85 (VIT). Asturias: (Ponga) Beleño, 600 m, 1970, Muñoz 6772 (hb. Frahm) and 5 Sep 1980, Casas s.n. (BCB); Pto. Ventana (Teberga), 1300 m, 3 Jun 1993, Ordoňez s.n. (hb. Frahm); Río Orio between El-Pontigon and Brieres, Sollman 66-701 (BCB). Burgos: Espinosa de los Monteros, Pico de la Miel, 1500 m, Infante 680/88 (VIT). Cáceres: Garganta de Santa Lucia, 600 m, 19 Mar 1983, Viera s.n. (MA); Garganta de Santa Lucia, Las Villuercas, 7 Feb 1982, Viera s.n. (MA). Coruña: (Capela) Caaveiro, ca 100 m, 5 Feb 1981, Reinoso s.n. (hb. Frahm); La Coruna Monfero, Fraga de Caaveiro, 20 m, 2 Sep 1987, Geissler s.n. (G). Lugo: Serra de Xistral, Coto da Cal, 580 m, 22 Sep 1995, Casas, Sérgio & Brugués s.n. (BCB). Gipúzcoa: La Haya sur Irun, Jul 1933, Allorge s.n. (PC); Pasajes, Jaizkibel, 100 m, Heras 338/93 (VIT); Oyarzun, Pto. Bianditz, 710 m, Heras 1151/93 (VIT) and Infante 1230/93 (VIT). León: (Boca de Huérgano), vega de Tarua, ca 1600 m, Muñoz 6190A (hb. Frahm); Branuelas, ca 1100 m, 9 Jun 1927, Allorge s.n. (PC); Pinar de Lillo, 18 Apr 1971, Izco & Carbó s.n. (BCB). Lérida: (Vall d'Arán) Bossost, ca 1100 m, 10 Jul 1966, Casas s.n. (hb. Frahm); Val d'Aran, Valarties, pujant a era Restanca, 1750 m and 2008 m, 14 Jul 1998, Brugués et al s.n. (BCB); (Vall Ferrera) Le Farga, ca 1500 m, 5 Nov 1981, Casas s.n. (ALTA, BRNM, hb. Frahm) & 227 (PAMP); Vall Ferrera, 5 Sep 1981 and 6 March 1992, Casas s.n. (BCB); Vall de S. Nicolau, 1800 m, 2 Jul 1959, Casas s.n. (BCB, BRNM); Vall de S. Nicolau, la Ermita del S. Esperit, 1800 m, 2 Jul 1959, Casas s.n. (o); Bossost, 9 Jul 1966, Casas s.n. (BCB, KRAM, PAMP); Bossost, Patielló, 10 Jul 1966, Casas s.n. (BCB); Valle de Colomers (Valle de Aran), 8 Jul 1966, Casas s.n. (BCB); Benasc.-La Renclusa- (Alta Ribagorça), 2000 m, 10 Oct 1981, Casas s.n. (BCB). Orense: Parque do Xurés, Rio Caldo subiendo a la Portela do Home, 530 m, sine dato, Casas, Sérgio & Brugués s.n. (BCB). Navarra: Lanz, 27 Nov 1980, Ederra s.n. (PAMP); Lakora, 800 m, 10 June 1983, Ederra s.n. (PAMP). Pontevedra: Monte de la Fracha, ca 500 m, 26 Aug 1990, Muñoz s.n. (hb. Frahm); Poyo, Luisier 73.1 (hb. Frahm); Loureza, 16 Aug 1930, Buch s.n. (H); Río Lerez, 9 Aug 1930, Buch s.n. (H). Vizcaya: Sarría, Peña Arralde, 950 m, Heras 1429/85 (VIT); Murua, Barranco Errekaseku, Hayedos, 830 m, Heras 1282/86 (VIT); Marquina, Barranco Ugalde, 800-950 m, Heras 615/86 (VIT).

SWEDEN, ÅNGERMANLAND, Härnösond: Härnön, Siöviken, 6 Dec 1944, Tuomikoski s.n. (s). BLEKINGE. Asarum: Rubens backe, 10 Nov 1917 Medelius s.n. (s); Sandvik, 26 Jun 1923, Medelius s.n. (s); Stenbackaskogen, 9 Mar 1918, Medelius s.n. (BR, G, S). Backaryd: Kläafben, 14 Jun 1948, Uggla s.n. (s). Hällaryd: Hällaryd, 21 Mar 1918, Medelius s.n. (s). Jämshög: Röan klippväg, 22 Mar 1920, Medelius s.n. (s); Hasslehult, 29 May 1923, Medelius s.n. (s). Lösen: Verkön, 29 Jul 1928, Florin s.n. (s). Ronneby: Djupadal, 8 Aug 1921, Medelius s.n. (s). Bo-HUSLÄN. Backa: Hökälla, 550 m, 16 Oct 1921, Johansson s.n. (s); Grindbo, 23 Dec 1900, Hjärne s.n. (H, S). Fiskebäckskil: Fiskebäckskil, 24 Jul 1911, Møller s.n. (s). Harestad: Heden, 30 Sep 1922, Stenholm s.n. (s). Hjärtum: Lödderstorp, Jul 1926, Kjellberg s.n. (s); Hjärtum, Jul 1925, Kjellberg s.n. (s). Hogdal: Svinesund, 18 Jul 1881 Grönvall s.n. (s). Högås: Tånga, 14 Jan 1925, Palmer s.n. (s). Jörlanda: Källsby, 1 Oct 1926, Stenholm s.n. (s). Klövedal: Valsäng, Selling 202 (s). Kville: Fjällbacka, Hvalö, 1 Jul 1922, Møller s.n. (H, S); Trättlanda, 1878, Thedenius s.n. (s). Läve: Hisingen, Hökälla, 22 Apr 1922, Stenholm s.n. (s). Ljung: Ljungskile, 8 Jul 1922, Åberg s.n. (s) and 31 Mar 1935, Krusenstjerna s.n. (s); Berg, 8 Jul 1922, Åberg s.n. (s); Lyckorna, Jul 1899, Bågenholm s.n. (s); Ulvesund, 19 May 1935, Krusenstjerna s.n. (s). Lycke: Klöverön, 4 Jun 1922, Stenholm s.n. (s). Lyse: Alsbäck, 10 Jul 1911, Møller s.n. (H, KRAM, POZG, S); St. Kornö, 30 Jul 1911, Møller s.n. (H, S). Morlanda: Skaftölandot, Lunnevik, 9 Jul 1911, Møller s.n. (S); Skaftölandot, Gåsö, 6 Jul 1911, Møller s.n. (CANM, S); Skaftön, Jun 1895, Jäderholm s.n. (s). Öddö: vid Tofterna, 3 Aug 1913, Larsson s.n. (s). Romelanda: Aleklätten, 12 Aug 1924, Johansson s.n. (s). Rödbo: am Vedbacka, 16 Aug 1924, Johansson s.n. (s). Rönnäng: N of Rönnängs hamn, 21 Sep 1945, Selling s.n. (s). Stenkyrka: vid Fagrefjäll, Selling 210 & 211 (s); Röra, Selling 78 (s); S of Krosse Kärr, 18 Sep 1945, Selling s.n. (s); Rösselvik V-sidan, 27 Sep 1945, Selling s.n. (s); Budalen (W of Djupvik), Selling 207 (s); Skärhamn, Selling 221 (s); Kållekårr, Selling 213 (s). Svarteborg: Steneked, Helsing 390 (s). Tanum: Grebberstad, 27 Jul 1939, Hülphers s.n. (s); Hede, 1878, Thedenius s.n. (s); Tanum, Oct 1879, Thedenius s.n. (s). Tjärnö: Rossön, Jun 1959, Erikson s.n. (s). Valla: Tönsäng, Selling 232 (s). ORUST ISLAND. Röra, Henån, 20 Jun 1930, Stenholm s.n. (s); Myckleby, Stillingsö, 16 Jul 1929, Stenholm s.n. (US, WTU). MARSTRAND ISLAND. Rosenlund, Koön, Jul 1889, Arvén s.n. (s). DALSLAND. Amåls: Korsbyn berg nära Barkerudssika, 26 May 1916, Larsson s.n. (s); Åmål, 26 Sep 1918, Tärnlund s.n. (s). Ånimskogs: Yttre Bodane, 2 Aug 1926, Larsson s.n. (s). Bäcke: Ödelepe, 21 Jun 1914, Bergström s.n. (s); Kårud, 7 Jun 1914, Bergström s.n. (s); Björtveten, 12 May 1913, Bergström s.n. (s); Kilevass, 5 Jul 1914, Larsson s.n. (s); Hjulserud, 29 Jun 1919, Bergström s.n. (s). Bolstad: Kvantensburg, 16 Jun 1920, Larsson s.n. (s). Dals-Ed: Bälsäs, 5 Sep 1932, Stenholm s.n. (DUKE). Dalskog: Teåker, 18 Jun 1910, Bergström s.n. (s); Båsane, 3 Jun 1928, Bergström s.n. (s); Edsleskog: Grättve, på Hafsåsen, 24 Aug 1913, Larsson s.n. (s); Kyrckohordebostället, på Gyllsberget, 18 Jul 1913, Larsson s.n. (s); Kyrkoherdebostället, på Presterndshöjden, 1 Jul 1915, Larsson s.n. (s); Kyrkoherdebostället, på Kenäsberget, 10 Sep 1915, Larsson s.n. (s); Bräcke, 6 May 1915, Larsson s.n. (s); Bergane, 24 Aug 1926, Larsson s.n. (s). Fargelanda: Norra Spångerud, 27 Aug 1916, Bergström s.n. (s). Fröskog: Hafsås, 11 Mar 1825, Hardin s.n. (s). Gunnarsnäs: Backa, 20 Sep 1914, Larsson s.n. (s). Holm: Framnås, 20 Jul 1919, Bergström s.n. (s); Framnås, Naren, 20 Jul 1919, Larsson s.n. (s). Järbo: Stora Bön, 19 Apr 1914, Bergström s.n. (s); Runsäter, 19 Apr 1914, Bergström s.n. (s). Laxarby: Heden, Kushålet, 16 Jul 1922, Larsson s.n. (s). Mo: Öjersbyn, 15 Sep 1916, Larsson s.n. (s); Vassbotten, Stockviken, 15 Jun 1922, Larsson s. n. (s). Nässemark: Rärbiken, 14 Aug 1932, Bergström s.n. (s). Ödsköld: Vången, 24 May 1915, Larsson s.n. (s). Rålanda: Tvållestad, 26 Sep 1927, Åberg s.n. (DUKE, S). Stensby: Jepplanda, 1 Jun 1914, Bergström s.n. (s); Jepplandaberget, 1 Jun 1914, Larsson s.n. (s). Valbo-Ryr: Vågsäter, 22 Aug 1927, Bergström s.n. (s). Varvik: Kråkviken, 24 Jun 1930, Bergström s.n. (s). DALARNA. Hedemora: Nås, Sep 1879, Indebton s.n. (s). Stora Tuna: Idkerbergs klack, 23 Apr 1927, Johansson s.n. (s). HAL-LAND. Älvsåker: Dala, 19 Jun 1923, Stenholm s.n. (s). Fagered: Lya, 9 Jul 1922, Stenholm s.n. (s). Fjärås: Eskebacka, 24 Jun 1922, Stenholm s.n. (s). Frillesås: Kyrketorp, 31 May 1922, Stenholm s.n. (s). Fröllinge: Getinge, Hovgard 726 (s). Gallared: Bresilt, 4 Jul 1923, Stenholm s.n. (s). Gunnarp: Esered, 2 Jul 1923, Stenholm s.n. (s). Lindome: Skeggared, 18 Apr 1922, Stenholm s.n. (s). Ölmevalla: Åsa, 29 May 1922, Stenholm s.n. (s). Simlangsdalen: Brunnshult, 21 Oct 1966, Holmen s.n. (H, PR). Slättåkra: Oskarström, 18 Jun 1923, Florin s.n. (KRAM, S); Lya, 7 Sep 1920, Medelius s.n. (s). Stråvalla: Läptakoro, 1 Nov 1922, Stenholm s.n. (s). Tölö: Höglunda, 12 Jun 1922, Stenholm s.n. (s). Ullared: Ullared, 17 Jul 1935, Hovgard s.n. (s). Veddige: Jonsjö, 30 May 1923, Stenholm s.n. (s). Hälsingland. Skog: Hemstanäs, 1849, Hartman s.n. (s). JÄMTLAND. Sundsjö: Vårsjöberged, 2 Jul 1941, Österlind s.n. (s). NÄRKE. Askersund: ca 1.5 km SE of Fagertärn, 5 Jul 1986, Hakelier s.n. (s). Hallsberg: Skålaklint, 21 Jun 1869, Hartman s.n. (s). Hammar: Mörssäter, 4 Jul 1874, Hartman s.n. (s). Hidinge: Lunnasjön, 16 May 1932, Waldheim s.n. (s). Kil: Ullaviklint, 1890, Jäderholm s.n. (s) and 24 Aug 1930, Waldheim s.n. (s); Stakadammama, 17 Jul 1933, Waldheim s.n. (s); Trolldalen, 6 Mar 1932, Waldheim s.n. (s). Lerbäck: Gropdalen, Jun 1870, Hartman s.n. (s). Svennevad: Skurkuget vid Skagaholm, 1870, Hartman s.n. (s); Sjölunda, Aug 1869, Hartman s.n. (BR, s); Skagaholm, Skeppkatta, 31 Jul 1869, Hartman s.n. (s). Tysslinge: Filipshyttan, 29 Jul 1965, Hakelier s.n. (s); Falkasjon, Falkaberget, 5 Jun 1900, Waldheim s.n. (s). Viby: Sumphallen, Jul 1853, Zetterstedt s.n. (s); Tystingsbörget, 28 Aug 1874, Hartman s.n. (ALTA, S); Tystingsbergen, Zetterstedt 72 (s). ÖSTERGÖTLAND. Blåviks: Lycköhål, 22 Jul 1933,

Florin s.n. (s). Kville: Gransjön vid Torsbag, 24 Jul 1878, Olsson s.n. (s). Kvillinge: Ågelsjö, 20 July 1922, Westerberg s.n. (s). Motala: Hålberget, 1842, Holmgren s.n. (s); Lemunda, Jul 1863, Holmgren s.n. (s). Regna: Regna, 28 Jun 1896, Nyman s.n. (s). Sund: Ydre, 5 Jul 1882, Arnell s.n. (s). Västra Ny: Gopö, sine dato, Holmgren s.n. (s). SKÅNE. Billinge: Bögerup, 10 Jul 1886, Grönvall s.n. (H, S). Bosjökloster: Bosjökloster, Sep 1864, Berggren s.n. (DUKE, S). Hästveda: Hallasnärje par. Hästveda, 27 May 1918, Hasslow s.n. (s, w). Höör: Höör, 15 May 1891, Møller s.n. (s) & Ahlfvengren s.n. (s) & 15 March 1885, Björling s.n. (s). Konga: Kongaö par Konga, 25 May 1926, Hovgard s.n. (s); Klofveröd, 1893, Alvthin s.n. (s). Sönnarslöv: Vastra, 8 Jun 1899, Alvthin s.n. (s). Stenestad: Klöfvahallar, 8 Jun 1899, Alvthin s.n. (s) and 13 Nov 1916, Medelius s.n. (s). Osby: Sibtorp, 12 Jul 1933, Tufvesson s.n. (s). Vånga: Bögesta Sågmölla o. Västervik, 30 Oct 1934, Halle s.n. (s). SÖDERMAN-LAND. Botkyrka: W of Tullngeberg, 24 Apr 1990, Hedenäs s.n. (s). Dalarö: Smådalarö, 16 Jul 1918, Westerberg s.n. (H, S). Grödinge: 1 km N of Kagghamra, 29 Sep 1954, Arnell & Persson s.n. (s). Helgona: Alla Helgona, Bönsta, 28 Jul 1915, Arnell s.n. (s). Huddinge: Balingsta, 30 May 1899, Arvén s.n. (H, KRAM, S); Vårbydalen, Gömmaren, Krusenstjerna 102 (s); Skrovensborg, Krusenstjerna 99 (s). Mörkö: Gustavsberg, 20 Jul 1985, Hedenäs s.n. (s). Nacka: Nacka, 15 Jun 1925, Møller s.n. (H, S); Nyckelviken, 1853, Lindberg s.n. (S); Saltsjö-Duvnäs, 15 Aug 1933, Tärnlund s.n. (s); Saltsjö-Duvnäs, 15 Aug 1933, Tärnlund s.n. (DUKE). Nynäshamn: Bedarö, Aug 1885, Forsell s.n. (s). Ornö: Kvarnö, Krusenstjerna 21 (s); Hässelmara, Hedenäs B11957 (s). Ösmo: Lund, Krusenstjerna 32 (s); Vinsberget, 11 Oct 1943, Halle s.n. (s). Östertälje: Vretaberg, 4 Jun 1961, Krusenstierna s.n. (s), Sorunda: Tärnan, 24 Jun 1929, Florin s.n. (CANM, S). Stockholm: between Finnboda and Soindersvik, 17 Aug 1937, Tärnlund s.n. (KRAM, S, WTU); Dalarö, Jul 1870, Holmgren s.n. (s); near Stockholm), Sillén (w) [Musci Frond. Scand Exs. No. 226]. Tyresö: Dyvik, 24 May 1942, Persson s.n. (s); Björndalen, 24 May 1942, Persson s.n. (s); Angnöo, 1878, Forsell (s); Långsjöns, 8 Oct 1933, Florin s.n. (s). Västerhaninge: Vitså, 9 Oct 1927, Florin s.n. (H, s); Presttorp, 22 Sep 1929, Florin s.n. (s). SMÅLAND. Almesåkra: Klintsaberg, 31 Jul 1865, Zetterstedt s.n. (s). Algutsboda: 1874, Scheutz s.n. (s). Åsenhöga: Granstöorp, 25 Jul 1959, Christoffersson s.n. (s). Femsjö: Hägnen, Aug 1859, Blomberg s.n. (s); Femsjö, 21 Sep 1924, Myrin s.n. (S). Gränna: Mogata, 6 Jul 1911, Arvén s.n. (BR, M, S). Hult: Skurugeta, 1869, Schenk s.n. (s); Hesslås dam, 11 Sep 1941, Larsson s. n. (s). Säaby: Gransbo, 27 May 1913, Persson s.n. (s). VÄRMLAND. Älga: Bergsklätten, Fransson 85/114 (s). Alster: Långenäs, 24 Aug 1926, Johansson s.n. (s). Arvika: Rackstadberget, Fransson 1988/137 (s); Djupdalshöjden, Fransson 1986/242 (s). Boda: Ronsnipan, 13 Aug 1923, Johansson s.n. (s); Valfjälet, S of Bärsbol, Fransson 1988/491 (s). Ed: SW of Segoltan, 10 Sep 1923, Johansson s.n. (s). Frykerud: Saxebyn, 3 Sep 1928, Johansson s.n. (s). Fryksände: Svenneby, Korpberg, Fransson 1986/527 (s). Gillberga: Gårdsjö, 29 Jun 1881, Kindberg s.n. (s). Glava: Sarvtjärns, Fransson 1987/311 (s). Gräsmark: Sandnäs, 21 Sep 1923, Åberg s.n. (s); Blabarskullen, 350 m, 18 Sep 1923, Åberg s.n. (s). Grava: Gråssbolstorp, 6 Aug 1926, Johansson s.n. (s); Klippväyg i Hjerpetansberget, 22 May 1926, Johansson s.n. (s). Grums: Malsjö, 31 Aug 1923, Johansson s.n. (s); Gullsjö, 24 Aug 1923, Johansson s.n. (s). Gunnarskog: Osmtjärsushöjden vid Vatterud, Fransson 1991/205 (s). Järnskog: Kronefjället, Fransson 1988/252 (s). Kil: Gunnita by, 19 Sep 1927, Johansson s.n. (s); Nilsby, 8 Aug 1927, Johansson s.n. (S); Kils Kyrka, 6 Aug 1923, Johansson s.n. (DUKE, S). Köla: Hugnsåsens nv. sida, Fransson 1987/661 (s). Kroppa: Gammelkroppa, 27 Jun 1920, Møller s.n. (H, S). Långserud: Ned. Kålsäter, Fransson 1989/165b (s). Nedre Ullerud: Karlshof, 8 Jul 1927, Johansson s.n. (s); Tjusbol, 16 Aug 1926, Johansson s.n. (s); Dömk, 2 Sep 1926, Johansson s.n. (s); Dömk, 25 Aug 1926, Johansson s.n. (s). Nor & Segerstad: Ranviken, 17 Sep 1926, Johansson s.n. (s). Östervallskog: Trångstad och Karlsman, Fransson 1985/500 (s). Segerstad: Ranvikens gard, 20 Oct 1926, Johansson s.n. (s). Skillingmark: Edstjarnet, Bryelsegrottorna, Fransson 1989/228 (s). Stavnäs: Hammarklätter vid Stömne, Fransson 1983/267 (s). Sunne: Maggeby, 22 Jul 1923, Åberg s.n. (s); Åneberg, 7 Oct 1922, Åberg s.n. (s); Tossebergstad, 300 m, 10 Sep 1922, Åberg s.n. (s); Snipan W of Gardsjön, Fransson 1989/173 (s). VÄSTERGÖTLAND. Alingsas Hareklätten, 24 Jun 1911, Møller s.n. (s). Angered: Agnesberg, 16 Mar 1918, Stenholm s.n. (s). Askim: Hovås, 19 Mar 1923, Stenholm s.n. (s). *Älvsered*: Toppered, 5 Jul 1922, Stenholm s.n. (s), **Backa**: Hisingen, 22 Apr 1922, Stenholm s.n. (s). Borås: Hultaberg, 31 Mar 1918, Söderberg s.n. (s). Eggby: Foxerna, Hunesträm, 22 Mar 1923, Stenholm s.n. (s).

Kestad: Kinnekulle, Zetterstedt 72 (s). Landvetter: Skallered, 11 Sep 1922, Johansson s.n. (s); Landvetter, 10 Mar 1918, Stenholm s.n. (s). Örgryte: Stora Selsjön, 17 Oct 1921, Johansson s.n. (KRAM); Stora Torp, 27 Sep 1903, Hjärne s.n. (s). Radä: Pixbo, 23 May 1922, Stenholm s.n. (s); Pixbo, 31 Mar 1918, Stenholm s.n. (JE, M, S); Mölulycke, 23 Mar 1918, Stenholm s.n. (s). Sandhem: Tunarp, 20 Jul 1887, Arnell s.n. (s). Sjötofta: Aggarp, 14 Sep 1923, Stenholm s.n. (s). Styrsö: Hallsvik, 1 Sep 1926, Stenholm s.n. (s). Svenljunga: Kvamsjön, 26 Jul 1946, Nyman s. n. (s). Tufve: Grimbo, 6 Mar 1922, Stenholm s.n. (s). Undenäs: Stenkällebergen, 15 Jul 1973, Silfversparre (s); Trehörningen, Stenkälla-reservatet, Krusenstjerna 195 (s). Utvängstorp: between Kyrkekvarn and Amurliden, 22 Aug 1929, Halle s.n. (POZG, S). Västra Frölunda: Önneröd, 10 Apr 1922, Stenholm s.n. (s); Torp, 14 Mar 1922, Stenholm s.n. (s). VÄSTMANLAND. Gorythyttans: Romkullen, 19 Jun 1961, Hakelier s.n. (s); Ormtorpberget, S of Mörttjärn, 27 May 1962, Hakelier s.n. (KRAM, S); Lampahöjden, 19 Jun 1961, Hakelier s.n. (S); St. Gällsjön (Skattjärnshöjden), 19 Jun 1961, Hakelier s.n. (s); Lönnhöjden, 27 Oct 1963, Hakelier s.n. (s). Hjulsjö: Kalklinten, 9 Jul 1960, Hakelier s.n. (s). Ljusnarsberg: Finnfall, Jämmerdalen, Koponen 10623 (H). Medåkers: Klöverhäll vid Hagby, 18 Sep 1933, Tärnlund s.n. (CANM, COLO, KRAM, s). Nora: Amboberget, 23 Apr 1961, Hakelier s.n. (s); Digerberget, 15 May 1961, Hakelier s.n. (s); Ekeberget, 19 May 1956, Hakelier s.n. (s). Vikers: Sibbosjön, 14 May 1961, Hakelier s.n. (s); Fagerbosjön, 14 May 1961, Hakelier s.n. (s). UPPLAND. Danderyd: Djursholm, Krusenstjerna 19 (s). Djurö: Harö, Jul 1920, Hülphers s.n. (s); Runö, 10 Jul 1932, Hülphers s.n. (s); Runmarö, Jul 1923, Hülphers s.n. (s). Gustavsberg: Skeviks klyfta, 17 Sep 1933, Florin s.n. (s). Hölö: Östervik, 9 Jul 1943, Hähnel s.n. (s). Ingarö: Vishamnsvik, 23 Aug 1942, Florin s.n. (s); Skalsmara by och Eknäs, 20 Sep 1942, Florin s.n. (s). Lidingö: Kyrkviken, 7 Jun 1928, Møller s.n. (s); Skärsätra, 7 Jun 1928, Møller s.n. (s). Ljusterö: Kornäs, 2 Sep 1928, Møller s.n. (DUKE, FH, KRAM, POZG, S). Lovö: Malmvik, 25 Oct 1942, Selling s.n. (s); Kjersön, 31 May 1942, Persson s.n. (s). Norrtälje: Svinskogen, 19 Apr 1932, Agelin s.n. (s). Österåkers: Svarttjärn, 8 July 1958, von Krusenstjerna 78 (s). Solna: Hagaparken, 5 Oct 1927, sine dato, Holmgren s.n. (s). Stockholm: Skansen, 15 Apr 1927, Tärnlund s.n. (s); Västan, 1 Oct 1927, Florin s. n. (s); Nackaasen vid Nackanas, 19 Sep 1926, Tärnlund s.n. (s); Djurgården, May 1846, Thedenius s.n. (0, s); Rosendal, Jun 1852, Lindberg s.n. (s); between Finnboda and Svindersvik, 17 Aug 1937, Tärnlund s.n. (CANM). Svennevad: Sjölunda, Aug 1869, Hartman s.n. (BR). Viby: Närke, Sumphallen, Jul 1855, Zetterstedt s.n. (KRAM); Viby, Jul 1855, Zetterstedt s.n. (DUKE); Lumphallen, Jul 1855, Zetterstedt s.n. (O).

SWITZERLAND. Bern: Guttannen, KW Handegg, 900 m, Maier 10574 (G) and 1300 m, Maier 10604 (G); Guttannen, 1360 m, Maier 10562 (G). Glarus: Stausee Garickti Rieselhang, 1630 m, Geissler 7267/2017 (G). Ticino: Tegna, Ponte Brolle, rocca Lungo la Maggia, 260 m, Geissler 11667 (G); Intragna, Casbozzei di Sotto, 370 m, Geissler 11052 (G); Intragna, Remagliaso, ca 360 m, Bisang 3525-26 (G); Tamaro, 1200 m, 7 Aug 1893, Conti s.n. (G); Mercoscia-Gorippo, 800 m, Keller 923 (G). Valais: Martigny, Finhaut, Lac d'Emosson, 1930 m, Lüth 3033 (hb. Lüth).

TURKEY. ANATOLIA. *Prov. Giresun*: Charshut between Fol et Eseli, Kisyl Ali Jalla, *ca* 1500–1600 m, *Handel-Mazzetti 718* (H, W). *Prov. Gumushane*: Ulugoba near Fol, *ca* 2000 m, *Handel-Mazzetti 679* (W); *Prov. Rize*: Kalopotomas Dere, Rize, 600 m, *Balls 1942* (E). *Prov. Trabzon*: Bakadjak S of Ordu, Kabak Deressi, *ca* 650 m, *Handel-Mazzetti 1079* (W); Ardeşen, Zil Kale castle, 700 m, 20 Jul 2001, *Papp s.n.* (BP).

UKRAINE. *Eastern Carpathians*: Černogora, Ivano-Frankovskaja Oblast, Nadvornjanskij Rajon, Mt. Pozizevskaja, 26 Sep 1963, *Uliczna s.n.* (KRAM); Zielona near Ivano-Frankivsk, 19 Aug 1886, *Wołoszczak s.n.* (KRAM).

MACARONESIA. AZORES. *Flores Island*: la Forcada prés Fazenda, 350 m, 12 Jul 1937, *Allorge s.n.* (CANM, COLO, F, MO) [*Bryo. Azor*: No 81].

CANARY ISLANDS. *Tenerife*: El Pijaral, NE of San Andrés, 800 m, *Holyoak 02-221* (hb. holyoak).

MADEIRA. Ribeiro Frio-Po do Suna, *ca* 900–1050 m, 9 Jul 1952, *Nobrega & Persson s.n.* (s); Pico Casado ou Parteiro, *ca* 1450 m, 7 May 1952, *Een & Persson s.n.* (ALTA, DUKE, s); between Encumeada and Caramujo, *ca* 1000–1100 m, 29 Jun 1952, *Nóbrega & Persson s.n.* (s); S. Juan sur la route entre Calheta et Topo, 11 Aug 1937, *Jorge s.n.* (PC); route entre Calheta et Topo, 13 Aug 1937, *Jorge s.n.* (PC); Ribeira do Passo, *ca* 1150–1300 m, between Caramujo and the origin of Rib. do Inferno, 1 Jul 1952, *Nóbrega & Persson s.n.* (s); Pico Grande, Curral das Freiras, *Nobrega 232* (s); between Falcos and Torrhinas, 5 Jun 1952, *Persson s.n.* (s).

6. *Codriophorus ryszardii* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra (Figs 55–57)

Codriophorus ryszardii (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. \equiv Racomitrium ryszardii Bednarek-Ochyra, Cryptogamie Bryol. 21: 276, f. 1–3. 2000. — TYPE CITATION: U. S. A. Alaska, Wrangell-Petersburg Co.: Mitkof Island, slopes near Crystal Lake, S of Petersburg, lat. 56°36' N, long. 132°50' W; alt. ca 200 ft, on boulder in opening, 22 Jun 1968, Worley, Schofield & Hamilton 8528 [Holotype: "Bryophytes of Southeast Alaska University of British Columbia Herbarium Rhacomitrium aquaticum (Brid. ex Schrad.) Brid. cfr on boulder in opening, ca. 200' Det.: W. B. Schofield, 1983 Slopes near Crystal Lake, Mitkof I., S. of Petersburg. 56°36' N, 132°50' W. June 22, 1968 Coll. I. A. Worley, W. B. Schofield & G. Hamilton No. 8528" – KRAM!].

Plants medium-sized to large, slender to rather robust, usually stiff and coarse, in dull, loose or occasionally compact, extensive tufts or mats, light to dark green, vellow-brownish or olive to green-brown, sometimes with a golden-reddish tinge above, light to dark brown below. Stems prostrate to ascending, (1-)2-7 cm or occasionally up to 10 cm long, irregularly sparsely branched, branches mostly decumbent, without short tuft-like horizontal branches, dark brown with varnish-like lustre, in transverse section circular or oval, consisting of 4-5 layers of small, thick-walled and dark brown cortical cells surrounding 8-10 layers of large, thicker-walled, hyaline or yellowish-hyaline medullary cells, central strand absent; rhizoids usually frequent at stem base, dark brown, glossy, smooth, branched; axillary hairs hyaline throughout, 11-12-celled, filiform, composed mostly of short, barrelshaped cells becoming elongate above. Leaves similar in size and shape on stems and branches, straight to slightly falcate, loosely appressed, erect to slightly secund or crisped when dry, erect-spreading when moist, lanceolate to linear-lanceolate from a broader base, (2.8-)3.2-4.0 (-4.2) mm long, 0.8-1.0(-1.1) mm wide, slenderly long acuminate, obtuse to subacute, slightly decurrent; margins unistratose throughout, broadly recurved on one side and narrowly recurved on the other side from the base to about ³/₄–⁷/₈ way up the leaf, plane above, irregularly bluntly eroso-dentate to papillose-crenulate at the extreme apex or rarely entire and cristate; costa single, intensely yellow to yellow-brownish, sharply demarcated from the laminal cells and only at the extreme apex less evident and gradually merging into them, subpercurrent, ending a few cells below the leaf tip, almost of the same width throughout or somewhat tapering above, (80–)90–120(–135) µm wide at base, mostly lying in a shallow groove, in transverse section plano-convex throughout, strongly convex dorsally, bistratose, crescent-shaped, with 2-3 ventral cells, flattened and frequently with a shallow groove on the dorsal side in the distal portion making the costa somewhat winged, becoming flattened-lunate dorsally, tristratose with occasional 4-stratose spots and 3-4 larger ventral cells in midleaf, and 4-stratose, reniform with 5-8 larger cells across the ventral side at leaf base; laminal cells unistratose throughout, with large, flat, conspicuous papillae over the cell walls and the larger part of the lumina leaving only narrow cavities, with strongly sinuose or nodulose very thick walls; upper cells irregularly rounded-quadrate, oval to short-rectangular, 8-22 µm long, 6-8(-10) µm wide, becoming short-rectangular in mid-leaf, 15-30 µm long, 7-8 µm wide, and longer rectangular, up to 40 µm long, 5-8 µm wide below; cells at the insertion rectangular, shorter and wider than the adjacent laminal cells, 15–20 μm long, 10–11 μm wide, less sinuose but porose, forming a distinct yellowish-brown or orange-yellow strip of 1-2 rows of cells; alar cells differing little from the adjacent cells at the insertion, or subquadrate to shortrectangular, 16–22 µm long, 12–17 µm wide, with thick, smooth to sinuose walls, forming distinct, orange-yellow, flat, pellucid, shortly decurrent auricles; supra-alar cells quadrate to short-rectangular, 9–11 µm wide, 15–25 µm long, thick-walled, sinuose, not pellucid, not markedly different from the adjacent laminal cells and not forming a distinct border. Dioicous. Perigonia bud-like, 1.0-1.2 mm long, sometimes quite frequent; outer perigonial bracts ovate-lanceolate with a strong and percurrent costa; inner perigonial bracts hyaline-brown, broadly ovate, acute, 1.1-1.2 mm long, strongly concave, with a costa ending well below the chlorophyllous, yellow-green apex; antheridia to 24 per perigonium, club-shaped, pale brownish, short-stalked; paraphyses lacking. Outer perichaetial leaves ovate-lanceolate, gradually narrowly acuminate, 3.5-3.7 mm long, 1.0-1.2 mm wide, with obtuse apex and laminal cells generally similar to those in the vegetative leaves; inner perichaetial leaves oblong-ovate to lingulate, rounded-obtuse to subacute at the apex, 2.0-2.5 mm long, 0.8–1.2 mm wide, entire, strongly concave, sheathing below, hyaline to pale yellowish, composed of thin-walled cells below, chlorophyllous in the upper third and composed of cells with incrassate and sinuose walls, the innermost hyaline throughout or with a row of chlorophyllous uppermost cells. Setae single in the perichaetium, straight, exserted, (4.5-)5.5-7.5(-9.0) mm long, pale brown above, dark brown below, becoming dark brown throughout with age, smooth, dextrorse when dry; vaginula dark brown, 0.9-1.1 mm long, with rectangular, sinuose epidermal cells. Capsules erect, straight, cylindrical, gradually narrowed towards the seta, (2.0-)2.3-3.0(-3.2) mm long, 0.9-1.0 mm wide, smooth, somewhat lustrous, pale brown becoming dark brown with age; operculum erect, long-rostrate, with a straight rostrum to 1.1 mm long; annulus separating, composed of 2-3 rows of pellucid, orange- to yellow-brown, thick-walled cells with an outer row of elongate cells and basal rows of short, isodiametric cells; exothecial cells of two kinds, short-rectangular to linear, mixed with others, irregularly hexagonal, 20–90 µm long, 10–20 µm wide, thick-walled, becoming rounded below the orifice and forming a distinct, 3-4-seriate reddish-brown rim; stomata few near the base of the urn in 2-3 rows, superficial, bicellular with rounded pores, variously oriented; *peristome* single composed of 16 teeth, 500–650 μ m long, dark yellow to orange-brown, regularly split nearly to the base into 2 filiform, terete, not clearly barred prongs, densely papillose with tall, spiculate papillae; *basal membrane* short, to 25 μ m high, finely papillose; *preperistome* present as high as the basal membrane. *Spores* globose, finely papillose, pale yellowish-brown, 10–16 μ m in diameter. *Calyptra* conic-mitrate, dark brown, distinctly papillose at the apex, naked, not plicate, 4–5-lobed at base.

Etymology — This specific name honours Professor Ryszard Ochyra, Cracow, in appreciation of his great contribution to bryology.

Diagnostic characters and differentiation—Codriophorus ryszardii is a distinct and unmistakable species that is characterised by the following set of features: (1) plants medium-sized and slender to large and robust, mostly stiff and coarse, green, yellow-brown to brown-green; (2) stem creeping to ascending, irregularly and sparingly forked; (3) leaves lanceolate to linear-lanceolate, slenderly long acuminate, obtuse to subacute, irregularly bluntly erosodentate, papillose-crenulate or cristate at the extreme apex, seldom entire to subentire, always lacking a hairpoint; (4) costa broad, (80-)90-120(-135) µm wide, usually situated in a shallow groove, ending a few cells below the leaf tip and diffusing into the laminal cells, strongly convex dorsally, bistratose, with 2-3 ventral epidermal cells, flattened and frequently winged on the dorsal side in the upper part owing to the presence of a shallow groove, tristratose, with 3-4 larger ventral cells and flattened-lunate in mid-leaf, and 4-stratose, reniform, with 5-8 larger cells across the ventral side at the leaf base; (5) leaf margin entirely unistratose, variously recurved on both sides, entire except for the apex; (6) laminal cells unistratose throughout, irregularly rounded-quadrate to oval near the apex, short-rectangular in mid-leaf and longer rectangular below; (7) basal marginal cells quadrate to short-rectangular, thick- and sinuose-walled, not pellucid, not forming a distinct border; (8) alar cells not differentiated or forming flat, orange-yellow, pellucid and shortly decurrent auricles; (9) innermost perichaetial leaves hyaline throughout with lax areolation or only sometimes with a marginal row of chlorophyllous cells with somewhat thickened walls at the apex; (10) setae 5.5–7.5(–9.0) mm long, dextrorsely twisted; (11) capsules erect, straight, cylindrical, 2.3-3.0 mm long, somewhat lustrous, brown, with a longrostrate operculum; (12) peristome teeth $500-650 \,\mu\text{m}$ long, regularly split nearly to the base into 2 terete, thread-like branches, densely spiculate papillose.

Codriophorus ryszardii is a rather isolated species, although from its costa structure it seems to be most closely related to *C. aquaticus* and *C. carinatus*, species which are united into a single subsection, subsect. *Hydrophilus*. *C. ryszardii* has been consistently mistaken for *C. aquaticus* and under this name it has long existed in the North American bryological literature (e.g., Schofield 1968, 1976; Lawton 1971; Anderson *et al.* 1990). However, it differs from C. aquaticus in a number of gametophyte and sporophyte characters, including its longer leaves, 3.2-4.0 mm on average, that are lanceolate to linear-lanceolate, narrowly long acuminate and end with an obtuse or subacute apex which is most often bluntly eroso-dentate giving it a cristate appearance. Only rarely is the leaf apex entire. Moreover, its leaf margins are recurved for $\frac{3}{4}-\frac{7}{8}$ of the leaf length, the costae are often bluntly winged dorsally in the distal portion, the laminal cells are entirely unistratose and the supra-alar cells are not differentiated from the adjacent laminal cells and do not form basal marginal borders. By contrast, the leaves in C. aquaticus are shorter, 2.5-3.0 mm on average, broadly lanceolate and more shortly acuminate into an obtuse and always entire, never cristate, apex. In addition, the leaf margins in this species are recurved for $\frac{1}{2}-\frac{3}{4}$ of the leaf length, the costae are symmetric and never winged dorsally, the laminal cells are sometimes bistratose distally and the supra-alar cells are quadrate to short-rectangular with relatively thick, smooth to slightly sinuose walls forming short but usually distinct, hyaline to yellowish-hyaline but otherwise pellucid marginal borders. The most distinctive sporophyte difference between C. ryszardii and C. aquaticus is in the peristome. The peristome teeth in the former are longer, 500-650 µm, and they are densely papillose with needlelike papillae, whereas in C. aquaticus the peristome teeth are shorter, mostly less than 500 μ m, and they are only finely papillose.

There have been only a few cases of confusion of *Codriophorus ryszardii* with the Asiatic *C. carinatus*, although some epilose phenotypes of this species have been determined as *Racomitrium aquaticum* in Japan (Noguchi 1974, 1988) and they may resemble *C. ryszardii*. Both species share narrowly lanceolate leaves which lack basal marginal borders but, typically, *C. carinatus* has short, denticulate hyaline leaf tips which immediately distinguish this species from *C. ryszardii*. On the other hand, epilose phenotypes of *C. carinatus* always have entire leaf margins, narrower, 2–3-stratose costae with 2 characteristic, much enlarged ventral epidermal cells in the upper part and often bistratose leaf margins in 1–3 rows of cells.

The eroso-dentate leaf apices of *Codriophorus ryszardii*, resulting in their cristate appearance, are very similar to those in *C. brevisetus*, *C. anomodontoides* and *C. corrugatus* of sect. *Fascicularia* but the costa in these species is situated at the base of a deep furrow and ceases well below the leaf apex, sometimes extending only to mid-leaf, and is bistratose throughout in transverse section. The oldest specimens of *C. ryszardii* from Washington (Cascade Mts, May 1929, *Grant s.n.*, o; Marysville, May 1930, *Grant s.n.*, MICH, WTU) were misnamed as *Racomitrium aciculare* which does have leaves dentate at the apex. However, leaves in this species are broadly lingulate and broadly rounded-obtuse at the apex and are completely unlike the lanceolate leaves of *C. ryszardii*.

Variability — *Codriophorus ryszardii* is a stenotypic species which exhibits little morphological variability in its diagnostic characters. The leaf apex is usually distinctly



FIGURE 55. *Codriophorus ryszardii.* — 1. Habit. 2. Portion of branch, wet. **3–12**. Leaves. **13**. Cross-section of stem. **14–26**. Cross-sections of three leaves, sequentially from base to apex. — [1-5, 13, 17-21 from *Worley, Schofield & Hamilton 8528* (holotype), KRAM; 6–8, 22–26 from *Schofield & Vaarama 23970*, DUKE; 9–12 and 14–16 from *Schofield 45262*, CANM]. — Scale bars: a – 0.5 cm (2); b – 1 cm (1); c – 100 mm (14–26); d – 100 µm (13); e – 1 mm (3–12). (Reproduced from *Cryptogamie, Bryologie*, **21**: 277, 2000, with permission from ADAC – Cryptogamie).



FIGURE 56. *Codriophorus ryszardii.* — 1–3. Leaf apices. 4. Upper leaf cells at margin. 5. Mid-leaf cells. 6. Basal juxtacostal cells. 7. Angular cells. 8–10. Axillary hairs. — [All from holotype, *Worley, Schofield & Hamilton 8528*, KRAM]. — Scale bar: 100 μm (1–10). (Reproduced from *Cryptogamie, Bryologie*, 21: 278, 2000, with permission from ADAC – Cryptogamie).

eroso-dentate to papillose-crenulate or cristate and subacute to narrowly obtuse but, occasionally, some leaves on the same plant have entire or subentire and more broadly obtuse apices. The costa shows some variation in stoutness, its width ranging from 80 to 135 μ m near the base, although it does not markedly taper upwards and is almost of the same width throughout its length. In transverse section, the costa is somewhat asymmetric in outline and rugged on the dorsal side and is often shallowly grooved below the leaf apex, resulting in the presence of more or less obscure wings. There is also some variation in thickness and number of the costal ventral epidermal cells but these features are strictly correlated with its stoutness and in general costal anatomical structure is relatively stable in *C. ryszardii*. The alar cells are either not much differentiated from the adjacent basal cells or they are subquadrate



FIGURE 57. *Codriophorus ryszardii.* — 1. Habit of plant with sporophyte, wet. 2. Perigonium. 3. Outer perigonial bract. 4–5. Inner perigonial bracts. 6. Innermost perigonial bract with antheridia. 7–10. Innermost perichaetial leaves. 11. Apex of innermost perichaetial leaf. 12. Epidermal cells of vaginula. 13. Cross-section of seta. 14. Cross-section of calyptra. 15. Calyptra. 16. Operculum. 17–18. Operculate capsules, wet. 19–20. Deoperculate capsules, wet. 21–22. Deoperculate capsules, dry. 23. Exothecial cells and stomata at urn base. 24. Exothecial cells in middle of urn. 25. Exothecial cells at orifice, annulus and peristome. 26. Spores. — [1, 21–22, 25–26 from *Schofield 30680*, NY; 2–6 from *Schofield 45262*, CANN; 7–11 from *Schofield & Vaarama 23970*, DUKE; 12–14, 19–20, 23–24 from *Worley, Schofield & Hamilton 8528* (holotype), KRAM; 15–16 from *Ireland, Lawton & Sharp 9104*, CANM; 17–18 from *Maskham & Mueller s.n.*, 9 Dec 1965, ALTA]. — Scale bars: a – 0.5 cm (1); b – 1 mm (2–6); c – 1 mm (15–16) and 100 μ m (11–14, 23–24); d – 1mm (7–10); e – 100 μ m (25–26); f – 1 mm (17–22). (Reproduced from *Cryptogamie, Bryologie*, 21: 280, 2000, with permission from ADAC – Cryptogamie).

to short-rectangular with thick and sinuose walls and form flat, transparent, orange-brown and shortly decurrent auricles. Both states are usually observable on the same plant and hence the alar cells have no taxonomic importance in this species.

The plants of *Codriophorus ryszardii* are rather uniform in size and branching and the length of the majority of stems varies from 2 to 7 cm. Plant colour varies according to light exposure, ranging from dark green to brown-green with a wide spectrum of intermediate hues such as yellow-brownish, olive-brown or, occasionally golden-reddish. Leaf form varies somewhat from straight to curved with length usually ranging from 3.2 to 4.0 mm, exceptionally from 2.8 to 4.2 mm.

Reproduction — The majority of populations produces profusely fully mature sporophytes, singly per perichaetium.

Taxonomic and nomenclatural notes — Codriophorus ryszardii has a short and straightforward taxonomic history. It was only recently described as a separate species, Racomitrium ryszardii, from material collected from south-east Alaska (Bednarek-Ochyra 2000), and subsequently transferred to Codriophorus (Ochyra et al. 2003). The species has been discovered at many sites on the north-west coast of North America and the majority of specimens were misdetermined as Racomitrium aquaticum (Schofield 1968, 1976; Lawton 1971). Although it is widely distributed and locally frequent and abundant, the first specimen of this species was collected by J. M. Grant as recently as 1929 in the Cascade Range of Washington and misidentified as *Racomitrium aciculare*. Apart from R. aquaticum, some specimens of C. ryszardii have been named Racomitrium varium and R. fasciculare in various herbaria.

Chromosome number --- Not available.

Habitat — Codriophorus ryszardii is a hydrophytic moss that thrives in damp or wet situations, although no data on its submergence or occurrence in running water are available. It can also tolerate seasonal drought and some specimens are described as having been collected in dry habitats. The species grows predominantly on acidic, mostly granite, basaltic and siliceous rocks, although occasionally it has also been collected from limestone (e.g., Horton 1369, ALTA). It is most often found in moist and shaded places, infrequently in open and drier sites, throughout coastal coniferous forest dominated by Chamaecyparis nootkatensis, Picea sitchensis and Tsuga heterophylla, on outcrops, rocks, boulders and cliff faces in or near streams and lakes, on outcrops in bogs and along waterfalls and seeps. C. ryszardii mostly grows in monospecific stands and only very rarely does it form mixed stands with C. acicularis.

Geographical distribution — *Codriophorus ryszardii* is a north-western North American endemic species. It is

widespread in coastal areas, ranging from Kodiak Island and south-east Alaska through British Columbia where it is mostly distributed on coastal islands, with a particular concentration of localities in the Queen Charlotte Islands with very rare occurrences on the mainland in the biogeoclimatic coastal western hemlock zone (Schofield 1988). It then extends southwards to the Olympic Mountains and Cascade Range of Washington, reaching its southernmost station on Mt Hood in the Cascade Range in north Oregon (Fig. 58). It occurs from sea level to the subalpine zone, attaining a highest elevation of 2130 m on Mt Rainier in the Cascade Range, Washington. However, it seems to occur most often at elevations below 1000 m, at least judging from the altitudinal data on the labels. Elliott & Moore (1989) reported Racomitrium aquaticum from the Glacier National Park in Montana (Schofield 12260) but the status of this record cannot be precisely established because I had no access to the herbarium holdings of this genus in UBC.

SPECIMENS EXAMINED

NORTH AMERICA. CANADA. BRITISH COLUMBIA. Capilano Canyon below Capilano Dam, Schofield & Jamieson 41437 (DUKE); Lynn Canyon Park, Lynn Creek, Lyford & Schofield 199 (osc); Golden Ears Provincial Park, Evans Creek Trail, Schofield & Taylor 67545 (NY); Kloiya Bay, 19 km E of Prince Rupert, Schofield 13852 (CANM); Calvert Island, Keith Anchorage, Kwakshua Channel, Schofield 86069A (CANM, DUKE) and Schofield & Williams 27061 (DUKE); same island, long lake at N base of Mt Buxton, Schofield & Williams 27883 (DUKE); S Sathe Road, ca 23 km from gate, Harrison Mills Logging Road, Schofield 57872 (DUKE). OUEEN CHARLOTTE ISLANDS. Chaatl Island: without closer data, Schofield & Boas 18889 (CANM, DUKE); N central coast, Schofield 100854 (DUKE). Graham Island: Skidegate Channel, E side of Trounce Inlet, Schofield 14003 (CANM, DUKE, NY, S); head of Van Inlet, Schofield & Krajina 39419 (DUKE); Goose Cove, Athlow Bay, Schofield & Spence 83641 (CANM, DUKE); Long Inlet, Lagins Creek, Schofield 30035 (DUKE). Hibben Island: NE side, Schofield 15260 (s). Lihou Island: at NW coast of Moresby Island, Schofield 15371B (NY). Louise Island: Mathers Lake, Schofield 37309 (DUKE). Lyell Island: Beljay Bay, Schofield & Vaarama 23968 (DUKE) & 23970 (CANM, DUKE). Moresby Island: NE cove Moresby Lake, 95 m, Vitt 12217 & 12294 (ALTA) and 95-153 m, Horton 1369 & 1485 (ALTA); Bigsby Inlet, Schofield 45213 (ALTA, CANM, DUKE) and Schofield & Vaarama 24075 (DUKE); Crescent Inlet, Schofield 45262 (CANM, MICH, NY, PR, UC); Skidegate Channel, S side of West Narrows, Schofield 30680 (CANM, DUKE, NY, POZG, S, US); Skidegate Channel, seaside cliffs of East Narrows, Schofield 14079 (CANM, S); Mine Mt, above Tasu, Schofield & Schofield 73556 (CANM, DUKE); Tasu Sound, Schofield 35025 (ALTA, CANM, DUKE, MO); Tasu Sound, W side of Fairfax Inlet, ca 1.5 km from Tasu, Schofield & Schofield 73604 (DUKE); Sewell Inlet, Schofield 57759 (DUKE); Peel Inlet area, mountain at head of W branch of Braverman Creek, Schofield 30486 (DUKE); Kootenay Inlet, N side, Schofield & Krajina 39513 (DUKE); Jedway area, Schofield 34660 (DUKE); Seal Inlet, Schofield 33759 (DUKE); Gray Bay, Schofield 34740 (DUKE). VANCOUVER ISLAND. Waterfall ca 37 km E of junction with Tofino-Ucluelet Highway, Schofield 38843 (CANM, DUKE, MICH); Nootka Sound, Mooyah Bay, mouth of Muchalat Inlet, Schofield & Halbert 40394 (DUKE); Muchalat Inlet, near mouth of Houston River & Tributary, Halbert 4725 (DUKE); Nootka Island, W of Crawfish Lake, Halbert 4862 (DUKE); Raza Island, Raza Passage, Schofield 64062 (ALTA, CANM, DUKE, NY) & 64038A (ALTA, KRAM).

U.S.A. ALASKA. Juneau Co.: SE Roberts Peak, ca 500 m, Hermann 21974 (CANM, S, US). Ketchikan Gateway Co.: Revillagigedo Island, Ketchikan, steep slope along East Channel, Hermann 22204 (CANM, DUKE, MICH, NY, S, US); vicinity of Ketchikan, Ward Lake, Tongas Natl. Forest, 10–20 m, Redfearn & Redfearn 36699 (MO). Kodiak Island Co.: Kodiak Island, stream valley N of road to Anton Larsen Bay beyond Buskin Lake, 30–50 m, Sharp 263 (NY, TENN). Skagway Hoonah-Angoon



FIGURE 58. Global distribution of Codriophorus ryszardii.

Co.: Yakobi Island, upper waterfall of Bohemia Creek, ca 250 m, Shacklette 4006 (MICH). Valdez-Cordova Co.: along Copper River highway about 4 miles E of Cordova, Chugach National Forest, 0–50 m, Norris 96466 (KRAM). Wrangell-Petersburg Co.: Coronation Island, Maskham & Mueller s.n. (ALTA); Etolin Island, stream from Kunk Lake to Zimovia Strait, Worley & Hamilton 8346 (DUKE); Wrangell Island, along road ca 13.5 km S of Wrangell, Worley 7551 (DUKE). WASHINGTON. Clallam Co.: Olympic Natl. Park, Deer Lake Trail near Soleduc Hot Springs, Schofield, Ireland & Boas 19444 (CANM, DUKE, WTU). Grays Harbor Co.: along Peter Creek Trail in Colonel Bob Wilderness, Olympic National Forest, 325–480 m, Norris 95435 (KRAM). Pierce Co.: Mt Rainier National Park, on N slope of Mt Rainier, trail to Berkeley Park, ca 2130 m, Ireland & Lawton 8303 (WTU). Jefferson Co.: Quinalt River, Meyer 130/B (G); along Dry Creek about 6.5 km S of Huelsdonk Ranch, *ca* 300 m, *Norris* 98801 (KRAM). *Snohomish Co.*: Schweitzer Creek, between Verlot and Silverton, road to Bear Lake, *ca* 500 m, *Ireland, Lawton & Sharp 9104* (CANM, NY); Mt Baker, Snoqualmie National Forest, S of Verlot, 700 m, *Norris* 86702 (UC); Mt Pilchuck, Rotary Creek, *Schofield, Ireland & Boas* 18528 (CANM, DUKE) and *ca* 850 m, *Lawton 4508* (WTU); Mt Pilchuck, 500–650 m, *Lawton 4689* (WTU); SE of Verlot, along road to Mt Pilchuck Lodge, Rotary Creek, *Ireland 7223* (CANM); Mt Baker National Forest, Verlot, Rotary Creek, *at 1000 m, Hermann 18450* (CANM, DUKE, MICH, US); Rotary Creek, Mt Pilchuck, *Schofield & Ireland 21708* (CANM); Marysville, May 1930, *Grant s.n.* (MICH, WTU); Monte-Cristo region, Cascade Range, My 1929, *Grant s.n.* (O). OREGON. *Multinomah Co.*: Cascade Range, W of Mt Hood, *ca* 700 m, *Rambo s.n.* (UC).

7. *Codriophorus carinatus* (Cardot) Bednarek-Ochyra & Ochyra (Figs 59–62)

Codriophorus carinatus (Cardot) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. \equiv *Racomitrium carinatum* Cardot, Bull. Herb. Boissier Sér. 2, 8: 335. 1908. — TYPE CITATION: Corée: île Quelpaert, à 1200 m. (n. 643). [Holotype: "Herb. J. Cardot. Rhacomitrium carinatum Card. <u>sp. nova.</u> Corée: île Quelpaert, Hallasan, 1200 m. Leg. Faurie, 1907. nº 643" – PC-Cardot!; isotypes: H-Brotherus!, s-Roth/Möller!].

Racomitrium aciculare (Hedw.) Brid. var. *brachypodium* Besch., Ann. Sc. Nat. Bot. Sér. 7, 17: 338. 1893. $\equiv R.$ *brachypodium* (Besch.) Cardot, Bull. Herb. Boissier Sér. 2, 8: 334. 1908. $\equiv R.$ *fasciculare* (Hedw.) Brid. var. *brachypodium* Besch. *ex* Sakurai, Musc. Jap.: 64. 1954, *nom. inval. in synon. err: pro* R. aciculare *var.* brachypodium. $\equiv R.$ *heterostichum* (Hedw.) Brid. var. *brachypodium* (Besch.) Nog., J. Hattori Bot. Lab. 38: 367. 1974. — TYPE CITATION: Yézo: sur les pierres dans le lit des ruisseaux, novembre 1886 (Faurie, n° 202). [Holotype: "Herbier Emile Bescherelle Rhacomitrium aciculare var. brachypodium Yezo – rochers Nov. 86 Japon – Abb. Faurie legit (N° 202)" – BM-Bescherelle!; isotypes: H-Brotherus!, PC!, PC-Cardot!, s-Roth!], *syn. nov.*

R. fauriei Cardot, Bull. Herb. Boissier Sér. 2, 8: 333. 1908. — TYPE CITATION: Japon: Hakkoda, pierres, à 1300 m. (n. 2921). [Holotype: "Herb. J. Cardot. Rhacomitrium Fauriei Card. <u>sp. nova.</u> Japon: Hakkoda, 1100 m. Leg. Faurie, 1904. nº 2921" – PC-Cardot!; isotypes: H-Brotherus!, NY!, s-Roth/Möller!], *syn. nov.*

R. sudeticum (Funck) Bruch & Schimp. var. *subellipticum* Cardot, Bull. Herb. Boissier Sér. 2, 8: 333. 1908. – *R. subellipticum* (Cardot) Sakurai, Bot. Mag. Tokyo 51: 105. 1937. — TYPE CITATION: Japon: Onikobe (n. 161); Iwakisan (n. 2634); Takayu, rochers, 1200–1600 m. (n. 2863, 2872, 2879); Ubayu, rochers, à 1300 m. (n. 2816, 3194); Hakkoda, pierres, à 1300 m. (n. 2935, 2938, 2951 in parte, 2952 in parte, 2953); Komagatake, rochers à 2300 m. (n. 3381, 3393, 3394, 3395, 3396). [Lectotype (*selected here*): "Herb. J. Cardot. (illegible *manu* G. Roth) Rhacomitrium sudeticum BS. var. subellipticum Card. cfr. (e specim. origin.). Japon: Ubayu, rochers à 1300 m. Leg. Faurie, 1904. n. 2816" – s-Roth!]; syntype: "Bryophyta Faurieanae. Herb. Bot. Inst. Sci. Dept. Imp. Univ. Kyoto. Rhacomitrium sudeticum (Funck) var. subellipticum Card. Faurie, No. 161 Onikobe Mense VII Anni 1897 Leg. Urbain Faurie" – KY0!], *syn. nov.*

Plants small to moderately sized, mostly gracile or, rarely, coarser, stiff and fairly rigid, loosely or densely caespitose, dull, dark green, olivaceous, olive-, yellow-, rufous- or golden-brown to dark brown above, brown to blackish-brown below, sometimes brown to golden-or vellow-brown throughout. Stems erect, arcuately ascending to prostrate, (1.0-)2.5-5.5(-9.0) cm tall, straight or flexuose, sparsely dichotomously or copiously fastigiately branched, rarely almost unbranched, densely or sparsely radiculose in the lower part with reddish- or rufous-brown, branching, smooth, lustrous rhizoids, sometimes scattered in clusters along the creeping stems, in transverse section circular to oval, lacking a central strand, consisting of 3-5 layers of stereid cortical cells with small lumina and strongly incrassate, dark brown walls, abruptly or gradually passing into 5-7 layers of large, hyaline, thicker-walled medullary cells; axillary hairs filiform, hyaline throughout, consisting of 8-11 short, barrelshaped cells. Leaves crowded, erect, appressed, flexuose or somewhat crisped on drying, erect-spreading on wetting, narrowly lanceolate to linear- or ovate-lanceolate, (1.9-)2.2-3.2(-3.8) mm long, 0.6-0.9 mm wide, slenderly long acuminate, shortly decurrent, carinate above, carinate-concave below; leaf apex acute to narrowly roundedobtuse, muticous or terminated with a short, denticulate, hyaline tip, up to 125 µm long, often reduced to a single apical, hyaline cell; margins entire throughout or denticulate at the hyaline tip, unistratose all around or bistratose in the distal part in 1-3 rows of cells, recurved on one side for $\frac{1}{2}-\frac{2}{3}$ of the leaf length, plane or slightly deflexed above, plane on the other side, rarely plane on both sides; costa single, percurrent or subpercurrent, brown to yellowbrown, sharply separated from the laminal cells, strong, 85-105 µm wide at the base, gradually narrowed towards the apex, 50-70 µm wide in the upper part, in transverse section strongly convex dorsally, elliptical to semi-terete, bistratose in the upper and central parts, with 2 very large, elliptical ventral cells in the central part, reniform, crescent-shaped to rectangular and flattened, 2-3-stratose in the basal part with a ventral layer of 3-4(-5) very large, elliptical cells and 1–2 layers of small stereid cells on the dorsal side; laminal cells unistratose throughout, except for occasional bistratose streaks and margins in the distal part, opaque, isodiametric, mostly irregularly angular to quadrate or oblate near the margins, $(6-)10-12(-15) \mu m$ long, (8-)10-12 µm wide, becoming sinuose-walled, isodiametric to short-rectangular below, (8-)10-15(-20) µm long, 8–10 µm wide, and longer rectangular above the base, (15-)20-35(-45) µm long, 8-10 µm wide; basal cells short- to long rectangular, 20-45 µm long, 8-12 µm wide, with strongly incrassate, nodose and porose walls, forming a distinct, bright olive-yellow strip along the leaf insertion, consisting of 2-3(-4) rows of cells; alar cells not differentiated from the adjacent basal cells or sometimes somewhat larger but not forming markedly distinct auricles; supra-alar cells not differentiated or quadrate to short-rectangular, (8-)10-20 µm long, 5-10 µm wide, esinuose, pellucid, forming a marginal border, often only on one side, consisting of 5-14(-24) cells. Dioicous. Perigonia gemmiform, about 1.5 mm long; outer perigonial bracts lanceolate, ca 1.5 mm long, 0.9-1.0 mm wide, with a distinct, subpercurrent costa; inner perigonial bracts ovate, about 1 mm long, broadly acute, deeply concave, the innermost one with 9-10 claviform, brownish antheridia, intermixed with a few, hyaline paraphyses, about half the length of the antheridia. Outer perichaetial leaves ovate-lanceolate, 2.3-3.0 mm long, 0.9-1.0 mm wide, with a subpercurrent costa; innermost perichaetial leaves oblong, broadly acute, blunt at the apex, 1.8-2.0 mm long, 0.8–0.9 mm wide, sheathing the seta, hyaline throughout. Setae single per perichaetium, very rarely geminate, erect, straight, (1.9-)3.0-5.5(-7.0) mm long, dextrorse, brown, smooth; vaginula about 1 mm long, brown, with oblong, sinuose- and firm-walled epidermal cells. Capsules erect, straight, obloid to short-cylindrical, (1.0-)1.5-2.1 mm long, 0.8-0.9 mm wide, brown, smooth, somewhat lustrous; operculum conical-rostrate, about 1 mm long, with a straight, fairly stout beak; annulus separating, 2-3-seriate, consisting of large, vesiculose, yellow-brown cells with strongly incrassate walls;


FIGURE 59. *Codriophorus carinatus.* — 1. Plant with mature sporophyte, wet. 2. Portion of branch, dry. 3. Stem section. 4–6. Axillary hairs. 7–22. Leaves. 23–25. Upper laminal cells at margin. 26–28. Mid-leaf cells. 29–30. Basal juxtacostal cells. — [1–2 from *Takaki 5839*, MAK; 3–9, 24, 26 from *Wu 1047*, MO; 10–11 from *Mayebara 1849*, MAK-B57673; 12–14, 25, 28, 30 from *Faurie 643*, H, isotype of *Racomitrium carinatum*; 15–16 from *Maeda s.n.*, 4 Aug 1950, MAK; 17, 20 from *Sakurai s.n.*, 23 Apr 1944, MAK; 18–19 from *Iishiba 927*, H; 21–23, 27, 29 from *Faurie 2921*, s, isotype of *R. fauriei*]. — Scale bars: a – 1 mm (2); b – 1 mm (7–22); c – 100 µm (3); d –100 µm (4–6, 23–30); e – 1 cm (1).

exothecial cells mostly oblong to rectangular, mixed with rounded-quadrate, $25-50(-60) \mu m \log$, $10-15 \mu m$ wide, firm-walled, becoming isodiametric in 3–5 rows at the mouth; stomata at the base of the urn 9–20, disposed in 1-2(-3) rows, superficial, bicellular, with rounded pori; peristome teeth 16, lanceolate, yellow- or orange-brown, densely spiculate-papillose throughout, $300-350 \mu m \log$, deeply divided into 2 or, rarely, 3 terete, weakly articulated branches, with a low basal membrane, to 50 μm long, and a distinct, low, hyaline preperistome. Spores spherical, very finely roughened, $(10-)12-15(-17) \mu m$ in diameter. Calyptra conical-mitrate, 5–6-lobed at the base, about 1.5 mm long, pale brown, coarsely papillose at the apex.

Etymology — The specific epithet derives from the Latin *carinatus* which means keeled, in reference to the distinctly keeled leaves.

Diagnostic characters and differentiation — Codriophorus carinatus has usually been poorly understood and misinterpreted and even in recent treatments (e.g., Noguchi 1974, 1988; Iwatsuki 1992, 2001, 2005) its various morphological expressions have been considered as separate taxa of the genus Racomitrium, namely R. carinatum, R. fauriei and R. heterostichum var. brachypodium. This has been the consequence of attaching too much importance to some otherwise variable characteristics and considering them to have diagnostic significance and simultaneously neglecting other fairly stable characters which actually best characterise C. carinatus. Most confusing are the form of the leaf apex and the stratosity of leaf margins in the distal portion. The type material of C. carinatus and most of its populations have shortly but distinctly hyaline tipped leaf apices. Such plants do not pose any problems with identification because the presence of the hyaline leaf apex is extremely unusual in the genus Codriophorus and is otherwise known only in the western North American C. varius and the South American C. laevigatus. On the other hand, the populations described as Racomitrium fauriei lack the hyaline hair-point and perfectly imitate Codriophorus aquaticus, these two taxa actually having been considered conspecific (Noguchi 1974). In fact, they are definitely distinct and R. fauriei is here reduced to synonymy with C. carinatus. The characters separating C. aquaticus and the epilose phenotypes of C. carinatus which were described as R. fauriei are discussed below.

The leaf margins are unistratose in most populations of *Codriophorus carinatus* but sometimes they are distinctly bistratose in the distal portion, and occasional bistratose spots also occur in the type material of this species (Fig. 61.5). The leaf margins are bistratose in the plants described as *Racomitrium aciculare* var. *brachypodium* (Bescherelle 1893) and *R. sudeticum* var. *subellipticum* (Cardot 1908a). These varieties were subsequently raised to species by Cardot (1908*a*) and Sakurai (1937*a*), respectively, as *R. brachypodium* and *R. subellipticum*. Noguchi (1974) considered them to be identical, the former name having priority, and reduced *R. brachypodium* to a va-

riety, *R. heterostichum* var. *brachypodium*. This taxon has obviously nothing to do with *Bucklandiella heterosticha* which differs, among other things, in having perfectly smooth laminal cells. However, the leaf areolation, cell papillosity and the structure of the costa clearly indicate the identity of *Racomitrium heterostichum* var. *brachypo- dium* with *Codriophorus carinatus*.

As presently understood, Codriophorus carinatus is diagnosed by the following set of features: (1) plants small to medium-sized, forming loose or dense tufts, green, olivaceous or yellow- to golden-brown, variously dichotomously or fastigiately branched; (2) leaves narrowly lanceolate to linear- or ovate-lanceolate, gradually long acuminate, distinctly carinate in the distal portion and carinate-concave in the proximal part; (3) leaf apex acute to narrowly rounded-obtuse, muticous or shortly hyaline tipped; (4) margins entire or denticulate at the hyaline apex, unistratose or bistratose in 1-3 rows of cells distally, recurved on one side to $\frac{1}{2}-\frac{2}{3}$ of the way up the leaf, plane on the other side; (5) costa strong, percurrent to subpercurrent, strongly convex dorsally, bistratose, elliptical to semi-terete in the distal and central parts, with 2 very large, transversely elliptical ventral cells in the median part, reniform, lunate to rectangular and flattened, 2-3-layered below, with 3-4(-5) elliptical ventral cells much larger than the stereid cells on the dorsal side; (6) upper and median laminal cells opaque, isodiametric to short-rectangular, unistratose or with bistratose streaks near the apex; (7) leaf auricles absent; (8) basal marginal border absent or usually present, composed of 5-14(-24) esinuose, pellucid cells; (9) innermost perichaetial leaves hyaline throughout; (10) setae short, (1.9-)3.0-5.5(-7.0) mm, dextrorse; (11) capsules obloid to short-cylindrical, (1.0-)1.5-2.1 mm long; (12) peristome teeth short, 300-350 µm, deeply divided into 2-3 prongs, densely spiculate-papillose throughout.

Actually *Codriophorus carinatus* can be correctly and unfailingly distinguished by the combination of two characters, namely the areolation of obscure, isodiametric to short-rectangular laminal cells in the upper and median parts of the leaves and the presence of two markedly enlarged and transversely elliptical ventral cells in the median part of the costa, visible in transverse section. These characters, coupled with the presence of the hyaline leaf tips, make the species very distinct and easily distinguishable from all other congeners. However, many populations of the species, known as *Racomitrium fauriei* and *R. brachypodium*, have muticous and acute to rounded-obtuse leaves and they have been interpreted as *C. aquaticus* (Noguchi 1974, 1988).

Codriophorus aquaticus differs from muticous expressions of *C. carinatus* in some structural characters, primarily in the costal structure and leaf shape and areolation. The costa in *C. aquaticus* is generally much broader and thicker, $100-180 \mu m$ wide near the base, most often tristratose and with 4–7 ventral epidermal cells in the middle of the costa. These are mostly rounded and similar to other cells in the central and dorsal rows, making the costa homogeneous in transverse section. In contrast, the



FIGURE 60. Codriophorus carinatus. — 1–9. Leaf apices. 10–13. Basal marginal cells. — [1–2, 12–13 from Faurie 2921, s, isotype of Racomitrium faurie; 3, 10–11 from Faurie 643, H, isotype of R. carinatum; 4 from Mayebara 1849, MAK-B57673; 5–7 from Deguchi s.n., 26 Jul 1974, HIRO; 8–9 from from Iishiba 927, H]. — Scale bar: 100 µm.

costa in C. carinatus is bistratose in the middle and has two very large, transversely elliptical cells on the ventral side which are much larger from those on the dorsal side and consequently the anatomy of the median part of the costa resembles very much that in Bucklandiella microcarpa. In the basal part, the costa in C. aquaticus is much broader and thicker, 3-6-stratose, with 7-15 ventral epidermal cells which are transversely elliptical and much larger than the lower stereid cells. Conversely, the costa in C. carinatus is much narrower and thinner in the basal part, 2-3-layered, with 3-4(-5) enlarged cells in the ventral row and much smaller, stereid cells in the dorsal row(s). The leaves of C. aquaticus are stiff and unchanged when dry, broader lanceolate and recurved on both sides in the lower half. Conversely, the leaves of C. carinatus are usually flexuose on drying, narrowly lanceolate, slenderly long acuminate and recurved only on one side to $\frac{1}{2}-\frac{2}{3}$ of the way up the leaf, plane on the other side. Both C. aquaticus and C. carinatus have quite similar leaf areolation but the cells are pellucid in the former, whereas those in C. carinatus are distinctly opaque.

The plants of *Codriophorus carinatus* with epilose leaves have sometimes been mistaken for *C. brevisetus* and both species share frequently bistratose leaf margins and short laminal cells in the distal part. This prompted Sakurai (1937*a*) to consider them as conspecific taxa. However, *C. brevisetus* has a distinctly erose-denticulate or notched-serrate leaf apex and its costa is bistratose throughout, except for some tristratose patches near the base. Occasionally, some specimens of *C. carinatus* have been misdetermined as *C. fascicularis* and *C. anomodontoides*, but these species are distinct at a glance in having elongate upper laminal cells and costae bistratose in crosssection. In the latter species the costa is also distinctly convex on the ventral side.

Confusion of *Codriophorus carinatus* with species of *Bucklandiella* sometimes occurs and the case of its synonymous name, *Racomitrium aciculare* var. *brachypodium*, is discussed above. The specimen of *C. carinatus* from Taiwan (*Shevock 18017*, CAS, KRAM, MO) so named by Cao *et al.* (2003) actually represents *Bucklandiella subsecunda*, the most widespread species of the genus in Asia (Frisvoll 1988), characterised by having a costa strongly flattened and broad in the proximal portion.

Variability — Although Codriophorus carinatus is a welldefined and fairly stable species in its basic diagnostic characters, it exhibits a certain amount of variation in some morphological and anatomical characters which has led to the misinterpretation of some plants. In most populations at least the upper leaves are hair-pointed. The hair-point is very short and actually it is only a denticulate, hyaline tip which varies in length from 20 to 125 μ m both within and between populations and very often it is reduced to one or a few hyaline apical cell(s). Furthermore, a goodly number of collections consist of plants with all leaves muticous, for example, those represented by the type specimens of *Racomitrium fauriei* and *R. sudeticum* var. *subellipticum* (Fig. 60). Hyaline hair-points are generally very variable throughout the Grimmiaceae and their length and presence or absence are evidently conditioned environmentally. Therefore this character has limited value as a diagnostic character.

The laminal cells and leaf margins are unistratose in most plants of *Codriophorus carinatus*, but in some populations the leaf margins are variously bistratose in the distal half in 1–3 rows of cells and the upper laminal cells sometimes possess bistratose streaks (Fig. 61). Such a character state also agrees with a general tendency in the Grimmiaceae and the genus *Codriophorus* itself, especially in species associated with aquatic habitats, and variously multistratose laminal cells and leaf margins are observed in such species as *C. acicularis*, *C. aquaticus*, *C. depressus*, and *C. brevisetus*. The leaf margins are distinctly recurved on one side and plane on the other side in *C. carinatus* but occasionally they are plane on both sides (e.g., *Mayebara 1849*, MAK).

Within individual populations of *Codriophorus carinatus*, the variation in seta length is generally less than two millimetres but it is considerably greater among various populations in general, for example, from 1.9 to 2.3 mm in one population (*Deguchi s.n.*, HIRO-13217) and in another from 6 to 7 mm (*Iwasaki 8080*, MAK). There is also some interpopulational variation in capsule length. The capsules are generally cylindrical, from 1.5 to 2.1 mm long, but occasionally they are obloid and very short, from 1.0 to 1.2 mm (*Deguchi s.n.*, HIRO-13217) and these short capsules are correlated with short setae supporting them.

Codriophorus carinatus varies in habit, size, colour and branching of plants and stems, but no excessive deviations from typical phenotypes have been observed. Most specimens examined are moderately sized and slender plants, with stems ranging from 2.5 to 5.5 cm in length, and the largest and fairly coarse plant has stems up to 9 cm long (*Iwasaki 1303*, MAK), whereas the smallest one collected in a dry site merely reaches about 1 cm (*Iwatsuki & Sharp 39D*, TENN). The stems are variously branched, dichotomously with a few elongate branches or fasciculately with many shorter branches, but sometimes they are filiform and almost unbranched (*Nakashima 3143 & 4357*, HIRO). The colour of the plants is typically olivaceous, dark green to yellow-, olive- or golden-brown and occasionally the plants are rusty-brown.

Reproduction — Codriophorus carinatus produces sporophytes frequently only in Japan, although even there not in great profusion. On mainland Asia, it is consistently sterile and sporophytes have so far been detected only in a single population from Korea (*Shevock 16377*, CAS, KRAM, MO) and Taiwan.

Taxonomic and nomenclatural notes — Codriophorus carinatus was recognised for the first time as a separate taxon by Bescherelle (1893) who described it as a variety, *Racomitrium aciculare* var. *brachypodium* from a single collection from Japan. Cardot (1908a) raised this variety to species, *R. brachypodium*, and provided an expanded description of the taxon, stressing the differences between



FIGURE 61. Codriophorus carinatus. — 1–5. Transverse sections of leaves. — [1 from Faurie 2921, s, isotype of Racomitrium fauriei; 2 from Wu 1047, MO; 3 from Iwatsuki & Smith 1002, NY; 4 from Deguchi s.n., 4 Aug 1973, HIRO; 5 from Faurie 643, H, isotype of R. carinatum]. — Scale bar: 100 µm.

it and *R. aciculare*, *R. nevii* and, newly described in the same paper, *R. fauriei* from Japan. He compared the last species to *R. protensum* and found it to be variable and distinguished two plants as a separate form, fo. *irrigatum*, but its status must remain uncertain since neither of the two syntypes has been located. Finally, in the same paper Cardot (1908*a*) described *R. carinatum* and *R. sudeticum* var. *subellipticum* which was later elevated to species rank by Sakurai (1937*a*). As discussed above, all these taxa are here considered identical. Interestingly, in 1908, three

specific names were proposed for these taxa which are now considered to represent a single species and actually any one of them could have been chosen as its final name. The epithet *carinatus* is accepted for this species since this name is firmly rooted in the literature (Noguchi 1974, 1988; Iwatsuki 1992, 2001, 2005; Cao *et al.* 2003). Moreover, as *Racomitrium fauriei* was treated as a synonym of *R. aquaticum* and *R. brachypodium* was considered to be a variety of *R. heterostichum* (Noguchi 1974, 1988), using either of these epithets could lead to confusion.

Chromosome number — Not available.

Habitat — Codriophorus carinatus is a rupicolous moss that grows in wet to moist or dry, shaded or open habitats on acidic granite or volcanic rocks. It has been found on stones and boulders in stream and river beds and on cliffs, rock outcrops and slabs, rarely on soil on banks of streams, streamlets and rivers throughout montane temperate broad-leaved, mixed hardwood-coniferous forest and in subalpine coniferous forest, occasionally also in subtropical bamboo forest and sometimes also in swamps in the alpine region. There is no information on the herbarium labels concerning its submergence or occurrence in running water, although some plants are encrusted with silt and this may indicate growing in at least temporarily inundated sites. It has been found growing in mixed stands with other species of the genus (C. corrugatus, C. anomodontoides, and C. brevisetus) as well as Niphotrichum barbuloides (Cardot) Bednarek-Ochyra & Ochyra and Dryptodon brachydictyon (Cardot) Ochyra & Żarnowiec.

Geographical distribution — Codriophorus carinatus is an East Asian species, with its main centre of occurrence in Japan and is scattered on mainland Asia from southern Kamchatka to Taiwan (Fig. 63). In Japan, the species extends from Rebun Island in the north to Yakushima Island in the south, with a remarkable concentration of localities in central Honshu, where it extends from coastal regions at an elevation of 100 m to the alpine zone with the highest locality at 2600 m on Mt Otensho and with most localities in the subalpine and alpine zones in this part of Japan. On Hokkaido and Kyushu the species occurs at lower elevations, from 150 to 1200 m, and only once was it recorded at 1700 m on Hokkaido. On the continent it is rare and scattered in South Korea where it occurs at altitudes from 500 to 1500 m, in Southeast China from 100 to 1320 m and in the alpine zone on Taiwan at elevations from 2100 to 2500 m. In addition, it is known from a single and highly isolated locality on southern Kamchatka (Bednarek-Ochyra & Czernyadjeva 2003). Cao et al. (2003) reported it from Liaoning Province in Northeast China but the material was not available for examination.

EXSICCATI

NOGUCHI & IWATSUKI – *Musci Japonici Exsiccati* No. **1341** (ALTA, BR, CANM, F, GZU, H, KRAM, MICH, MO, NY, POZG, S, TENN, US).

SELECTED SPECIMENS EXAMINED

ASIA. CHINA. ANHUI PROV. She Xian Co.: Huang Shan, 1320 m, 20 May 1982, Gao Chien s.n. (MO). JIANGSU PROV. Yixing Co.: Yangdian, Taikua, Qian-Yun-Jie, 100–300 m, Pan-cheng Wu & Y.-X Jin 2126 (MO). ZHEJIANG PROV. Lin-an Co.: Mt Xi-tian-mu, Wu Pan-cheng 1047 (MO).

JAPAN. HOKKAIDO. Abashiri Pref.: Mt Rausu, Shari-cho, Sharigun, 950 m, Deguchi s.n. (HIRO-12555); Mt Rausu, Shari-gun, Shari-cho, (Okhotsk-tenbo (460 m) - Ginreisui (1020 m), Seki s.n. (HIRO-24172); Mt Shari, Kamishari-mura, Shari-gun, 800 m, Deguchi s.n. (HIRO-12508). Kamikawa Pref .: Mt Ashibetsu, Furano-city, 1140 m, Deguchi s.n. (HIRO-12359) and 1700 m, Deguchi s.n. (HIRO-12384); Mt Ponkaun -Ten' ninkyo gorge, Biei-cho, Kamikawa-gun, 1200 m, Deguchi s.n. (HIRO-12319); Mt Daisetsu, Kawakami-gun, Tsujibe s.n. (MAK-B9226). Sôya Pref.: Mt Rebun, Rebun-cho, Rebun-gun, Rebun Island, 426 m, Deguchi s.n. (HIRO-11997); Himenuma, Higashi-Rishiri-cho, Rishirigun, 130 m, Deguchi s.n. (HIRO-12157), Mt Rishiri, Higashi-Rishiri-cho, Rishiri-gun, 350 m, Deguchi s.n. (HIRO-12075A). Sorachi Pref.: Minami'shokan mountain hut - Uryu bog, Uryu-cho, Uryu-gun, 600 m, Deguchi s.n. (HIRO-12653). Tokachi Pref.: near Tomuraushi spa, Shintoku-cho, Kamikawa-gun, 450 m, Deguchi s.n. (HIRO-11769), 480 m, Deguchi s.n. (HIRO-11690 & 11768) and 500 m, 25 June 1973, Deguchi s.n. (HIRO-11757); Mt Haku'un, lakeside of Shikaribetsu, Shikaoi-cho, Kato-gun, 1000 m, Deguchi s.n. (HIRO-12440 & 12443); E foot of Mt Rakkodake, Hidaka Mountains, 200-400 m, Inoue 19805 (TNS). HONSHU. Aichi Pref.: Kitashidara-gun, Mt Horaiji, Iwatsuki 531 (NICH); Hachigome, Kita-keryu, Mt Hongusan, border of Nukada-gun and Hoi-gun, Takaki 5839 (MAK-B57672). Akita Pref.: Akita City, Koie 218 (MAK); Yuri-gun, Kisakata-machi, Shishigabana, 520 m, Higuchi 21596 (TNS); Prov. Rikuchiu, Sukawa, Uematsu 1116 (H); Mt Sukawa, Jul 1906, Uematsu s.n. (H). Aomori Pref.: Aomori-shi, Mt Hakkoda, Sugayu Spa, ca 1000 m, Watanabe 17358 (NICH); Hakkoda, 1100 m, Faurie 2921 (FH, H, KRAM, NY, PC, S, type of Racomitrium fauriei); Mt Hakkoda, Odake, ca 900 m, 3 Aug 1954, Noguchi s.n. (WTU); Aomori, Faurie 202 (ВМ, Н, РС, s, neotype of R. aciculare var. brachypodium). Fukushima Pref .: Nishigo-mura, Nishishirakawa-gun, Higuchi 104 (MAK); Nishi-shirakawa-gun, Nishigo-mura, Kannko Spa, 900 m, Suzuki s.n. (HIRO-20759); Mt Handayama, Koori-machi, Date-gun, sine collector (MAK-B57665); Mt Hiuchigatake, Hinoemata-mura, Minamiaizu-gun, Maeda s.n. (MAK-B57759) and Yagi 991 (MAK); Kawamata, Prov. Iwashiro (old name for central and western parts of Fukushima Pref.), 2 Aug 1918, Yasuda s.n. (CAS); Mt Azuma, Higuchi s.n. (MAK-B57683A). Gifu Pref.: Takayama-shi, Deguchi s.n. (HIRO-13133); Prov. Hida (old name for N part of Gifu Pref.), Kamidakara-mura, Yoshiki-gun, Sasaoka 1287 (0). Gunma Pref .: Mt Shibutsu, Tone-gun, Yagi 1051 (MAK); Mt Tanigawa-dake, Tone-gun, Sakurai s.n. (MAK-B6987A); Mt Shirane, border of Tochigi Pref. and Gunma Pref., Tezuka s.n. (MAK-B57761); Mt Akagi (Mt. Kurobi), Fujimi-mura, Seta-gun, 1450 m, Deguchi s.n. (HIRO-17109), 1460 m, Deguchi s.n. (HIRO-17112) and 1520 m, Deguchi s.n. (HIRO-17118); Mt Haruna, Haruna-cho, Gunma-gun, Sakurai s.n. (MAK-B910); Kotsuka, Mt Haruna, Sakurai 910 (H); Kadoka, Mt Akagi, Tsunoda 1395 (H). Hiroshima Pref.: Hiramidani, Togouchi-cho, Yamagata-gun, ca 590 m, Nakashima 3697 (HIRO); Mt Ohouki yama, Nukui, Kake-cho, Yamagata-gun, 530 m, Nakashima 3811 (HIRO); Shimoyama, Togouchi-cho, Yamagata-gun, ca 430 m, Nakashima 3068 (HIRO), ca 450 m, Nakashima 4263 (HIRO) and ca 460 m, Nakashima 3143 (HIRO); Shimoyama, Togouchi-cho, Yamagata-gun, Riv. Osa, ca 460 m, Nakashima 4292 & 4357 (HIRO); Hibayama Mountains, Kenashiyama, 1110 m, Ando s.n. (HIRO-28053); Mt Ungetsu, 28 May 1961, Ando s.n. (PR). Hyogo Pref .: Yabu-gun, Sekinomiya-cho, Mt Hyônosen, 1200 m, Miyata 4607 (NICH); Taki-gun, Tannan-cho, 350 m, 8 Jue 1969,

FIGURE 62. *Codriophorus carinatus.* — 1. Portion of branch with mature capsule, wet. 2. Perigonium. 3. Outer perigonial bract. 4. Inner perigonial bract. 5. Innermost perigonial bract and antheridia. 6–8. Perichaetial leaves, sequentially from outermost to innermost. 9. Apex of innermost perichaetial leaf. 10. Epidermal cells of vaginula. 11. Transverse section of seta. 12–13. Operculate capsules, wet. 14–15. Deoperculate capsules with destroyed peristomes, wet. 18. Deoperculate capsule with peristome, wet. 17. Operculum. 18. Calyptra. 19. Transverse section of calyptra. 20. Exothecial cells in mid-urn. 21. Exothecial cells at base of urn and stomata. 22. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 6–8, 12–13, 16–22 from *Takaki 5839*, MAK; 2 from *Takahashi s.n.*, MAK-5057; 3–5, 9, 11 from *Ikegami s.n.*, 13 Apr 1947, MAK; 10 from *Maeda s.n.*, 4 Aug 1950, MAK; 14–15 from *Deguchi s.n.*, 14 Aug 1973, HIRO]. — Scale bars: a – 1 mm (12–18); b – 100 μ m (9, 20–22); c – 100 μ m (10–11, 19); d – 1 mm (6–8) and 2.5 mm (1); e – 1 mm (2–5).





FIGURE 63. Global distribution of Codriophorus carinatus.

Nakajima s.n. (ALTA, BR, CANM, F, H, KRAM, MICH, MO, S, TENN, US) [Musci Jap. Exs. No. 1341]. Ibaraki Pref.: Mt Tsukuba, Tsukuba-machi, Tsukuba-gun, Hisauchi s.n. (MAK-B7035, TNS) and sine collector (MAK-B101962). Ishikawa Pref.: Ishikawa-gun, Shiramine-mura, Iwama-Spa, 720 m, Ando s.n. (HIRO-26360). Iwate Pref.: Prov. Rikuchu, between 3-gome and Aion-zawa, Kadomaguchi, Mt Hayachine, ca 850 m, Takaki 36669 (TNS); Mt Hayachine, Iishiba 1272 (H); Prov. Rikuzen, Mt Omae, Iishiba 720 (H); Iwate-gun, Matsuo-mura, Hachimantai, ca 1400 m, Watanabe 5008A (NICH). Kanagawa Pref.: Hakone, 8 Jul 1947, Abel s.n. (PC). Mie Pref.: Mt Komono, Komono-cho, Mie-gun, Iwasaki 1303 (MAK); route from Dōgura mountain lodge to Momonoki mountain cottage, Miyagawa-mura, Taki-gun, 720 m, *Deguchi s.n.* (HIRO-7991); Owasetsuji – Kaminari pass, Miyama-cho, Kitamuro-gun, 1500 m, *Deguchi s.n.* (HIRO-10107). *Miyagi Pref.*: Tenshudai, Sendai, 20 Oct 1907, *Iishiba s.n.* (H); Mt Zao, *Iishiba 379* (H); Onikobe, *Faurie 161* (KYO – syntype of *Racomitrium sudeticum* var. *subellipticum*). *Nagano Pref.*: Mt Kurohime, Shinano-machi, Kamiminochi-gun, *Iwasaki 5825* (MAK); Mitsumata – Mt Chogatake, Horigane-mura, Minami-Azumi-gun, 1450 m, *Deguchi s.n.* (HIRO-12848) and 2080 m, *Deguchi s.n.* (HIRO-12855); Mt Komagatakekomanoyu, Kisofukushima-cho, Kiso-gun, 2440 m, *Deguchi s.n.* (HIRO-13069); Mt Otensho – Mt Nishidake, Azumi-mura, Minami-azumi-gun, 2600 m, *Deguchi s.n.* (HIRO-12915); Mt Togakushi, Togakushi-mura, Kami-mizuuchi-gun, 1700 m, Deguchi s.n. (HIRO-13202); Mt Togakushi, Kamiya 163A (H); Mt Shirouma, Lake-Ôike, Takaki 304 (F); Mt Shirouma, 1 Aug 1949, Takaki s.n. (S) and Iishiba 1274 (H, PC) &1250 (H); Minami-azumi-gun, Azumi-mura, Mt Yarigadake, ca 2100 m, Watanabe 11468 (NICH); Shimotakai-gun, Mt Yokote, 2200 m, Jinno s.n. (HIRO-14731). Nara Pref.: Mt Odaigahara, Yoshinogun, Toyama 761 & 775 (MAK); Mt Oodaigahara, ca 1600 m, 6 Aug 1970, Kodama s.n. (ALTA, BISH, DUKE, hb. Frahm, MICH, PR); Yamato, Mt Oodaigahara, 1000 m, Anonymous 775 (s); route from Ozasano-yado to Mt Shofugen (1580 m), Yoshino-gun, 1560 m, Deguchi s.n. (HIRO-6613); route from Shiokaradani valley to Sengokugura via Nakanotaki fall, Kamikitayama-mura, Yoshino-gun, 1300 m, Deguchi s.n. (HIRO-7948); Masakigahara, Kami'kitayama-mura, Yoshino-gun, ca 1600 m, Deguchi s.n. (HIRO-5114); route from Ushi'ishigahara to Daijagura, Kamikitayamamura, Yoshino-gun, 1480 m, Deguchi s.n. (HIRO-7864); Shônoiwaya -Mt. Daifugen, Kamikitayama-mura, Yoshino-gun, 1580 m, Deguchi s.n. (HIRO-10584); Sanjogatake, en route from Seijo-Ochashi to summit of Mt Sanjo, Tenkawa-mura, Yoshino-gun, 1000 m, Deguchi s.n. (HIRO-6389); Mt Wasamata - Shônoiwaya, Kamikitayama-mura, Yoshino-gun, 1400 m, Deguchi s.n. (HIRO-10508); Mt Togakushi, Shinano (old name for Nagano Prefecture), Iishiba 910 & 927 (H) and Kamitani 230 (H). Niigata Pref.: Mt Yukyu-zan, Nagaoka City, Iwasaki 6136 (MAK); Mt Myoko-san, Nakakubiki-gun, Iwasaki 2674, 4919 & 8080 (MAK); Mt Myoko, Nakakubiki-gun, Sakurai 1006 (мак); Mt Myoko, Myokokogen-cho, Naka-kubiki-gun, 1400 m, Deguchi s.n. (HIRO-12977); Mt Futaoji, Kitakanbara-gun, Yagi 888 (MAK); Kanatsu, Niitsu City, Ikegami 8849 (MAK); Mt Kurosawa-dake, Nakakubiki-gun, Yagi s.n. (MAK-B57763); Mt Kinpoku-san, Sado-gun, Ikegami 6488 (MAK); Kanazu, Niitsu City, Yagi s.n. (MAK-B57757); Haraigawa, Kamikawa-mura, Higashikanbara-gun, Yagi 382 (MAK); Gomisawa, Irihirose-mura, Kitauonuma-gun, Ikegami 11647 (MAK); Iwafune, Sekikawa, Sawa, 100 m, Ikegami 49974 (TENN); Yashiro, Arai City, Iwasaki s.n. (MAK-B57675). Saitama Pref.: Chichibu-gun, Mt Kobushi, 2300 m, Jinno s.n. (HIRO-14698); Chichibu-gun, Jumonji Pass, ca 2000 m, Jinno s.n. (HIRO-14691). Shimane Pref .: Nitamaki, 14 Aug 1964, Nishida s.n. (WTU); Fusigama (=Ushigama), Aug 1888, Miyoshi s.n. (H). Tochigi Pref.: Uramino-taki, Nikko Citv, Mizushima s.n. (MAK-B57669); Nikko Citv, Osada s.n. (MAK-B6979); Mt Nikko, Kono 41 (H) AND Okamura 693 (H); Prov. Shimotsuke (old name for Tochigi Prefecture), Mt Konsei (near Nikko), Sasaoka 6591 (BM); Mt Nantai, Osada 6572 (BM) & 6473A (BM, FH). Tokyo Pref .: Hikawa-machi, Mt Tenso, 6 Jul 1940, Hattori s.n. (NICH); Tokyo Met., Mt Takamizu, Ome City, Tezuka s.n. (MAK-B33776). Toyama Pref.: Midagahara, Mt Tateyama, 2000 m, Iwatsuki et al. 144A

(TENN) and 2000-2100 m, Iwatsuki & Sharp 42A (TENN); prov. Etchu (old name for Toyama Prefecture), Sekidô, Sasaoka 1287 (BM); Mt Isurugi, 20 Aug 1915, Sasaoka s.n. (BM). Wakayama Pref.: Shingu; route from Ichinotaki fall to Ninotaki fall, Nachikatsuura-cho, Higashi murogun, 380 m, Deguchi s.n. (HIRO-6963 & 7021). Yamagata Pref.: Mt Gassan, Higuchi 9 (MAK). Yamanashi Pref.: Hirogawara - Shirane-oike mountain hut, Ashiyasu-mura, Nakakoma-gun, 1920 m, Deguchi s.n. (HIRO-13217); Kai (old name for Yamanashi Prefecture), Mt Taomoku, Tamura 85 (H). KYUSHU. Kagoshima Pref.: Yakushima Island, Tainokawa valley, 150-450 m, Iwatsuki et al. J-1075 (NY) and 250-450 m, Iwatsuki, Sharp & Sharp 15627 (NICH); Yaku-sugi Kanshorin, ca 1000 m, Iwatsuki & Smith J-1002 (NY); Yakushima Island, ca 420 m, Iwatsuki & Smith J-934 (NY); along the valley of the Suzukawa between Onoaida and the falls, 150-500 m, Iwatsuki & Sharp 15581 (TENN); near "Wilson's Tree" above Kosugidani, 1000-1200 m, Iwatsuki & Sharp 15140 (TENN). Kumamoto Pref .: Kikuchisuigen, ca 400 m, 28 Nov 1967, Noguchi s.n. (NICH, WTU); Hitoyoshi, Yotoyoshi City, 200 m, Mayebara 3455 (MAK) and 300 m, Mayebara 1849 (MAK). Miyazaki Pref.: Mt Sobo-san, Nishiusuki-gun, Takahashi 102 (MAK); Ebino-Cho, Iwatsuki & Smith J-106 (NY); Kirishima, circumference of the Onami, Kuwahara 42A (NY). Oita Pref .: Mt Sobo, ca 800 m, 18 Oct 1952, Noguchi s.n. (WTU) and 3 Nov 1931, Noguchi s.n. (NICH). SHIKOKU. Ehime Pref.: Mt Ishizuchi, Kono 231 (H); Mt Ishizuchi, Senzokuyama, Saijo City, Kochi s.n. (MAK-B57678 & 57670); Mt Daitenjo-dake, Minamiazumi-gun, Maeda 1223 (MAK) & Sugiuchi s.n. (MAK-B57676).

RUSSIA. FAR EAST. Kamchatka Prov. West Kamchatka, basin Left Kihchik River, Czernyadjeva 116 (KRAM, LE).

SOUTH KOREA. Ile Quelpaert (=Cheju Island), 1200 m, Faurie 643 (H, PC, s, type of Racomitrium carinatum). CHEJU-DO PROV. Pukcheju-gun Co.: Hallasan National Park, along Songp'anak Trail toward Mt Hanna at Chiaallachat-daep'iso Camp west of highway 11 from Songp'anak Rest Area, 1500 m, Shevock 16377 (CAS, KRAM, MO). KYONGGI-DO PROV. Nowan-gu Co.: Uijongbu Region, Tobongsan area, trail to Tobongsan from trailhead W of Tobongsan train station and highway 3, 500–700 m, Shevock 16128 (CAS, KRAM, MO). Tobong-Gu Co.: Puk'ansan National Park, along trail to Paegundae, on N side of Seoul, 700 m, Shevock 16062 (CAS, KRAM, MO).

TAIWAN. *Pingtung Co.*: Kwai-ku, 2190 m, *Ching-chang Chuang* 1402 (mo); Ako, Mt Daibu, (Ako – Japanese name of Kaohsiung including Pingtung), *Matsumura 1311* (H). *Taichung Co.*, Hsueh Shan Shan Mo, hardwood forest just below Anma-shan, *ca* 2100 m, *Iwatsuki & Sharp 1365* (TENN); Hsueh Shan Shan Mo, 17 km above Anma-shan, near Chunghsueh-shan, *ca* 2500 m, *Iwatsuki & Sharp 913* (TENN).

A3. Subsection Depressi Bednarek-Ochyra, subsect. nov.

Plantae magnae robustaeque, laxe caespitosae. Folia sicca erecto-appressa, humida erecto-patentia, homomalla, lanceolata, oblongo-lanceolate vel late ovata, apice obtusa vel acuta, concavo-canaliculata, nervo latissimo lato planiusculo, margine medio revoluta, superne reflexa, apice integerrima vel denticulis remotis irregularibus obtusis instructa, cellulis laminae laevissimis vel minutissime papillosis, superioribus ovatorotundatis, frequenter bistratosis, medianis et basilaribus elongatis. Capsula in pedicello brevi, dextrorsi, subcylindrica, nonnumquam gibbosa. Dentes peristomii bifidi vel tripartiti, cruribus inaequalibus vel liberis, superne papillosis.

Type: Codriophorus depressus (Lesq.) Bednarek-Ochyra & Ochyra (Racomitrium depressum Lesq.).

Plants large and coarse, forming loose or dense tufts, dull, olive-, yellowish- or blackish-green, olive-brown, olivaceous or black, prostrate, ascending or erect, simple to dichotomously or fasciculately, rather sparingly branched. *Leaves* crowded to distant, erect-imbricate on drying, erect-spreading when wet, often homomallous, straight to weakly curved, sometimes falcate, lanceolate, oblong- or ovate-lanceolate to broadly ovate, acute or obtuse, muticous at the apex, broadly concave to canaliculato-concave; *margins* entire throughout or bluntly, irregularly dentate or sinuate at the apex, variously recurved on one or both sides to $\frac{1}{2}-\frac{3}{4}$ of the way up the leaf, unistratose throughout to variably bistratose near the apex; *costa* subpercurrent, flat and very broad, in cross-section reniform to sub-elliptical, 2–3-stratose in the upper and median parts, with 4–7(–10) ventral cells, becoming transversely rectangular, strongly flattened and convex on the dorsal side, situated at the bottom of a shallow, wide-angled channel in the lower half, with 7–11(–15) enlarged ventral cells; *laminal cells* unistratose throughout or variously bistratose in the distal part, isodiametric to short-rectangular in the upper part, becoming long rectangular in the median and lower parts; basal cells with strongly incrassate, nodulose and porose walls; alar cells not differentiated or large, with thick and porose walls forming enlarged, decurrent auricles; supra-alar cells not differentiated or forming a short marginal border of 2-8, esinuose, pellucid cells. Dioicous. Innermost perichaetial leaves oblong to oblong-ovate, rounded to broadly acute at the apex, yellowish-hyaline throughout. Setae short, dextrorse. Capsules exserted, obloid to cylindrical, straight or slightly curved and gibbous; *operculum* long rostrate, with a long oblique beak; exothecial cells rectangular, firm-walled; peristome teeth erect, curved inwards when dry, reddishto yellowish-brown, two thirds divided into 2-3, terete, irregular, papillose prongs, with a low, finely papillose to nearly smooth basal membrane. Spores globose, light brownish, finely papillose. Calyptra long rostrate, 4-5lobed at the base, papillose at the apex.

Codriophorus subsect. Depressi is a monotypic taxon that consists only of C. depressus. This taxon is characterised by the following set of characters: (1) leaves straight to weakly curved, strongly concave below, broadly canaliculato-concave in the distal part; (2) leaf apex acute to obtuse, muticous, entire, sinuate or with some blunt, irregular teeth; (3) costa very broad and flattened, lying at the base of a shallow, wide-angled groove below, with a row of 7-11(-15) enlarged ventral cells and 3-4 layers of stereid cells, reniform to sub-elliptical, 2-3-stratose in the median and upper parts; (4) laminal cells entirely unistratose to variously bistratose in the upper part, smooth to finely papillose, rounded-quadrate to short-rectangular above, long rectangular below; (5) innermost perichaetial leaves yellowish-hyaline throughout; (6) capsules obloid to cylindrical, straight to weakly curved and gibbous; (7) peristome teeth bifid or tripartite to two thirds into irregular, papillose, terete branches.

Morphologically, *Codriophorus depressus* is certainly most closely related to *C. acicularis* and *C. aquaticus* and, as suggested in the original description by Lesquereux (1868), it is intermediate between these two species which are classified into two different subsections within the type section of *Codriophorus* and are characterised primarily by having distinctly papillose laminal cells. However, *C. depressus* does not fit either of them. Therefore, its smooth or only very slightly papillose laminal cells, as well as the extraordinary structure of its costa, coupled with the occasionally asymmetric capsules and frequently tripartite peristome teeth fully warrant recognition of a separate subsection to accommodate this anomalous and aberrant species.

Ecologically, *Codriophorus depressus* is also quite distinctive in its habitat specificity from both *C. acicularis* and *C. norrisii* which occur in perennial aquatic systems generally along streams and rivers where they are seasonally submerged on rocks and boulders. However, *C. depressus* is distributed along intermittent streamlets, rivulets, and sheet rock drainages where the plants are hydrated during snowmelt. Plants of *C. depressus* therefore can form mats that can extend for metres over rock slabs and rock terraces. The growth form of *C. depressus* is

rather prostrate across the substrate. Plants of *C. depressus* are generally wet during the snowmelt period between late May through early July, then dry until the habitat is under snow from November to May. In *C. acicularis* and *C. norrisii*, the plants are hydrated during the winter rain season since these taxa occur in lower elevations, and are then submerged when this habitat is near flood stage.

Codriophorus depressus (Lesq.) Bednarek-Ochyra & Ochyra (Figs 64–66)

Codriophorus depressus (Lesq.) Bednarek-Ochyra & Ochyra, Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. = *Racomitrium depressum* Lesq., Mem. Calif. Acad. Sci. 1: 14. 1868. — TYPE CITATION: Falls of the Yosemite Valley, *Bol.[ander]*. [Holotype: "Racomitrium depressum sp nov Mem Cal Acad Not Vol 1 p 51 f. viii Racomitrium acicular var ?? Intermediate between R. aciculare & R. cataractarum Braun I will see more of it when I have fruit Yosemite valley Bol. 1. – FH-Lesquereux!; isotype: NY!].

Plants large, robust and coarse, occasionally fairly gracile, stiff and rigid, loosely to densely caespitose or forming extensive patches, dull to slightly glistening, olive- or yellowish-green, olive-brown, olivaceous, golden- or rufous-brown to blackish-green above, brown to blackish brown below, sometimes dark blackish-green to black throughout. Stems erect, ascending or procumbent, (2-)4-10(-13) cm long, tough, often denuded and appearing bristly below due to erosion of the leaf laminae except for the costae in rapidly flowing water, sparingly dichotomously branched with a few long branches or profusely fastigiately branched with shorter branches, sometimes with a few short lateral branchlets, sometimes almost unbranched, not or sparsely to densely radiculose in the lower part with blackish- or reddishbrown or brown, glossy, branching rhizoids, in transverse section circular, lacking a central strand and consisting of a 2-4-stratose cortex of sclerenchymatous cells with small lumina and incrassate walls and a 6-8-layered medulla of large, hyaline, moderately thick-walled cells; axillary hairs filiform, hyaline throughout, composed of 10-18 cells, short or elongate distally. Leaves densely set to distantly spaced, loosely erect-appressed, often homomallous when dry, erecto-patent when moist, straight, weakly curved to falcate, lanceolate, oblong- or ovate-lanceolate to broadly ovate, (2.1-)3.0-4.5(-5.0) mm long, (0.8-)1.0-1.3(-1.5) mm wide, acute or obtuse at the apex, epilose, broadly concave below, broadly canaliculate-concave or only occasionally narrowly canaliculate above, often dilated and semi-auricled at the shortly decurrent base; margins entire, sometimes sinuate or with a few blunt, irregular teeth at the apex, unistratose throughout or bistratose distally in several rows of cells, broadly recurved to $\frac{1}{2}-\frac{3}{4}$ of the the leaf length on one side, plane to more narrowly recurved to mid-leaf on the other side, occasionally plane on both sides; costa single, subpercurrent, clearly delimited from the laminal cells but often less so towards the apex and merging with the bistratose laminal cells, occasionally weakly spurred above, strong,



FIGURE 64. Codriophorus depressus. — 1. Habit, wet. 2. Portion of branch, wet. 3–19. Leaves. 20. Stem section. — [1-2 from Bolander 373, US; 3-4 from Flowers 5449, COLO; 5-7 from Flowers 5452, ALTA; 8–11 from Shovers 2437, WTU; 12–14 from Bolander 511, FH, holotype of Racomitrium depressum; 15–17 from Lavin 572D, WTU; 18–20 from Shevock 17525, KRAM]. — Scale bars: a – 1 mm (3–19); b – 10 µm (20); c – 1 cm (1); d – 0.5 cm (2).

(80-)100-200 µm wide at the base, gradually tapering upwards, 55-80(-130) µm wide in the upper part, in transverse section strongly flattened, situated in a shallow, wide-angled furrow, 3-4(-5)-stratose at the base, consisting of 7-11(-15) enlarged ventral cells and 2-3(-4)layers of small, stereid cells, forming a distinctly convex band on the dorsal side, flat or somewhat concave on the ventral side, becoming 2-4-stratose in mid-leaf and 2-3stratose in the distal part, with 4-7(-10) ventral cells, not or scarcely differentiated from those in the central and dorsal rows, reniform to sub-elliptical, U-shaped on the ventral side, scarcely convex dorsally, usually nearly as thick as the lamina; laminal cells unistratose throughout or entirely to partially bistratose in the distal part, smooth or very slightly papillose on young leaves, pellucid, quadrate, rounded-quadrate to short-rectangular, with strongly thickened and weakly sinuose walls in the upper part, (8-)10-20 µm long, 8-10 µm wide, becoming rectangular in mid-leaf, (13-)20-45 µm long, 5-8 µm wide, with thick and sinuose walls, and long rectangular above the base, 30-75 µm long, 5-8 µm wide; basal cells long rectangular, 50-70 µm long, 7-10 µm wide, with strongly incrassate, nodose and porose walls, forming a 2-3-seriate, yellow- or orange-brown strip along the leaf insertion; alar cells similar to the adjacent basal cells or larger, 40-100 µm long, 10-18 µm wide, with strongly incrassate, porose and nodose walls, forming convex, decurrent, dark brown or dark yellow auricles; supra-alar cells not differentiated or 2-8 cells hyaline, with esinuose walls, forming a short marginal border. Dioicous. Perigonia bud-like, 2.5-3.0 mm long; outer perigonial bracts ovate, acuminate, 2.2-3.0 mm long, 1.0-1.1 mm wide, entire, with a narrow, distinct, subpercurrent costa; inner perigonial bracts ovate, broadly acute, 1.7-1.8 mm long, 0.9-1.0 mm wide, pale brown, deeply concave, the innermost one comprising 10-12 brown antheridia intermingled with a few pale hyaline-brownish, short paraphyses. Outer perichaetial leaves lanceolate to oblong-lanceolate, 3.0-3.6 mm long, 1.0 mm wide, similar to the vegetative leaves; innermost perichaetial leaves oblong to oblong-ovate, 1.8-2.3 mm long, 0.8-1.0 mm wide, broadly rounded to acute at the apex, with a faint subpercurrent costa, yellowish-hyaline throughout. Setae single or, rarely, 2-3 per perichaetium, erect, straight, 4.5-7.0 mm long, brown, smooth, dextrorse; vaginula dark brown, ca 1 mm long, with sinuose- and moderately thick-walled epidermal cells. Capsules exserted, erect, obloid to cylindrical, 1.8-3.0 mm long, 0.8-1.0 mm wide, straight and symmetric or slightly curved and gibbous, brown to reddish-brown, lustrous, pachydermous; operculum conical-rostrate, with a slanted beak, 1.2-2.0 mm long, dark brown below, light brown above; annulus deciduous, 2-3-seriate, reddish-brown, composed of vesiculose cells with strongly incrassate walls; exothecial cells mostly rectangular, 25-60 µm long, (12-)15-20(-25) µm wide, moderately thick-walled, becoming short-rectangular to rounded-quadrate in 4-5 rows at the mouth; stomata 9-10 per capsule at the base of the urn, disposed in 2(-3) rows, rounded, 37-42 µm wide, superficial, bicellular, with rounded pori; *peristome teeth* 16, erect, curved inwards when dry, arising from a low basal membrane, 350–500 µm high, lanceolate but irregular in outline, reddish- or yellowish-brown, finely papillose to nearly smooth below, densely low-papillose above, deeply bifid or tripartite down for two thirds of their length, with unequal, terete, articulate, free or cohering prongs, often with irregular openings below; *preperistome* low, to 50 µm tall, hyaline. *Spores* spherical, light brownish, very finely roughened, (10-)12-15(-17) µm in diameter. *Calyptra* long rostrate, 2.0–2.2 mm long, 4–5-lobed at the base, light brown below, dark brown, distinctly verrucose at the tip.

Etymology — The specific epithet derives from the Latin *depressus* which means flattened from above and somewhat sunken at the centre and it refers to the shape of the costa.

Diagnostic characters and differentiation — Codriophorus depressus is differentiated from all other species of Codriophorus by a combination of the following of diagnostic characters: (1) semi-aquatic plants, large and coarse, with tough, moderately branched stems; (2) leaves lanceolate, oblong- or ovate-lanceolate to broadly ovate, acute or obtuse at the apex, epilose, broadly canaliculate-concave above and broadly concave below; (3) margins entire throughout or bluntly dentate or sinuate at the apex, unistratose throughout or variably bistratose at the apex, variously recurved on one or both sides to about $\frac{3}{4}$ of the leaf length; (4) costa subpercurrent, very broad and strongly flattened, lying in a shallow and wide-angled groove in the basal part, 3-4(-5)-stratose with a row of 7-15 enlarged ventral cells near the base and 2-4 layers of stereid cells, reniform to sub-elliptical above, weakly convex dorsally and U-shaped ventrally; (5) laminal cells unistratose throughout to variously bistratose near the apex, smooth or very weakly papillose, quadrate, rounded-quadrate to short-rectangular in the upper part, long rectangular below; (6) alar cells not differentiated or enlarged, with strongly incrassate and porose walls forming swollen and decurrent auricles; (7) basal marginal border wanting or very short, consisting of 2-8 cells; (8) innermost perichaetial bracts yellowish-hyaline throughout; (9) seta short, dextrorse; (10) capsules obloid to cylindrical, straight or somewhat gibbous; (11) peristome teeth curved inwards when dry, divided into 2-3papillose prongs for two thirds of the tooth length, with a low basal membrane.

Codriophorus depressus is primarily characterised by the costa which is exceptionally broad, strongly flattened and weakly convex on the dorsal side and U-shaped ventrally in the distal part. The combination of this feature and leaves that are broadly concave to broadly canaliculate as well as laminal cells that are smooth or only very slightly papillose is so distinctive that *C. depressus* can scarcely be mistaken for any other species of *Codriophorus*.

Codriophorus depressus is externally similar to *C. acicularis* and *C. norrisii*, with which it shares habit and a dark green or olive-green plant colour due to conver-



FIGURE 65. *Codriophorus depressus.* — 1–2. Leaf apices. 3–4. Upper laminal cells at margin. 5. Mid-leaf cells. 6. Lower mid-leaf cells. 7. Angular cells. 8. Basal juxtacostal cells. 9–23. Transverse sections of five leaves, sequentially from base to apex. 24–26. Axillary hairs. — [1, 9–11, 24–26 from *Shevock 17525*, KRAM; 2–3, 5–8, 12–15 from *Flowers 5449*, COLO; 4, 21–22 from *Bolander 511*, FH, holotype of *Racomitrium depressum*; 16–20 from *Lavin 572D*, WTU; 23 from *Wiggins C-88*, FH]. — Scale bars: a – 100 µm (1–8, 24–26); b – 100 µm (9–23).

gence stimulated by living in summer drought habitat conditions. However, the leaves in these other species are broadly lingulate, acute to broadly rounded and usually distinctly dentate or eroso-dentate at the apex and the costa is generally narrower and crescent-shaped on the dorsal side. Particularly reliable for distinguishing *C. acicularis* and *C. norrisii* are the prominently papillose laminal cells which sharply contrast with the smooth or only finely roughened cells in *C. depressus*. Moreover, *C. norrisii* has distinctly limbate leaves almost all around and the innermost perichaetial leaves are chlorophyllous in the upper third.

The European Codriophorus aquaticus is unlikely to be confused with C. depressus for phytogeographical reasons, although some of its phenotypes have broad and robust costae of comparable size to those in C. depressus. However, its costae are distinctly crescent-shaped on the dorsal side throughout or flattened only at the base but then deeply grooved. In addition, the laminal cells of the European endemic are clearly papillose, not smooth as those in the Californian endemic. Nonetheless, the two species do indeed show external similarity and Lesquereux (1868) considered his newly described species Racomitrium depressum to be intermediate between R. aciculare and R. protensum. In fact, Frye (1917) determined as R. depressum the specimen from British Columbia distributed in Macoun's Canadian Musci as No. 620 under the name R. protensum, and consequently markedly extended its geographical range northwards. Lawton (1972) re-determined this specimen as a muticous form of R. heterostichum (Hedw.) Brid. but Ireland & Spence (1987) and Frisvoll (1988) proved that this specimen correctly represents Bucklandiella pacifica and actually it is one of the paratypes of this species name. The latter is quite likely to be confused with C. depressus as both species have epilose leaves. However, B. pacifica has smaller leaves, less than 3 mm long and 1 mm wide, and its costae are narrower, less than 120 µm, distinctly narrowly canaliculate above and lying at the bottom of a deep and narrow-angled groove, partly enclosed in the lower part. Moreover, B. pacifica is a lowland species, whereas C. depressus is a montane moss.

In the anatomical structure of the costa, *Codriophorus depressus* resembles very much another European endemic, *Bucklandiella obtusa* (Brid.) Bednarek-Ochyra & Ochyra. However, this species has strongly recurved to revolute leaf margins, much narrower leaves, 0.5–0.7 mm wide, and grows in less wet habitats.

Variability — There is a certain amount of variation in the habit, size, colour, branching pattern and leaves of *Co*-

driophorus depressus but its extent is typical for aquatic mosses and is evidently environmental, having no taxonomic importance. Although the plants are 5-9 cm long on average, some specimens are as long as 13 cm, for example the type material itself, but sometimes they may reach only 2 cm (e.g., Dillingham 1305, KRAM). In this context, the measurements of plant size for this species (10–15 cm) given by Jones (1933) are somewhat strange. The leaf size varies correspondingly with the size of the plants. The shape of the leaves varies from lanceolate through oblong-lanceolate or ovate-lanceolate to broadly ovate. The leaves are generally straight or somewhat curved but, occasionally, they are distinctly falcate (e.g., Showers 2437, WTU; Fig. 64.8-10). Frisvoll (1988) described the leaves of C. depressus as being "often soft and flaccid" but this is a misleading statement since they are actually always stiff and rigid. Frisvoll's specimen's leaves also have narrower costae, 80-100 µm wide at the base, but their areolation and other structural characters do not deviate from those of typical expressions of the species and therefore such plants do not deserve taxonomic recognition.

The colour of the plants varies markedly, with most being olive-green, olive-brown, olivaceous, golden- or rufous-brown, but sometimes those growing submerged in rapids of snowmelt streamlets are dark blackish green to entirely black (e.g., *Shevock et al. 15718 & 18505* and *Shevock & Bourell 13967*, CAS, KRAM).

There is some variation in the microscopic characteristics of this taxon. The laminal cells are described as unistratose throughout (Jones 1933; Frisvoll 1988) and actually this is the case with the type material. However, quite often the laminal cells are variously bistratose in the distal portion of the leaves. Only seldom are they entirely bistratose and usually the bistratose laminae are furrowed with broader or narrower unistratose strands. Not infrequently the proportions are reversed and the unistratose laminal cells are furnished with bistratose streaks from one to a few cells broad. A tendency for multiplication of the laminal cells is often observed in aquatic mosses, especially those growing in rapids, waterfalls and fast running streams and is evidently an adaptation to the rheophilous habitat conditions. The laminal cells are generally smooth but on some young leaves they are quite weakly but nonetheless distinctly roughened because of clear depressions over the centre of the cell cavities and slight elevations over the lateral parts of the lumina and walls.

The costa of *Codriophorus depressus* varies markedly in robustness, its width ranging from 80 to 200 μ m but such costa variation is typical for all rheophytic mosses. The alar cells are variable and they are either not markedly

FIGURE 66. *Codriophorus depressus.* — 1. Portion of branch with mature capsule, wet. 2. Perigonium. 3–5. Perigonial bracts, sequentially from outermost to innermost. 6. Innermost perigonial bract and antheridia. 7–11. Perichaetial leaves, sequentially from outermost to innermost. 12–14. Operculate capsules, wet. 15. Deoperculate capsule. 16. Transverse section of seta. 17. Operculum. 18–19. Calyptrae. 20. Transverse section of calyptra. 21. Epidermal cells of vaginula. 22. Apex of innermost perichaetial leaf. 23. Exothecial cells at base of urn and stomata. 24. Exothecial cells in mid-urn. 25. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 12–15 from *Bolander 373*, US; 2–6 from *Leiberg 5478*, NY; 7–11, 16–21, 23–25 from *Shevock 17525*, KRAM; 22 from *Flowers 5452*, ALTA]. — Scale bars: a – 0.5 cm (12–15, 17–19); b – 0.5 cm (1) and 200 µm (23–25); c – 1 mm (3–6); d – 100 µm (16, 29); e – 100 µm (21–22); f – (2, 7–11).



different from the adjacent basal cells or are clearly larger with distinctly incrassate walls and form dilated, swollen and decurrent auricles. Frisvoll (1988) erroneously described the angular cells as "thin-walled" but at the same time he illustrated them as clearly "thick-walled".

The species is not particularly variable in sporophyte characters. The capsules vary in shape from obloid to shortly cylindrical but their most outstanding feature is the frequently observed asymmetry, making them slightly curved and gibbous. This is really a unique capsule shape in *Codriophorus* because those of other taxa within the genus are always symmetrical, except for some aberrant specimens.

Reproduction — Fertile plants have been found in about one third of all the *Codriophorus depressus* specimens examined but, generally, sporophytes are not produced abundantly.

Taxonomic and nomenclatural notes — Codriophorus depressus was described as Racomitrium depressum by Lesquereux (1868) from a specimen collected by H. N. Bolander, a meritorious collector of Californian mosses, in Yosemite National Park in the Sierra Nevada. It was considered to be closely related to *C. acicularis* and, more precisely, an intermediate species between this species and *C. aquaticus*. This affinity was confirmed by Watson (1880), Lesquereux & James (1884) and Jones (1933) who positioned it in Racomitrium subg. Dryptodon close to *R. aciculare*.

Lawton (1972) questioned this relationship and suggested the close affinity of *Codriophorus depressus* to *Bucklandiella heterosticha* (Hedw.) Bednarek-Ochyra & Ochyra. This conclusion was based primarily on the basis of the similarity of this species to the specimen from British Columbia (*Macoun 620*, WTU) which has been discussed above under the "Diagnostic characters and differentiation" heading. Frisvoll (1988) accepted this suggestion and transferred *C. depressus* to *Racomitrium* sect. *Laevifolia* (Kindb.) Nog. and considered it to be most closely related to *R. pacificum*.

It is worth noting that Fritsch (1991) placed *Racomitrium depressum* in synonymy with *R. aciculare*, probably on account of the statement in the treatment of Steere *et al.* (1954) in which these authors suggested the close relationship of these species. Finally, Ochyra *et al.* (2003) transferred *R. depressum* to *Codriophorus*.

Chromosome number — In a single population examined cytologically from California the chromosome count of n = 14 was established (Steere 1954; Steere *et al.* 1954).

Habitat — Codriophorus depressus is a semi-aquatic saxicolous moss growing directly attached to or on soil over granite boulders, walls, stones and slabs along the banks of intermittent flowing streams, creeks and streamlets or in stream beds. It is most often found on seasonally wet or moist, shaded or diffusely lit sites, rarely in open, permanently or seasonally dry habitats throughout subalpine mixed coniferous forests dominated by *Abies concolor* (Gordon & Glend.) Lindl., *A. magnifica* Andr., *Pinus murryana* Grev. & Balf., *P. monticola* Doug. and *P. jeffreyi* Grev. & Balf. Quite often, it grows submerged in swiftly flowing water in the rapids of intermittent streams or in cascading streamlets, on dripping rocks and seeps over exposed granite rock terraces during snowmelt that then become dry by mid-summer.

Geographical distribution — Codriophorus depressus is a narrow endemic of western North America, restricted in its distribution to California, with a single record in the border area of adjacent Nevada at Lake Tahoe (Fig. 67). It has its main centre of occurrence in the Sierra Nevada, extending northwards to the Cascade Range south of the Pit River, and the Klamath Mountains and Coast Range in north-western California. In addition, it was once recorded at a disjunct station in the San Jacinto Mountains in the southern part of the state. C. depressus is an altimontane species, occurring predominantly in the subalpine zone, with more than half of its known records originating in areas above 2000 m, and the remaining ones, except for a few, above 1600 m. The highest known locality is from an altitude of 2760 m in the Central Sierra Nevada in Mono County. Only very rarely does the species descend below 1500 m, with the lowest known station at an elevation of 1325 m in the Northern Sierra Nevada of Plumas County.

The records of *Codriophorus depressus* from British Columbia (Frye 1917; Jones 1933), based on the specimens distributed in Macoun's *Canadian Musci* No. 620 and Holzinger's *Musci Acrocarpi Boreali-Americani* No. 620, are incorrect and actually represent *Bucklan-diella pacifica*. Additionally, Jones (1933) cited Labrador as part of the range of *C. depressus*, without indicating definite specimens, but Ireland *et al.* (1980) and Favreau & Brassard (1988) excluded this species from the moss flora of Canada and Labrador, thus, inferentially, acknowl-edging the latter report as erroneous.

SELECTED SPECIMENS EXAMINED

NORTH AMERICA. USA. CALIFORNIA. Alpine Co.: Central Sierra Nevada, Stanislaus National Forest, Carson-Iceberg Wilderness, 1 km from Sword Lake, ca 2100 m, Shevock 21046 (CAS, KRAM). El Dorado Co.: Placervill Road, Case 32a (NY). Fresno Co.: Sierra National Forest: along Ross Landing Road, N of Ross Meadow, ca 2320 m, Shevock & Ertter 13493 & 13496 (CAS, KRAM); S of Wishon Reservoir, ca 1980 m, Shevock & Ertter 13555 (CAS, KRAM); along Forest Service trail 34E04 to Cliff Camp below Wishon Reservoir, North Fork Kings River, ca 2010 m, Shevock & York 13581 (CAS, KRAM); S slope of Bear Mountain above Swamp Lake at tributary of Laurel Creek, ca 2590 m, Shevock & York 17412 (CAS, KRAM); Rock Creek Road at Glen Meadow, ca 1920 m, Shevock & Bourell 13967 (CAS, KRAM); Ross Crossing Road at Deer Creek, ca 2010 m. Shevock & Ertter 13520 (CAS, KRAM); S of Portal Forebay ENE of Huntington Lake, 2500 m, Norris 88160 (UC); off of Rock Creek Road along Rock Creek, a tributary to Dinkey Creek, North Fork Kings River drainage, ca 2040 m, Shevock & York 13936 (CAS, KRAM); Kings Canyon National Park, LeConte Canyon, Middle Fork Kings River at LeConte Ranger Station, ca 2650 m, Shevock & Haultain 18624 (CAS, KRAM). Humbolt Co.: Oregon Creek N of Trinity Summit Guard Station, 1700-1830 m, Norris & Creek 50170 (UC, WTU). Madera Co.: Sierra National Forest: Beasore Road 4 km



FIGURE 67. Global distribution of Codriophorus depressus.

E of junction with road to Mammoth Pool and 18 km from Mugler Creek near Globe Rock, *ca* 2075 m, *Shevock & Kellman 19662* (CAS, KRAM); Minarets Road, E base of Shuteye Peak, Chiquito Ridge, *ca* 1 km from Shakeflat Creek, *ca* 1585 m, *Shevock & Kellman 19746* (CAS, KRAM); tributary of Norris Creek, just S of Ansel Adams Wilderness boundary, *ca* 2410 m, *Shevock 24171* (CAS, KRAM); SE base of Chiquito Ridge, Shuteye Peak, *ca* 2030 m, *Shevock 24117* (CAS, KRAM). *Mariposa Co.*: Yosemite National Park: below Half Moon Meadow along trail to Ten Lakes, *ca* 2640 m, *Shevock, Wilken & Fritzke 18505* (CAS, KRAM); Yosemite Valley, [prior 1868], *Bolander s.n.* (FH, NY – type of *Racomitrium depressum*) and June 1870, *Bolander 335* (NY), *375* (BM, E, FH, MO, NY, US, WTU) & *379* (NY); Yosemite Point, *Hirstel 305* (CAS).

Mono Co.: Toiyabe National Forest, along the Pacific Crest Trail about 1.5 km below Harriet Lake near junction of trail toward Cascade Falls, 2760 m, *Shevock et al. 24414* (CAS, KRAM). *Nevada Co.*: Bear Valley, *Bolander & Kellog 339* (US); Northern Sierra Nevada, Tahoe National Forest, at Fuller Lake Day Use Area between Bowman Lake and California Hwy 20, 1600 m, *Shevock, Ertter & Morosco 15718* (CAS, KRAM); Tahoe National Forest, W of Sugar Bowl, *ca* 2135 m, *Shevock 22602* (CAS, KRAM). *Placer Co.*: Cisco, *MacFadden 17171* (MO, NY). *Plumas Co.*: Buck's Ranch, North Fork of Feather River, *ca* 1680 m, *Leiberg 5414* (NY, US) & *5478* (FH, NY, US); middle areas of North Fork of Feather River basin, *Leiberg 552* (US). **Plumas National Forest**: 9 km NE of Quincy along Cashman Creek, *ca* 1560 m, *Dillingham 1407* (KRAM); 6 km NE of Quincy in headwaters of Chandler Creek, ca 1325 m, Dillingham 1305 (KRAM); South Fork of Long Valley Creek, 6 km E of Cromberg, ca 1780 m, Dillingham 1573 (KRAM); 12 km NE of Quincy at headwaters of Taylor Creek, ca 1935 m, Dillingham 1672 (KRAM). Riverside Co: San Jacinto Mountains, San Jacinto State Park, north fork of the San Jacinto River along the Seven Pines trail, Harpel 1097 (KRAM). Shasta Co.: Lassen Volcanic National Park, Flatiron Ridge, 1830 m, Showers 2437 (WTU). Siskiyou Co.: Dunsmuir Quad., trail from Cedar Lake to Cliff Lake, 1680-1770 m, Norris 52966 (DUKE, KRAM, UC). Tehama Co.: along Hwy 36 at milestop 96, Sec 32, T29N, R5E, ca 1500 m, Norris 55978 (KRAM). Tuolumne Co.: Stanislaus National Forest: Gooseberry Camp near Pinecrest, Wiggins C-88 (FH); between Long Barn and Strawberry, ca 1700 m, Howell 194 (CAS, MO); along Wheat's Meadow Trail near Whittaker's Dardanelles, 2100 m, Sommer 87 (UC); ca 1 km below County Line Trailhead, S slope of The Dardanelles, ca 2100 m, Shevock 21058 (CAS, KRAM); Stanislaus National Forest, Eureka Valley Campground between Sonora Pass and Pine Crest in the Sierra Nevada, ca 1860 m, Spjut, Norris & Koponen 6256 (UC). Yosemite National Park: ca 7.2 km NE of Tamarack Flat junction and 1.5 km NE of bridge crossing of South Fork Tuolumne River, ca 2120 m, Shevock 18475 (CAS, KRAM). Tulare Co.: Sequoia National Forest: Kern Plateau, Ernest C. Twisselmann Botanical Area,

along S side of Sirretta Pass in canyon paralleling Sirretta Pass trail 34E12, ca 2680 m, Shevock 17524 & 17525 (CAS, KRAM); Kern Plateau, W of Cherry Hill road from Poison Meadow, ca 2290 m, 13 June 2002, Laeger 1461 (CAS, KRAM); E slope of Slate Mountain, along the Summit trail 31E14 about 3.5 km S of Quaking Aspen, tributary to Peppermint Creek, ca 2480 m, Shevock 15677 (CAS, KRAM); near Red Hill Grove, W slope of Slate Mountain along the Crawford Road, ca 6 km from Windy Gap and 11.5 km from Western Divide highway, ca 2010 m, Shevock 18436 (CAS, KRAM); near Red Hill Grove, W slope of Slate Mountains along the Crawford Road, ca 2010 m, Shevock 18433 (CAS, KRAM); along Generals highway 1 km S of junction with Big Meadows road and just past crossing of Woodward Creek, ca 2270 m, Shevock 15623 (CAS, KRAM); Big Meadows Campground, W of bridge crossing of Big Meadows Creek, ca 2290 m, Shevock & York 13695 (CAS, KRAM). Sequoia National Park: Clover Creek just E of Wuksachi Lodge, ca 2650 m, Shevock 18283 (CAS, KRAM); between Fresno and General Grant Grove, MacFadden 21881 (CAS, MO, NY, US, WTU); Giant Forest, W of Crescent Meadow, 2010 m, Rundel 3152 (DUKE); with no closer locality data, 1890 m, Flowers 5452 (ALTA, COLO, MO, NY, OSC, WTU) and 1950 m, Flowers 5449 (COLO);. NEVADA. Washoe Co.: Lake Tahoe Basin, Management Unit, Lake Tahoe, ca 1.5 km N of Sand Harbor, 2135 m, Lavin 5720 (WTU).

A4. Subsection Andicola (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

Codriophorus subsect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. ≡ *Racomitrium* subsect. *Andicola* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 64. 1995. — Type: *Codriophorus dichelymoides* (Herzog) Bednarek-Ochyra & Ochyra (*Racomitrium dichelymoides* Herzog).

Plants medium-sized, fairly slender, loosely or densely caespitose, dull, dark green, blackish- or dirty green to golden-brown, prostrate, ascending to suberect, fairly stiff, copiously or sparsely branching. Leaves crowded to distant, falcato-secund or circinate to weakly curved, lanceolate to oblong-lanceolate, gradually acuminate, subacute to narrowly rounded-obtuse, epilose at the apex, broadly canaliculate to subtubular distally, broadly concave in the basal part; margins entire, unistratose throughout, plane to erect; costa strong, subpercurrent, forked at the apex, in cross-section distinctly flattened, plane or weakly convex on the ventral side, weakly or prominently convex near the base dorsally, bistratose in the upper part, 3-5-stratose in the proximal portion, with a single row of enlarged ventral cells and 2-4 layers of dorsal stereid cells; laminal *cells* unistratose throughout, smooth or weakly papillose on young leaves, short-rectangular to subquadrate at the apex, becoming long rectangular downwards; basal cells long rectangular, with nodulose and porose, incrassate walls in 3-4 rows, forming a dark yellow to orange-brown strip along the leaf insertion; alar cells differentiated, forming flat or swollen decurrent auricles; supra-alar cells undifferentiated or forming a marginal border, consisting of up to 14 pellucid cells with esinuose walls. Dioicous. Innermost perichaetial leaves lanceolate, straight, gradually acuminate, somewhat plicate, entire, with a distinct subpercurrent costa, chlorophyllous throughout, with elongate cells with thick and sinuose walls. Setae erect, straight, twisted clockwise, with a single sinistrorse torsion immediately below the urn. Capsules erect, obloid to short-cylindrical; operculum conical-rostrate, with a stout, straight beak; exothecial cells obloid to rectangular, thickwalled; *peristome teeth* very short, arising from a fairly tall basal membrane, finely papillose below, densely papillose above, irregularly divided into 2–3 branches to the middle or somewhat below. *Spores* spherical, finely papillose. *Calyptra* conical-mitrate, dark brown, finely verrucose at the apex.

Codriophorus subsect. Andicola is a monotypic taxon that comprises only C. dichelymoides, a North Andean endemic. It is diagnosed as follows: (1) leaves strongly falcato-secund to circinate, strongly concave below, broadly canaliculate to subtubular in the acumen; (2) leaf margins entire and unistratose throughout, plane to erect; (3) costa vanishing below the apex, forked at the tip, not situated in a furrow, strongly flattened and weakly convex on the dorsal side (except for the extreme base where it is composed of a row of large ventral cells and 2-4 layers of small cells with strongly incrassate walls forming a prominent dorsal stereid band), flat or weakly convex on the ventral side; (4) laminal cells unistratose throughout, smooth or weakly papillose on young leaves, long rectangular; (5) innermost perichaetial leaves chlorophyllous throughout; (6) peristome teeth short, with a fairly tall basal membrane, split to the middle or somewhat below into 2-3irregular prongs.

Codriophorus subsect. *Andicola* was originally recognised as a subsection within *Racomitrium* sect. *Stenotrichum* (Bednarek-Ochyra 1995) and subsequently transferred to *Codriophorus* (Ochyra *et al.* 2003). Here, this subsection is raised to section on account of the aforementioned set of diagnostic characters which, tout ensemble, do not fit well any other subdivision of the genus. The generic position of this species may seem debatable because the laminal cells may appear to be smooth. However, careful examination of the leaf sections reveals fine papillosity of the laminal cells on young leaves whereas it is hardly visible or missing on older leaves. The young leaves are finely rough on both ventral and dorsal surfaces due to the presence of shallow but otherwise distinct hollows over the lumen centres which are separated by large but very low, flat cuticular elevations situated over the walls and lateral parts of the lumina. They are eroded with age and consequently the leaf surfaces appear to be smooth. Similar papillosity of the laminal cells is also present in C. depressus but this species is rather distantly related to C. dichelymoides and differs in a number of structural characters, the most important of which are the hyaline innermost perichaetial leaves, variously multistratose laminal cells, as well as different costa structure. The reduction of the leaf papillae is evidently an ecological adaptation to the aquatic environment and the best evidence confirming this notion is the form of leaf papillosity in C. norrisii which is remarkably reduced in comparison with that in its close relative, C. acicularis.

The taxonomic position of Codriophorus dichelymoides has not been discussed hitherto. Herzog (1934) did not comment on this issue when describing this species as new and compared only its leaves to those of two other rheophytic moss species, Dichelyma falcatum (Hedw.) Myrin and Cinclidotus aquaticus (Hedw.) Bruch & Schimp. Churchill & Linares (1995) suggested a relationship between this species with Bucklandiella cucullatifolia, a North Andean endemic species. The latter species is very odd in having, among other things, its costa vanishing far below the apex, convolute perichaetial leaves that are truncate at the apex, with the innermost ones being entirely chlorophyllous and having entirely smooth laminal cells. Bednarek-Ochyra (1995) placed it in a separate subsection, subsect. Cucullaria Bednarek-Ochyra, within Racomitrium sect. Stenotrichum, close to subsect. Andicola. Although Bucklandiella cucullatifolia shares the aforementioned characters with Codriophorus dichelymoides, the two species differ markedly, among other things, in the anatomical structure of the costa which precludes their close phylogenetic relationship. B. cucullatifolia is closely related to and probably conspecific with B. subsecunda.

9. *Codriophorus dichelymoides* (Herzog) Bednarek-Ochyra & Ochyra (Figs 68–70)

Codriophorus dichelymoides (Herzog) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. \equiv *Racomitrium dichelymoides* Herzog, Hedwigia 74: 103, *f. 9.* 1934. — TYPE CITATION: Columbia: Schluchten und Quellen im Bergwaldgürtel über Chapinero, 2800 m (n. 2111) [Holotype: "Rhacomitrium dichelymoides Herzog n. sp. 2111 Fl. v. Columbia Schluchten u. Quellen im Bergwaldgürtel über Chapinero b/ Bogotá ca 2800 m leg. C. Troll, 1929" – JE-Herzog!; isotypes: FH!, M!, s!].

Plants of moderate size to fairly large, rather slender but elongate, pretty stiff, in loose or dense tufts or mats

submerged at high water, dull, dark to blackish-, olive- or dirty green or bright golden-brown throughout, olivaceous to olive-green above, brown below. Stems trailing and prostrate to ascending or suberect, (3-)6-9(-12) cm long, tough, copiously or sparingly fastigiately or dichotomously branched, often denuded at the base due to erosion of the leaf laminae, sparsely or sometimes densely radiculose at the base with blackish-brown, glossy, smooth, branching rhizoids, in cross-section circular to elliptical, with a 2-4stratose cortex of stereid cells with small lumina and incrassate, dark to blackish-brown, brown or yellow-brown walls, 7-8-layered medulla of large, hyaline, moderately thick-walled cells and without a central strand; axillary hairs filiform, hyaline throughout, composed of 9-11 cells, short at the base, elongate above. Leaves distant to fairly crowded, erect to erect-spreading, falcate, recurved to falcato-secund, often circinate and penicillate at the stem and branch apices, less often nearly straight when dry, erecto-patent when moist, lanceolate to oblong-lanceolate, 3-4 mm long, 0.7-1.0(-1.2) mm wide, gradually tapering to a narrow, broadly canaliculate to subtubular acumen, obtuse or subacute, epilose at the apex, broadly concave below, not plicate, not or shortly decurrent; margins entire, plane, erect to incurved, unistratose throughout; costa single, extending to 5% of the way up the leaf, forked at the apex, dark green to brown, clearly delimited from the laminal cells, strong, $85-100 \mu m$ wide at the base, gradually narrowed towards the apex, in transverse section strongly flattened, nearly as thick as the lamina, except for the extreme base, flat or weakly convex on the ventral side, bistratose above, composed of uniform cells, 3-5-stratose near the base, with a ventral row of 9-11 enlarged cells and 2-4 layers of stereid cells on the dorsal side; laminal cells unistratose throughout, smooth or very weakly papillose on young leaves, short-rectangular to subquadrate at the apex, $(10-)15-25 \mu m \log, 5-8(-12)$ µm wide, with thick or thin, sinuose walls, becoming long rectangular downwards, reaching a length of 20-45 µm in mid-leaf and 30-60 µm above the base; basal cells long rectangular, 30–70 µm long, 8–10 µm wide, with strongly incrassate, nodulose-porose walls, forming a 3-4-seriate, dark yellow or orange-brown strip along the leaf insertion; alar cells short-rectangular to subquadrate, thin- to firm-walled, 25-40 µm long, 10-18 µm wide, forming flat or swollen, not or shortly decurrent auricles, concolorous with the adjacent basal cells; supra-alar cells not differentiated from the laminal cells or, rarely, subquadrate to short-rectangular, 13-15 µm long, 10-12 µm wide, esinuose, forming a short, pellucid marginal border extending to 14 cells up the margin. Dioicous. Perigonia gemmiform, fairly large, 2.0-2.5 mm long; outer perigonial bracts falcate, 2.0-2.5 mm long, ovate-lanceolate, gradually narrowed to a short, curved acumen, entire, with a distinct costa vanishing below the apex; inner perigonial bracts ovate, broadly short-acuminate, 1.0-1.5 mm long, 1.0–1.2 mm wide, entire, with a faint, percurrent costa; innermost perigonial bract broadly ovate, ca 1 mm long, strongly concave, bearing about 16 claviform, pale brown antheridia, with a few filiform, pale brown paraphyses reaching about half the length of the antheridia. Outer perichaetial leaves lanceolate, straight, gradually acuminate, 2.2-3.2 mm long, 1.0-1.2(-1.5) mm wide, somewhat plicate, entire, with a distinct costa ceasing well below the apex; innermost perichaetial leaves similar in size and shape to the outer ones, clasping the seta, chlorophyllous throughout, with the laminal cells thick- and sinuose-walled, 20–50 μ m long, (5–)7–8(–10) μ m wide in the distal portion. Setae single or geminate in the perichaetium, erect, straight, fairly stout, 9-10 mm long, lustrous, light brown above, blackish-brown to dark brown below, dextrorse, with a single torsion to the left immediately below the capsule; vaginula dark brown, 1.5-2.0 mm long, with oblong to irregularly elongate epidermal cells with moderately thin and weakly sinuose walls. Capsules exserted, erect, obloid to shortly cylindrical, 2.0–2.5 mm long, 0.9–1.0 mm wide, light brown, smooth, somewhat lustrous, pachydermous; operculum conical-rostrate, rather stout, 1.1-1.5 mm long, straight, light brown; annulus tardily deciduous, 2-3-seriate, composed of large, vesiculose cells with strongly incrassate walls; exothecial cells mostly oblong to rectangular, but mixed with irregular to rounded-quadrate ones, thickwalled, 15-50 µm long, 15-20 µm wide, becoming rounded-quadrate to short-rectangular, dark brown in 3-4 tiers at the mouth; stomata not numerous, 8-11 per urn, arranged in 2 rows at the base of the urn, superficial, bicellular, with circular openings; peristome teeth 16, with a fairly tall basal membrane, to 75 µm, lanceolate but rather irregular in outline, short, 350-400 µm tall, bright yellow and finely papillose below, orange-brown and densely covered with tall conical papillae above, irregularly split to the middle or somewhat below into 2-3 weakly articulated prongs. Spores spherical, light brown, delicately papillose, 13-18 µm in diameter. Calyptra conical-mitrate, to 2 mm long, 4-5-lobed at the base, dark brown, not plicate, delicately verrucose at the apex.

Etymology — The specific epithet is coined from the generic name *Dichelyma* and the Greek suffix *-ides* designating affinity. The species was named by reference to its resemblance in habit and ecological requirements to the aquatic species *Dichelyma falcatum*.

Diagnostic characters and differentiation — Codriophorus dichelymoides is a very curious and impressive species with muticous leaves that are falcato-secund to circinate and strongly hooked at the tips of the stems and branches. They give the plants a peculiar appearance which makes the species immediately distinguishable not only from all other congeners, but also from other taxa of the Racomitrioideae, a subfamily comprising segregates of the former genus *Racomitrium s. lato.* Exceptionally, strongly falcato-secund leaves have been found in specimens of *C. fascicularis* from Newfoundland (*Tuomikoski 5622*, H) and *C. depressus* from the Lassen Volcanic National Park in California (*Showers 2437*, WTU). Such a plant habit is extremely rare in the Grimmiaceae as a whole and so far it has been observed only in some spe-

cies of *Schistidium* subg. *Canalicularia* Ochyra, including *S. falcatum* (Hook.f. & Wilson) B.Bremer, an amphiatlantic south-temperate species (Ochyra 1998, 2003), and *S. pacificum* (E.Lawton) S.P.Churchill, a western North American endemic (Lawton 1979). Nonetheless, the typical "racomitrioid" leaf areolation of the cells with strongly sinuose longitudinal walls immediately indicates the affiliation of this species to the Racomitrioideae.

Codriophorus dichelymoides is diagnosed by the following combination of characters: (1) plants mediumsized to rather large, growing mostly submerged in the water of streams, with stems that are copiously to sparingly branched; (2) leaves lanceolate to oblong-lanceolate, falcate to falcato-secund or circinate, canaliculate to subtubular in the acumen, broadly concave in the proximal portion; (3) margins entire and unistratose throughout, plane to erect; (4) costa strong, ending a short distance from the leaf apex, strongly flattened and nearly as thick as the lamina, bistratose in the distal half, 3-5-layered in the basal part, with 2-4 layers of stereid cells on the dorsal side; (5) laminal cells smooth or with very low papillae over the walls and major part of the lumina; (6) supra-alar cells not differentiated or forming a pellucid border of up to 14 cells; (7) innermost perichaetial leaves entirely chlorophyllous, with areolation similar to that of the vegetative leaves; (8) setae stout, dextrorse, with a single torsion to the left immediately below the urn; (9)capsule obloid to short-cylindrical; (10) peristome teeth short, irregularly divided into 2-3 prongs to the middle or slightly below, finely papillose near the base, densely papillose in the upper part.

Codriophorus dichelymoides is unlikely to be mistaken for any other moss. Externally, it may be taken for *Dichelyma falcatum* or *Cinclidotus aquaticus* which are rheophytic aquatics having similar falcato-secund leaves and a similar dark green to blackish-green or goldenbrown colour. However, microscopic examination should dispel any doubts regarding the identity of this moss since these other species lack the characteristic leaf areolation of strongly sinuose-walled laminal cells.

Variability - Codriophorus dichelymoides is one of the least variable species of the genus in its most essential taxonomic characteristics, although it varies, as usual, in features that are readily modifiable by environmental conditions, including the size and colour of the plants. Typically, they are medium-sized, 6-9 cm long, but sometimes the stems are to 12 cm or only 3 cm long. Surprisingly, the colour of the plants is most variable and ranges from dark blackish-green to bright golden-brown with all possible intermediates between these extremes. The leaves vary from strongly falcate and circinate to weakly curved. The costa has a rather stable anatomical structure. Typically, it is strongly flattened from above and somewhat sunken at the centre, but sometimes it may be slightly convex ventrally. It is also rather weakly convex on the dorsal side and not markedly thicker than the laminal cells. Only at the base is it somewhat thicker because of two welldeveloped dorsal rows of stereid cells while occasion-



FIGURE 68. *Codriophorus dichelymoides*. — 1. Sterile plant, wet. 2. Portion of branch, wet. 3–10. Leaves. 11–12. Axillary hairs. 13–24. Transverse sections of two leaves, sequentially from base to apex. — [1, 6–19 *Churchill & Rengifo 17478*, KRAM; 2–5 from *Troll 2111*, JE (holotype of *Racomitrium dichelymoides*); 20–22 from *Cleef & 't Hart 2425*, NY; 23–24 from *Cuatrecasas, Murillo & Jaramillo 25641*, FH]. — Scale bars: a – 100 µm (13–22); b – 100 µm (11–12) and 0.5 cm (1); c – 1 mm (3–10); d – 1 mm (2).



FIGURE 69. *Codriophorus dichelymoides.* — 1. Transverse section of stem. 2–4. Leaf apices. 5. Upper laminal cells at margin. 6. Mid-leaf cells. 7. Basal juxtacostal cells. 8–9. Angular cells. — [1–2, 5–8 from *Churchill & Rengifo 17478*, KRAM; 3–4 from *Alston 7451*, FH; 9 from *Troll 2111*, JE (holotype of *Racomitrium dichelymoides*)]. — Scale bar: 100 μm (1–9).

FIGURE 70. Codriophorus dichelymoides. — 1. Plant with immature capsule, wet. 2. Perichaetium with two mature capsules, wet. 3. Perigonium. 4–6. Perigonial bracts, sequentially from outermost to innermost. 7. Innermost perigonial bract and antheridia. 8–10. Perichaetial leaves, sequentially from outermost to innermost. 11. Apex of innermost perichaetial leaf. 12. Epidermal cells of vaginula. 13. Transverse section of seta. 14. Calyptra. 15. Transverse section of calyptra. 16. Operculate capsule, wet. 17–18. Deopeculate capsules with destroyed peristomes, wet. 19. Exothecial cells at base of urn and stomata. 20. Exothecial cells in mid-urn. 21. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 8–15, 17–18 from *Churchill & Rengifo 17478*, KRAM; 2–7, 16 from *Cleef & 't Hart 2425*, NY; 19–21 from *Cleef 19–21*, U]. — Scale bars: a – 0.5 cm (2) and 200 µm (11); b – 1 mm (4–7); c – 100 µm (12, 15); d – 100 µm (13, 19–21) and 1 cm (1); e – 1 mm (3); f – 1 mm (8–10); g – 1 mm (14, 16–18).





FIGURE 71. Global distribution of Codriophorus dichelymoides.

ally it is prominently convex dorsally with four layers of small stereid cells (e.g., *Cuatrecasas, Murillo & Jaramillo 25641*, FH).

Papillosity of the laminal cells is normally hardly visible and is lacking on older leaves. However, on some young leaves both leaf surfaces are finely rough owing to the presence of shallow but otherwise distinct hollows over the lumen centres separated by large, scarcely raised and equally thickened flat cuticular elevations situated over the walls and lateral parts of the lumina. These are eroded with age, making the leaf surfaces smooth.

The alar cells are usually only slightly differentiated forming flat, non-decurrent groups, but sometimes they comprise swollen, auriculate and somewhat decurrent groups (e.g., *Churchill & Rengifo 17478*, KRAM). The supra-alar cells are usually similar to the adjacent laminal cells but occasionally they are distinct from them, forming a pellucid marginal border, for example in the type material of this species name (Fig. 69.9). The leaf apex varies from subacute to obtuse and both forms can be found even on the same plant (e.g., *Alston 7451*, FH; Fig. 69.2–4). The same situation occurs with the leaf acumen which varies from broadly canaliculate to subtubular (e.g., *Churchill & Rengifo 17478*, KRAM; Fig. 68.16–18). Variability in the sporophyte characters cannot be evaluated precisely because of the scarcity of mature sporophytes.

Reproduction — Codriophorus dichelymoides very seldom reproduces by spores. So far, only a few mature and several immature or old sporophytes have been found in three (of ten known) specimens of this species, namely from Caldas Departamento (*Cleef & 't Hart 2425*, ALTA, G, MICH, MO, NY, TNS and 2426, KRAM) and Nariño Departamento (*Churchill & Rengifo 17478*, MO, NY, KRAM). In the latter specimen some perigonia have also been discovered.

Taxonomic and nomenclatural notes — Codriophoris dichelymoides has a simple and straightforward taxonomic history. It was described by Herzog (1934) as Racomitrium dichelymoides from a single collection made in 1929 by C. Troll near Bogota and subsequently was transferred to the genus Codriophorus (Ochyra et al. 2003). The next specimen of this species was found in 1939 by A. H. G. Alston on Páramo de Guasca in Cundinamarca Departamento and reported by Bartram (1953). This author initially intended to describe it as a new species and the name of this undescribed species is seen crossed out on the herbarium label. Later, the author changed his mind with regard to the identity of the specimen as expressed in his letter of 6 August 1951 to the collector. An excerpt of it is attached to the specimen at BM and it reads: "I have just discovered that the moss you collected in Colombia which I named <u>Rhacomitrium Alstonii</u> sp. nov. was described by Herzog in Hedwigia, Band 74, pp 103–4, 1934 as <u>Rhacomitrium dichelymoides</u>. I have not seen the type material but the description and figures leave little doubt about the identity of your No. 7451.". Later, only a few additional collections of *C. dichelymoides* have been made, some of which have been published (Florschütz-de Waard & Florchütz 1979; Churchill & Linares 1995).

Chromosome number — Not available.

Habitat — Codriophorus dichelymoides is a rheophytic species growing attached to boulders in rivulet and stream beds, often in fast-moving water in rapids and in waterfalls, rarely on pockets of soil in temporarily dried up river beds and in springs. The moss tufts are monospecific and no associates have been recorded; only in one specimen are its shoots intermingled with filamentous algae.

Geographical distribution — *Codriophorus dichelymoides* is a narrow endemic species of the Colombian Andes which has most localities in the Cordillera Oriental, with solitary stations in the Cordillera Central and Cordillera Occidental (Fig. 71). It is an altimontane moss, occurring primarily in the páramo zone, reaching its highest elevation of 4520 m in the Cordillera Central, and rarely descending to the forest belt at 2800 m (type locality) in the Cordillera Oriental. Churchill *et al.* (2000) reported the lowest locality of the species at 1500 m and this elevation was erroneously given by Bartram (1953) for the specimen from Páramo de Guasca in Cundinamarca Departamento. In fact, the altitude on the label is 11500 feet, i.e. *ca* 3500 m.

SPECIMENS EXAMINED

SOUTH AMERICA. COLOMBIA. CALDAS. Nevado del Ruiz, Arenales, 2 km SW of Refugio, 4520 m, *Cleef & 't Hart 2425* (ALTA, G, MICH, MO, NY, TNS), 2426 (G) & 2434 & 2446 (KRAM). CUNDINAMARCA. Guasca, 3150 m, *Gradstein & Aguirre 3683* (FLAS, KRAM, MO, NY, S); Páramo de Guasca, *ca* 3500 m, *Alston 7451* (BM, FH, FLAS, KRAM); Macizo de Bogotá, eastern drainage, Páramo de Palacio, Quebrada de Casarreales, 3450 m, *Cuatrecasas, Murillo & Jaramillo 25640 & 25641* (FH, US); Chapinero over Bogota, 2800 m, *Troll 2111* (FH, JE, KRAM, M, S). NARIÑO. Volcán Galeras, S of Pasto, 3740–3900 m, *Churchill & Rengifo 17478* (MO, NY, KRAM).

B1. Section Fascicularia (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

Codriophorus P.Beauv. sect. *Fascicularia* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. ≡ *Racomitrium* sect. *Fascicularia* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 130. 1995. — Type: *Codriophorus fascicularis* (Hedw.) Bednarek-Ochyra & Ochyra (*Trichostomum fasciculare* Hedw.).

Plants medium-sized and fairly gracile to large, robust and coarse, mostly stiff and rigid, forming dull, loose or fairly dense, yellow, green, olive-brown to brownishgreen tufts or extensive patches. Stems erect, ascending or creeping, sparingly or freely, irregularly, dichotomously to fasciculately branching, often subpinnately branched with numerous short, tuft-like, lateral, horizontal branchlets, giving the plants a nodose appearance, usually sparsely radiculose at the base or with clusters of rhizoids scattered along the prostrate stems. Leaves crowded, straight to somewhat curved, rarely falcate, erect and appressed to loosely erecto-patent when dry, erect-spreading or patent, occasionally squarrose-recurved when wet, ovatelanceolate, narrowly lanceolate to linear-lanceolate, from an ovate, oblong- or ovate-lanceolate, not or distinctly plicate base, gradually short- or long-acuminate, often with a long, subulate, canaliculate-concave, straight or sometimes wavy to serpentine acumen; leaf apex muticous, acute, subacute to narrowly rounded-obtuse, entire or dentate, denticulate-cristate to papillose-crenulate, epilose or terminated with a hyaline to yellowish-hyaline, denticulate hair-point; margins recurved to revolute on both sides to varying extent, but usually from near the base to the apex or only somewhat below, entire or dentate to denticulate-cristate at the apex, unistratose throughout to variously bistratose in 1-2(-3) rows of cells, forming fleshy, bulging thickenings; costa single, vanishing in mid-leaf to subpercurrent or percurrent, entire throughout or spurred distally and forked at the tip, in the proximal part lying at the base of a deep, wide- or narrow-angled furrow, open or partly enclosed by the strongly infolded leaf base, in transverse section bistratose throughout, occasionally with tristratose spots or entirely 3-4-stratose near the base, flattened or convex on the ventral side, not prominently convex, lunate or flattened on the dorsal side, with cells in the dorsal and ventral rows of similar size and shape or with 1-2 dorsal rows composed of small stereid cells in the lower half or at the extreme base; *laminal* cells unistratose, long-rectangular to linear throughout, exceptionally variously bistratose, short-rectangular to isodiametric in the distal part, transparent, with thick and sinuose longitudinal walls; basal cells rectangular, with strongly incrassate, nodulose and porose walls, forming an intensely bright yellow or yellow-brown, 1-2(-3)-seriate strip along the leaf insertion; alar cells scarcely to strongly differentiated, quadrate to short-rectangular, with moderately thick to strongly incrassate walls, forming mostly distinct, yellow, brown to orange-brown, flat or somewhat swollen, not or shortly decurrent auricles; supra-alar cells subquadrate to rectangular, with thin to thick, straight walls, forming a transparent, 1(-2)-seriate marginal border consisting of 5-25 cells, rarely scarcely differentiated. Dioicous. Innermost perichaetial leaves oblong, oblong-lanceolate or oblong-ovate to elliptical, convolute, scarcely to strongly longitudinally plicate, subacute or rounded-obtuse, truncate or shortly apiculate at the apex, hyaline throughout or with an areolation of chlorophyllous, thick- and sinuose-walled cells in the distal portion. Setae 1-3 per perichaetium, erect, twisted once to the left immediately below the urn, dextrorse below. Capsules exserted, erect, straight, ovoid, obloid to cylindrical, smooth, lustrous, brown, fairly pachydermous; operculum conical-rostrate, with a straight rostrum, nearly as long as the urn or shorter; peristome teeth 16, lanceolate, 0.35-1.8 mm long, with a low basal membrane, brown to yellow- or reddish-brown, densely papillose throughout to almost smooth, deeply cleft nearly to the base into 2(-3)filamentous prongs. Spores spherical, brownish, finely papillose, 12-20 µm in diameter. Calyptra conical-mitrate, 4–5-lobed at the base, scabrous at the apex.

Codriophorus sect. *Fascicularia* is primarily characterised by its peculiar anatomical costal structure. The costa is situated at the bottom of a deep groove that is mostly narrow-angled and partly enclosed by the plicate leaf base, less often wide-angled and open and it extends to mid-leaf or vanishes just below or in the leaf apex. In transverse section the costa is bistratose, except for the lower half or the extreme base where it has tristratose spots or, rarely, it is entirely 3–4-layered. Both ventral and dorsal costal layers are composed of uniform cells and only in the proximal portion or near the extreme base only does the dorsal layer consist of small and thick-walled stereid cells. In addition, the costa varies from slightly prominent on the dorsal surface to nearly of the same thickness as the lamina. It is flat or convex on the ventral side and not prominently convex and crescent-shaped or flattened on the dorsal side and exceptionally in *C. varius* and one specimen of *C. fascicularis* from Japan (*Deguchi s.n.*, HIRO-7126) is the costa distinctly convex on the dorsal side in the lower half or near the base only, with three or four, often incomplete, rows of stereid cells.

Some species of section *Fascicularia* (*Codriophorus fascicularis*, *C. laevigatus*, *C. varius*) often have a characteristic bunched manner of branching owing to the presence of many short, tuft-like, horizontal, lateral branchlets and actually the name of the section (from the Latin *fasciculus* = fascicle) refers to this peculiar branching pattern. Branching of this type is almost unknown in the type section of *Codriophorus*. In all species of sect. *Fascicularia* (except for *C. brevisetus*) the leaf areolation is composed of elongate cells throughout the lamina, and the cauline leaves are straight, lanceolate to ovate-lanceolate, gradually tapering to a short or long, canaliculate acumen. Additionally, the seta is dextrorse but with a single torsion to the left immediately below the capsule.

Codriophorus sect. *Fascicularia* embraces six species which are subdivided into three subsections, namely subsect. *Fasciformes*, subsect. *Chrysei* and subsect. *Piliferi*. The former is recognised as new to accommodate four species of the Northern Hemisphere belonging within the *C. fascicularis* complex, whereas the latter two comprise only a single species each, *C. laevigatus*, a south-temperate amphiatlantic species, which is the only species of the genus known exclusively from the Southern Hemisphere, and *C. varius*, which is endemic to western North America.

B1. Subsection *Fasciformes* Bednarek-Ochyra, *subsect. nov.*

Plantae mediocres vel magnae grossaeque, elongatae, erectae, adscedentes vel prostratae, irregulariter vel fasciculato-ramosae, frequenter nodoso-ramulosae. Folia sicca erecta vel erecto-patula sursum retrorsum curvata, ex elongata basi anguste lineali-lanceolata, mutica, acuta vel obtusiuscula, integerrima vel apice denticulata cristataque, canaliculato-concava, cellulis elongatis, nervo tenui in medio vel in apice evanido, in sulco profunde sito, apice frequenter bifido, in sectione transversali bistratoso, e cellulis aequalibus fabricato. Calyptra tota vel apice fere papillosa. Capsula ovoidea vel breviter cylindrica, fusca, solida, pedicello breviore crassiusculo proxime infra urnam semel dextrorso. Operculum aciculare. Peristomi dentes longi, tota longitudine vel infra medio in cruris duo filiformia nodosa papillosa divisi.

Type: Codriophorus fascicularis (Hedw.) Bednarek-Ochyra & Ochyra (Trichostomum fasciculare Hedw.).

Plants moderately sized to large and robust, mostly coarse and rigid, loosely caespitose, forming dull, yellow, green, olive-brown to brownish-green tufts, sparsely or freely, irregularly, dichotomously to fasciculately branching, often with a nodose appearance due to many short, tuft-like, lateral, horizontal branchlets. *Leaves* straight to curved, sometimes falcate, erect and appressed to loosely erecto-patent when dry, erect-spreading or patent when wet, gradually tapering from an ovate, oblong- or ovate-lanceolate base to a long, subulate, canaliculate-concave, straight or sometimes wavy to serpentine acumen; *leaf apex* epilose, acute, subacute to narrowly rounded-obtuse, entire or dentate, denticulate-cristate to papillose-crenulate; *margins* recurved to revolute on both

sides from near the base to the apex, entire throughout, except for the apex, unistratose throughout to variously bistratose in 1-2(-3) rows of cells; *costa* single, ending in mid-leaf to subpercurrent, situated at the bottom of a deep, narrow- or wide-angled groove below, in transverse section bistratose throughout, with occasional tristratose spots near the base, flattened or convex on the ventral side, weakly convex, lunate or flattened on the dorsal side, with costal cells of similar size and shape or with a dorsal row composed of stereid cells at the extreme base; *laminal cells* unistratose, long-rectangular to linear throughout, rarely variously bistratose, short-rectangular to isodiametric in the distal part; *alar cells* differentiated, forming flat or somewhat swollen, not or shortly decurrent auricles; supra-alar cells subquadrate to rectangular, straightwalled, forming a pellucid, 1(-2)-seriate marginal border consisting of 5-25 cells. Dioicous. Innermost perichaetial leaves oblong, oblong-lanceolate or oblong-ovate to elliptical, convolute, not or slightly plicate, rounded-obtuse to shortly apiculate at the apex, hyaline throughout. Setae 1-2(-3) per perichaetium, erect, twisted once to the left immediately below the urn, clockwise below. Capsules exserted, erect, straight, ovoid, obloid to shortly cylindrical, smooth, lustrous, brown; operculum conical-rostrate, with a straight rostrum nearly as long as the urn; peristome teeth lanceolate, with a low basal membrane, brown to yellow- or reddish-brown, densely low or spiculate-papillose throughout, divided nearly to the base into 2(-3) filamentous branches. Spores spherical, brownish, minutely papillose. Calyptra conical-mitrate, 4-5-lobed at the base, scabrous at the apex.

Subsection Fasciformes consists of four species which constitute the Codriophorus fascicularis complex, namely C. fascicularis, C. anomodontoides, C. brevisetus and C. corrugatus. They are distributed exclusively in the Northern Hemisphere, except for the former two which only occasionally penetrate into the tropics in the Pacific region. The subsection is recognised by the following set of characters: (1) leaves lacking a hyaline hair-point; (2) leaf apex entire or dentate, serrate, denticulate-cristate to papillose-crenulate; (3) leaves not or scarcely plicate at the base; (4) alar cells with thin to moderately thickened walls, forming flat or somewhat swollen, indistinct and not or shortly decurrent auricles; (5) innermost perichaetial leaves weakly plicate or smooth, subacute to rounded-obtuse, hyaline throughout or sometimes with a few thicker-walled cells at the extreme apex. These characters are unknown in Codriophorus laevigatus which is morphologically quite similar to some phenotypes of C. fascicularis with short, lateral tuft-like branchlets and in the anatomy of the costa it is identical to C. anomodontoides. The essential difference between these two subsections is in the completely different form of the innermost perichaetial leaves that are hyaline throughout and not or only slightly longitudinally plicate in species of subsect. Fasciformes, whereas those in subsect. Chrysei are strongly plicate with an areolation of chlorophyllous cells.

Codriophorus fascicularis (Hedw.) Bednarek-Ochyra & Ochyra (Figs 72–76)

Codriophorus fascicularis (Hedw.) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. ≡ Trichostomum fasciculare (Schrad.) ex Hedw., Spec. Musc. Frond.: 110. 1801 ["Bryum fasciculare Schrad." in Gmel., Syst. Nat. Ed. 13, 2(2): 1332. 1791, non rite publ.; "Trichostomum fasciculare Schrad.", Spic. Fl. Germ.: 61. 1794, non rite publ.]. ≡ Racomitrium fasciculare (Hedw.) Brid., Mant. Musc.: 80. 1819. ≡ Grimmia fascicularis (Hedw.) Müll.Hal., Syn. Musc. Frond. 1: 809. 1849. — TYPE CITATION: Dill. hist. musc. p. 370 t. 47 f. 28. [Lectotype (vide Bednarek-Ochyra & Ochyra 2005: p. 1070): [icon in] Dillenius (1741): f. 28 on pl. 47; epitype (vide Bednarek-Ochyra & Ochyra 2005: p. 1070): the second specimen from the left on the sheet labelled "28. Rhacomitrium fasciculare 1892. n. 28. Bryum hypnoides, hirsutie virescens, fasciculare, alpinum *Hist. Musc.* p. 370. n. 28" – OXF-Dillenius!].

Bryum lutescens Dicks, Fasc. Pl. Crypt. Brit. 4: 14. 1801. \equiv Trichostomum lutescens (Dicks.) P.Beauv., Prodr.: 91. 1805. — TYPE CITATION: [Britannia] ad saxa in montibus frequens and a reference to "f. 28 on pl. 47" in Dillenius (1741). [Lectotype (*vide* Bednarek-Ochyra & Ochyra 2005: p. 1070): [icon in] Dillenius (1741): f. 28 on pl. 47]. First synonymised with *Trichostomum fasciculare* by Smith (1804: p. 1243).

Racomitrium fasciculare (Hedw.) Brid. fo. *rivulare* J.E.Zetterst., Rev. Grimm. Scand.: 123. 1861. $\equiv R.$ fasciculare var. rivulare (J.E.Zetterst.) H.Möller, Ark. Bot. 24A(2): 130, f. 25. 1931. — TYPE CITATION: Zett. Grimm. et Andr. exsicc. n. 32. [Lectotype (selected here): "32. Racomitrium fasciculare Brid. Schimp. Syn. musc. eur. p. 233. Zett. Rev. Grimm. scand. p. 121. forma rivularis glacialis Zett. 1. c. p. 123. In rivulis e niveliquefacta ortis juxta pedem montis Sneehætten alpium Dovrensium. 18 $^{2}/_{8}$ 58. J. E. Zetterstedt" – s-Möller!; isotypes: CANM!, M!], syn. nov.

R. virescens Lindb., Acta Soc. Sci. Fenn. 10: 68. 1871 ['*Bryum hypnoides* L. var. [γ] *virescens* Retz.', Fl. Scand. Prodr. 2: 214. 1779, *non rite publ.*]. — TYPE CITATION: Flora Danica (Liebmann 1849) "Tab. 2497, fig. 1" and references to pl. 47, f. 28 in Dillenius (1741) via Retzius (1779: p. 214). [Lectotype (*vide* Bednarek-Ochyra & Ochyra 2005: p. 1070): [icon in] Dillenius (1741): f. 28 on pl. 47]. First synonymised with *Racomitrium fasciculare* by Hartman (1871: p. 87).

R. fasciculare var. *nigricans* Warnst., Schrift. Naturw. Ver. Harz Wernigerode 2: 71. 1887. — TYPE CITATION: [...] Missionar O. J. Spindler im Jahre 1886 bei der Missionstation "Neuherrenhut" an der Südostküste von Grönland [...]. [Lectotype (*selected here*): "Herbarium Haussknecht, Jena 6. Rhacomitrium fasciculare nigricans Warnst. Grönland: Neuherrenhut 1886 leg. O. J. Spindler com. Warnstorf" – BR!; isotype: JE-Schliephacke!], *syn. nov.*

R. fasciculare var. *haplocladon* Kindb., Ottawa Natural. 7: 18. 1893. — TYPE CITATION: St. Paul's Island, Behring Sea, July 6th. 1892. (J. M. Macoun). [Holotype: "246. Ex Herb. Geological Survey of Canada. British Behring Sea Commission collection. Racomitrium fasciculare, Brid. var. haplocladon Kindb. St. Paul Island Collector, Jas. M. Macoun July 3rd 1892" – BM!], *syn. nov.*

R. papeetense Besch., Ann. Sc. Nat. Bot. Sér. 7, 20: 25. 1894. \equiv *Co-driophorus papeetensis* (Besch.) Bednarek-Ochyra & Ochyra, Cens. Cat. Polish Mosses: 141. 2003 ['papeetense']. — TYPE CITATION: Tahiti: Papeete, Jardin. [Holotype: "Rhacomitrium protensulum papeitense Besch Taiti Jardin Papeiti – Taiti 1852" – BM-Besch!; isotype: PC!], syn. nov.

Racomitrium microcarpon (Hedw.) Brid. var. *palmeri* Kindb. *in* Macoun, Cat. Canad. Pl. 6: 267. 1892. $\equiv R. palmeri$ (Kindb.) Kindb., Rev. Bryol. 23: 19. 1896. — TYPE CITATION: Amer. Arctic distr., r. Alaska: Palmer [Holotype: "St. Paul island June 10, 1890 W^m. Palmer N^o 169 <u>Racomitrium microcarpum</u> Brid. (Grimmia ramulosa Lindb., Braithw.) var. <u>Palmeri</u> Kindb., n. var. Differs in the leaves long-subulate, hairless, the upper cells longer and more confluent, the alar ones great and rectangular, the capsule shorter-pedicellate. Differs also from Racom. sudeticum in the deeply cleft peristome teeth, the long upper leaf cells etc. Linkoeping 18/3 1892 N. Conr. Kindberg." – CANM!; isotype: US!]. First synonymised with *Racomitrium fasciculare* by Jones (1933: p. 54).

R. tenuinerve Kindb., Rev. Bryol. 23: 19: 1896. — TYPE CITATION: Amer. Pacific distr., r. Canada: Macoun. Alaska: J. M. Macoun. [Lectotype (*selected here*): "Racomitrium tenuinerve Kindb. Alaska, S. Pauls ö 3/7 92 J. M. Macoun" – s-Kindb!; isolectotype: s!; syntype: "Racomitrium tenuinerve Kindb. n. sp. Canada, B. C., Revelstoke, rocks 19/5 90 Macoun" – s-Kindb!]. First synonymised with *Racomitrium fasciculare* by Möller (1931: p. 121). *R. fasciculare* var. *atroviride* Cardot, Bull. Herb. Boissier Sér. 2, 8: 334. 1908. – TYPE CITATION: Japon: Kamitsuge (n. 822); Takayu, rochers à 1200 m. (n. 2871, 2873); Hakkoda, à 1300 m. (n. 2927, 2928). [Lectotype (*selected here*): "Herbarium of Edwin B. Bartram Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. atroviride Card. <u>sp. nova.</u> Japon: Takayu. Leg. Faurie, 1904. n° 2873" – FH-Bartram!; syntype: (1) "Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. atroviride Card. (<u>e specim.origin.</u>) Japon: Takayu, rochers, 1200 m. Leg. Faurie, 1904 n. 2871" – s-Roth!; (2) "Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. atroviride Card. <u>var. nova.</u> Japon. Hakkoda, 1300 m. Leg. Faurie, 1904 n° 2927 " – NY!], *syn. nov.*

R. fasciculare fo. *nigrescens* H.Winter, Hedwigia 49: 296. 1910. — TYPE CITATION: [Norway] Snehätta ..., Knudshö. [Lectotype (*selected here*): "Herbarium Haussknecht, Jena Central Norwegen Racomitrium fasciculare Brid. nigricans Abhänge des Snehätta juli 1904 leg. Dr Winter" – JE-Winter!], *syn. nov.*

R. fasciculare fo. *submersum* H.Winter, Hedwigia 49: 296. 1910. — TYPE CITATION: [Norway] in Gletscherbächen des Snehätta...., Foksstuhö. [Holotype: "Herbarium Haussknecht, Jena [illegible] Central Norwegen Racomitrium fasciculare Brid. var. fluitans m. submersum Snehätta, in Schneewasser Tümpels Juli 1904 leg. Dr Winter" – JE-Winter!], *syn. nov.*

R. fasciculare fo. *validius* H.Winter, Hedwigia 49: 296. 1910. — TYPE CITATION: [Norway] Snehätta. [Holotype: "Herbarium Haussknecht, Jena Central Norwegen Racomitrium fasciculare Brid. validius Abhänge des Snehätta Juli 1904 leg. Dr Winter" – JE-Winter!], *syn. nov.*

Plants medium-sized to large and robust, fairly coarse, less often small to very small and slender, rather stiff and rigid, densely or loosely caespitose or forming extensive patches and mats, dull, yellow, yellow-, olive- to goldenbrown, yellow-green to green, brown to blackish-brown above, brown, dark brown to blackish-brown below, sometimes brown or black throughout. Stems procumbent, erect or ascending, (1-)4-10 or, sometimes, as much as 20 cm long, sparsely or freely fasciculate- to pinnate-branched, often with many short, tuft-like, lateral, horizontal branchlets, rarely almost unbranched, sparsely radiculose at base with dark brown to blackish-brown, smooth, lustrous, scarcely branched rhizoids, less often with bundles of rhizoids scattered along prostrate stems, in transverse section circular, lacking a central strand, with a 4-6-stratose cortex of small cells with dark brown, reddish- to blackish-brown, strongly incrassate walls and small lumina, surrounding 5-6 layers of large, thickwalled, yellow-brown medullary cells; axillary hairs numerous, hyaline throughout, consisting of 9-11 cells, short below becoming cylindrical distally. Leaves erect, loosely appressed with spreading to homomallous apices, sometimes closely imbricate when dry, erect-spreading when moist, straight to somewhat curved, occasionally falcate, broadly canaliculate-concave, narrowly lanceolate to linear- or ovate-lanceolate, (1.5-)2.2-3.6(-4.0) mm long, 0.5-1.0(-1.5) mm wide, from an oblong- or ovate-lanceolate, not or weakly plicate base gradually tapering to a long, channelled acumen, acute to narrowly rounded-obtuse, lacking a hair-point, entire but papillose-crenulate at the apex; margins entire and unistratose throughout, very rarely with solitary bistratose spots, variously recurved on both sides from the base nearly to the apex; costa single, unbranched, not or occasionally minutely spurred or forked at the apex, extending to $(\frac{2}{3})^{3}_{4}-5^{6}$ of the leaf length, well- or poorly defined, often concolorous and imperceptibly merging with the laminal cells above or bright to dark yellow-brown and clearly delimited from the laminal cells, (40-)50-70(-80) µm wide at the base, gradually tapering upwards, not prominent dorsally, situated at the bottom of a rather deep, wide-angled and open groove, in transverse section bistratose throughout, except for tristratose patches at the extreme base, composed of homogeneous cells, flat and consisting of 2-4 epidermal cells on the ventral side, flattened to somewhat curved and weakly convex on the dorsal side, composed of 4-7 ventral cells of the same size as the dorsal ones or the latter somewhat smaller and substereid at the extreme base; laminal cells unistratose throughout, densely covered on both surfaces with large, flat papillae, with strongly sinuose to nodulose, thick longitudinal walls, short- to long-rectangular, $(10-)20-30(-50) \mu m \log_{10} (5-)7-8(-10) \mu m$ wide in the upper part, becoming more linear-rectangular downwards, (25-)30-60(-70) µm long, with more nodulose walls in the suprabasal part; basal cells long-rectangular, with incrassate, porose and nodulose walls, (25-)30-50(-65) µm long, 8-10 µm wide, forming an orange- or yellowbrown biseriate strip along the leaf insertion; *alar cells* subquadrate to short-rectangular, 30-40(-50) µm long, 12-17(-20) µm wide, with thin to moderately thickened, straight to sinouse walls, often forming distinct, somewhat decurrent, brown auricles; supra-alar cells rectangular to subquadrate, (15-)20-30(-40) µm long, 8-10(-15) µm wide, hyaline to yellowish-hyaline, pellucid, straight- and thin-walled, forming a distinct, uniseriate, or occasionally biseriate, transparent border extending to (5-)7-18 cells up the margin. Dioicous. Perigonia bud-like, to 2 mm long; outer perigonial bracts lanceolate, to 2 mm long, 0.8 mm wide, similar to the cauline leaves; inner perigonial bracts ovate, shortly acuminate, with a blunt, rounded apex, 0.9-1.0 mm long, 0.8-1.0 mm wide, strongly concave and convolute, bearing up to 20 club-shaped, short-stalked greenish to brownish antheridia, intermixed with a few hyaline paraphyses about half the length of the antheridia. Outer perichaetial leaves similar to the vegetative leaves, narrowly linear-lanceolate, 3-4 mm long, 0.9-1.0 mm wide; inner perichaetial leaves loosely convolute, oblong-lanceolate to elliptical, 2.0-2.5 mm long, 0.8-0.9 mm wide, concave, broadly acute to rounded-obtuse at the apex, yellowishhyaline throughout, with a thin-walled areolation. Setae single per perichaetium, sometimes geminate, straight,

FIGURE 72. Codriophorus fascicularis. — 1. Habit. 2. Portion of branch, wet. 3. Portion of branch with capsules, dry. 4–8. Leaves. 9. Transverse section of stem. 10–13. Axillary hairs. 14–15. Alar cells. 16. Mid-leaf cells at margin. 17. Mid-leaf cells. 18–20. Leaf apices. 21–27. Transverse sections of leaves, sequentially from base to apex. — [All from *Limpricht 126*, KRAM]. — Scale bars: a - 1 mm (2-8); b - 1 cm (1); $c - 100 \mu \text{m} (9–27)$. (Reproduced from *Fragmenta Floristica et Geobotanica Series Polonica*, 2: 133, 1995, with permission).



erect, (2-)3-8(-11) mm long, reddish- to blackish-brown, smooth, twisted clockwise, with a single torsion to the left immediately below the capsule; vaginula dark-brown to reddish-brown, 1.0-1.2 mm long, with elongate, thickand sinuose-walled epidermal cells. Capsules exserted, erect, straight, ellipsoid, obloid to cylindrical, (1.0-)1.2-2.5(-3.1) mm long, 0.7–0.9 mm wide, smooth, lustrous, brown, pachydermous; operculum erect, long- and straightrostrate; annulus 2-3-seriate, deciduous, composed of large, vesiculose cells with strongly incrassate walls; exothecial cells isodiametric to elongate, oval, subquadrate to rectangular, 20-50 µm long, 10-20 µm wide, thick-walled with distinct corner thickenings, becoming quadrate, dark brown in 3-4 tiers at the mouth; stomata at the extreme base of the urn in 1-3 rows, numerous, 10-20 per capsule, superficial, bicellular, with rounded pori; peristome single, consisting of 16, reddish-brown, densely spiculate-papillose teeth, 550-600(-800) µm long, split nearly to the base into to 2 filiform, weakly barred prongs, with a low basal membrane, to 50 µm tall, and a distinct hyaline preperistome. Spores globose, brownish, 12-15(-17) µm in diameter, finely papillose. Calyptra conic-mitrate, verrucose at the apex, naked, 4-5-lobed at the base.

Etymology — This specific epithet is coined from the Latin *fascicularis* meaning connected or drawn into a fascicle or little bundle, in reference to the short lateral tuft-like branchlets.

Diagnostic characters and differentiation — Codriophorus fascicularis is a distinct and easily recognisable species that is unlikely to be mistaken for any other species of the genus throughout its wide geographical range in the Holarctic, except for East Asia where three other species of subsect. Fasciformes are known to occur and determination of some of them may sometimes be problematical. This is especially so because these otherwise distinct and clearly defined species have often been considered merely as varieties of the broadly circumscribed C. fascicularis and the amalgamation of all these species into a single taxon has markedly obscured the taxonomic concept of the central species of this complex.

After examination of a great number of specimens of Codriophorus fascicularis from across the world and typification of the species name (Bednarek-Ochyra & Ochyra 2005), this species is characterised by the following set of characters: (1) plants very variable in size and stature, ranging from small and slender to large and robust, growing in loose or dense tufts or forming extensive patches or mats, basically yellow-green, yellow-brown or green, but usually in various combinations of these and similar colours and their tints; (2) stems prostrate, ascending or erect, sparingly or abundantly fasciculateto pinnate-branched and also often bearing numerous, short, tuft-like, lateral, horizontal branchlets; (3) leaves narrowly lanceolate to linear- or ovate-lanceolate, not or weakly plicate at the base, gradually narrowed to a long, subulate, canaliculate acumen, straight or curved, broadly canaliculate-concave; (4) leaf apex muticous, acute to

narrowly rounded-obtuse, entire, papillose-crenulate; (5) margins entire and unistratose throughout; (6) costa extending to $\frac{3}{4}-\frac{5}{6}$, very rarely to $\frac{2}{3}$ of the way up the *leaf*, spurred or forked at the apex, situated at the base of a moderately deep, wide-angled and open channel, in transverse section bistratose throughout, flat ventrally, flattened to somewhat curved dorsally; (7) laminal cells unistratose, short- or long-rectangular to linear-rectangular throughout; (8) alar cells subquadrate to shortrectangular, thin- to moderately thick-walled, usually forming somewhat decurrent auricles; (9) supra-alar cells rectangular to subquadrate, with straight thin walls, hyaline to yellowish-hyaline, forming a uniseriate or, sometimes, biseriate, pellucid border consisting of 5-18 cells; (10) setae straight, erect, (2-)3-8(-11) mm long, reddish- to blackish-brown, smooth, dextrorse, with a single torsion to the left immediately below the capsule; (11) capsules ellipsoid, obloid to cylindrical, (1.0-)1.2-2.5(-3.1) mm long; (12) peristome teeth reddish-brown, densely spiculate-papillose, 550-600(-800) µm long, split nearly to the base into 2 filiform branches, with a low basal membrane.

Codriophorus fascicularis is closely related to the remaining three species of subsect. *Fasciformes* and has often been confused with them. The entire leaf apex is the principal character which accurately separates *C. fascicularis* from *C. brevisetus*, *C. anomodontoides* and *C. corrugatus*. In all these species the apex is papillose-crenulate because of the protruding cell papillae, but in the last three species it is additionally variously denticulate-cristate, dentate or serrulate, although on some leaves the denticulation may be obscure and indistinct. However, if some supplementary characters are taken into account they should in combination ensure accurate identification of the species.

Codriophorus anomodontoides is easily distinguished in doubtful cases by the shape of its costa which is distinctly convex on the ventral side and quite often also canaliculate dorsally. This gives the costa a curved appearance as is nicely visible in transverse section. In contrast, the costa is entirely flat on the ventral side in *C. fascicularis*. The flat costa on the ventral side is also typical for *C. brevisetus* and *C. corrugatus*. However, the former is distinct by having short distal laminal cells, 5–15 µm long, whereas the upper laminal cells in *C. fascicularis* are 20–30 µm long, with only some solitary cells being shorter. In addition, in most populations of *C. brevisetus* the leaf margins are variously bistratose and this combination of characters should suffice for the correct identification of the material.

Finally, *Codriophorus corrugatus* shares with *C. fascicularis* the elongate upper leaf cells that are unistratose throughout the lamina and the flat costa on the ventral surface. However, the corrugate, ruffled and wavy leaf acumen should preclude confusion because in *C. fascicularis* the leaf acumen is always plane and straight. Additionally, the costa in *C. corrugatus* is short and typically vanishes in mid-leaf, whereas in *C. fascicularis* the costa ends at least three quarters of the way up the leaf.

Confusion of Codriophorus fascicularis with other species of the genus is minimal but in some regions possible. In Asia, it may be mistaken for C. carinatus and actually Cardot (1908a) in the original description of the latter species remarked on its similarity in size and habit to C. fascicularis. C. carinatus is quite variable and its epilose phenotypes are likely to be confused with C. fascicularis unless carefully studied. However, C. carinatus is at once distinct in having short, isodiametric distal laminal cells, frequent bistratose leaf margins and, in particular, different costal anatomy. The costa in this species is strongly protruding on the dorsal side, semi-terete to crescent-shaped, but it is 2-3-layered in the proximal half, with a distinct dorsal 1-2-stratose stereid band and markedly large, 3-4 ventral epidermal cells. Additionally, many populations of C. carinatus have short, hyaline and denticulate leaf tips, whereas C. fascicularis always has muticous leaves.

In Pacific North America Codriophorus fascicularis has occasionally been mistaken for C. varius. Typically, the latter species has piliferous leaves and very longcylindrical capsules with very long peristome teeth and these characters coupled with the very robust habit of the plants make C. varius a very distinct species. However, some populations of C. varius lack hyaline hair-points on the leaves and may resemble those in C. fascicularis, especially as they may possess short, tuft-like, lateral branches. However, the leaves strongly plicate at the base, subquadrate to short-rectangular upper laminal cells and a tristratose costa in the proximal half should preclude confusion of the two species.

Variability — Codriophorus fascicularis has been a misunderstood and incorrectly described species, especially in East Asia, where Noguchi (1974, 1988) circumscribed it very broadly and merged with it three other species of the complex which are now considered to be species in their own right. As is the case with other widely distributed species showing a broad ecological amplitude, C. fascicularis varies correspondingly but its variability is phenotypical and mostly conditioned by environmental factors. The main morphological differences within this species are relative and difficult to classify, although occasionally some characteristic phenotypes were distinguished as separate taxa. For example, plants growing submerged in flowing water in montane streams in Norway were described as Racomitrium fasciculare fo. rivulare (Zetterstedt 1861) or R. fasciculare var. rivulare (Möller 1931) and R. fasciculare fo. submersum (Winter 1910). They are merely irregularly and sparingly branched phenotypes with eroded leaves and denuded stems in the lower parts which otherwise share all diagnostic characters of the species.

In general, *Codriophorus fascicularis* exhibits great variation in the stature of the plants and their size and robustness range from small and gracile to large, robust and coarse. The largest plants were collected in Greenland and reached 20 cm (*Hamann 69-774*, c), whereas small, stunted forms reaching about 1 cm are not rare at

altimontane elevations or in polar regions. The branching pattern of the species is particularly subject to variability. Typically, it commonly has a bunched or nodose appearance due to numerous short, lateral, tuft-like branchlets. However, very often they are lacking in many populations, especially in the Arctic, and the plants are variously, freely or sparingly and irregularly to subpinnately branched. Sometimes, the plants are poorly ramified and are represented by single, almost unbranched shoots as for example in populations from the Bering Sea near Alaska which were described as Racomitrium fasciculare var. haplocladon (Kindberg 1893) or those from British Columbia which consist of thread-like and fairly delicate plants (Schofield, Vitt & Horton 72655, DUKE). Likewise, the coloration of the plants is subject to great variation. Apart from the commonly occurring colours, such as yellow-brown, yellow-green or olive-green, the plants are sometimes golden-brown or golden-rufous and blackish to deeply black. The latter phenotypes were given taxonomic recognition in Greenland as R. fasciculare var. nigricans (Warnstorf 1887) and in Norway as R. fasciculare fo. nigrescens (Winter 1910).

The leaves of *Codriophorus fascicularis* vary much in size and in general this variation is correlated with the robustness of the plants. In extreme cases the leaves can be as little as 1.5 or as much as 4.0 mm long, but in general they average 2.2–3.6 mm long. The shape of the leaves is lanceolate, ovate- or linear-lanceolate to lanceolate-subulate. The leaves are mostly straight or slightly curved and homomallous. However, they are sometimes distinctly falcato-secund, giving the plants a 'drepanocladoid' appearance, for example in Newfoundland (*Tuomikoski 5622*, H) (Fig. 73.32–35).

The leaf apex is also variable in shape, from subulate or setaceous (e.g., *Schofield & Spence 84215*, DUKE), through acute to narrowly rounded-obtuse. The last form of the leaf apex is particularly frequent in cold parts of the range of the species, for example in Chukotka (e.g., *Afonina s.n.*, 13 Aug 1991, KRAM) (Fig. 75.11). The leaf margins are typically narrowly to broadly recurved or revolute on both sides from the base nearly to the apex, although occasionally they are plane in the upper $\frac{1}{4}-\frac{1}{5}$ of the leaf length. They are consistently unistratose throughout and only in a very few cases from about one thousand sectioned plants have there been found solitary bistratose spots, for instance in the type material of *Racomitrium papeetense*.

The costa of *Codriophorus fascicularis* is relatively stable and varies little so it has diagnostic value for this species. It is relatively long and vanishes at ${}^{3}\!\!/_{4}$ - ${}^{5}\!\!/_{6}$ of the way up the leaf and only very rarely does it end in some leaves at ${}^{2}\!\!/_{3}$ of the leaf length, for example in the type of *Racomitrium tenuinerve*, but its width lies within the limits typical for the genus. The costae are mostly 50–70 µm wide, but sometimes they are broader, to 80 µm, or narrower, to 40 µm. The plants with broad costae were distinguished as a separate taxon, namely *Racomitrium fasciculare* fo. *validius* in Norway (Winter 1910). Interestingly, despite its name, *R. tenuinerve*, described from Alaska and British

Columbia in North America (Kindberg 1896), has a relatively broad costa but it is concolorous with the laminal cells and gives the impression of slenderness. As well, leaf areolation varies little in *C. fascicularis* and in general the laminal cells are elongate throughout the leaf. The leaves with long-acuminate to subulate apices have longrectangular to linear distal cells (Fig. 75.1–9), whereas in the short-acuminate leaves with narrowly rounded-obtuse apices the apical cells are shorter, but otherwise rectangular, not isodiametric (Fig. 75.10–11).

There is some variation in sporophyte characters in Codriophorus fascicularis, especially in the seta length and the capsule size and shape, but it generally follows the trends commonly observed in other species of the genus. The capsules are mostly obloid to short-cylindrical, 1.2-2.5 mm long, supported by setae of medium length, 4–8 mm long. Occasionally, the capsules are very large, 3.0–3.1 mm long, cylindrical, seated on long setae to 11 mm (e.g., Hermann 22206, KRAM) and such plants have been mistaken for C. varius. In contrast, some plants (e.g., Kincaid s.n., 27 Jul 1899, WTU) have very small, ellipsoid capsules, 1.0-1.1 mm long on very short setae, 2-3 mm long, which are produced in great abundance. The peristome teeth are mostly short, about 600 µm, but occasionally they may reach 800 µm (e.g., Hagen s.n., 14 Мау 1888, н).

Reproduction — Codriophorus fascicularis is a prolific species which produces sporophytes in great profusion in temperate latitudes and at low montane elevations. Its fecundity is markedly reduced in areas with harsh and severe climatic conditions in the Low and High Arctic as well as in the alpine zone in mountains. For example, only sterile specimens are known from Spitsbergen, Jan Mayen, Chukotka, Kamchatka, Arctic Siberia, Arctic Alaska and the Yukon Territory, whereas in Greenland only about five fertile specimens have been detected amongst over 60 specimens examined. Likewise, sporophytes are rarely found in Iceland, the Aleutian Islands and Japan.

Taxonomic and nomenclatural notes — Codriophorus fascicularis was distinguished for the first time as a separate species by Dillenius (1741) in his Historia muscorum. This author assigned to it the phrase-name Bryum hypnoides, hirsutie virescens, fasciculare alpinum and provided a detailed description and illustration which were based upon a specimen from Snowdon in Wales. Linnaeus (1753, 1763) accepted this taxon but considered it only as an unnamed variety $[\beta]$ within his "Bryum hypnoides" (=Racomitrium lanuginosum). He provided no description of this taxon and cited only the Dillenian phrase-name along with a reference to the plate and figure in Historia muscorum. This taxon was subsequently accepted by Hudson (1762), Necker (1771), Reichard (1780), and Hull (1799), but without an epithet. It was only Retzius (1779) who introduced a formal name to this variety, "Bryum hypnoides var. virescens", providing a direct reference to Dillenius (1741). As this was done earlier than the starting point for moss nomenclature (1801), it was obviously not a validly published name. This varietal designation was formally elevated to species rank by Lindberg (1871) as *Racomitrium virescens* Lindb., but this name has long been considered illegitimate because, according to the compilers of *Index muscorum* (Wijk *et al.* 1967), it included an earlier name, *Racomitrium fasciculare* (Hedw.) Brid. based on *Trichostomum fasciculare* Hedw.

Codriophorus fascicularis was recognised as a separate species and given a name in a binomial combination, "Bryum fasciculare", by H. A. Schrader (in Gmelin, 1791). Three years later this author transferred this species to the genus Trichostomum sensu Hedwig (1782), as "T. fasciculare", and provided its first detailed description. The species immediately gained wide acceptance in various contemporary Floras and botanical treatments (e.g., Laicharding, 1794; Hoffmann, 1796; Bridel, 1798; Swartz, 1799; Röhling, 1800; Roth, 1800), and Hedwig (1801) validated T. fasciculare when accepting this species in his Species muscorum frondosorum which is accepted as the starting point for moss nomenclature (Sphagnum excepted). He provided only a brief diagnosis of the species excerpted from Gmelin (1791) but neither a description nor discussion were presented. Bridel (1819) transferred Trichostomum fasciculare to Racomitrium and under this generic name it has appeared as R. fasciculare in most Floras and botanical handbooks in Europe. Müller (1849) transferred R. fasciculare to his catch-all genus Grimmia Hedw., but this concept has largely been ignored since the genus Racomitrium has been universally accepted by bryologists.

Bednarek-Ochyra & Ochyra (2005) carefully investigated the early taxonomic history of Codriophorus fascicularis and found that only two collections of this species were known in the pre-1801 period, namely from Snowdon in Wales (J. J. Dillenius) and Mt Brocken in the Harz, Germany (H. A. Gmelin). Neither is to be found in the personal herbarium of J. Hedwig at Geneva and there is not the slightest evidence that Hedwig (1801) could have seen and examined them during preparation of the validating diagnosis of Trichostomum fasciculare. Therefore they are not eligible to be selected as a lectotype. The only element that is eligible for typification of this species name is figure 28 on table 27 in Historia muscorum of Dillenius (1741) and this was actually selected as the lectotype of T. fasciculare (Bednarek-Ochyra & Ochyra 2005). This illustration is inadequate for accurate identification of the species since it lacks many microscopic details that are crucial for its correct circumscription, especially the anatomy, length and shape of the costa, the leaf areolation and the shape of the leaf apex. Consequently the corresponding specimen preserved in the Dillenian herbarium at Oxford (Druce & Vines 1907) was designated as epitype in order to preserve the current usage of T. fasciculare. The epitype material is in excellent condition, consisting of vigorous plants with numerous sporophytes which have been illustrated and described in detail by Bednarek-Ochyra & Ochyra (2005).

Despite its morphological variability, *Codriophorus* fascicularis has been accurately interpreted by bryolo-



FIGURE 73. Codriophorus fascicularis. — 1–35. Spectra of vegetative leaves. — [1–4 from Afonina s.n., 13 Aug 1991, KRAM (Chukotka); 5–7 from De Sloover 2264, BCB (Belgium); 8–10 from Váňa s.n., 8 Sep 1959, PRC (Czech Republic); 11–13 from Voroblev s.n., 25 Jul 1946, LE (Kuril Islands); 14–16 from Schofield & Spence 84215, DUKE (British Columbia); 17–18 from Loof E124, MICH (Alaska); 19–21 from Iwatsuki & Sharp 76A, TENN (Honshu); 22–25 from Jardin s.n., 1852 – type of Racomitrium papeetense (Tahiti); 26–27 from Jury 5962, BCB (Scotland); 28–31 from Faurie 2873, FH – lectotype of Racomitrium fasciculare var. atroviride (Japan); 32–35 from Tuomikoski 5622, H (Newfoundland)]. — Scale bar: 1 mm.

gists and is one of very few species which have not been redundantly described in Europe under different names, a common practice in the case of polymorphic species. Dickson (1801) described *Bryum lutescens* from Britain but this name was soon reduced to synonymy with *Trichostomum fasciculare* (Smith 1804). There have been some disagreements with regard to the legitimacy of the name *B. lutescens* and the compilers of *Index muscorum* (Wijk *et al.* 1959, 1969) considered it to be illegitimate because of the supposed inclusion of *Racomitrium fasciculare*. Bednarek-Ochyra & Ochyra (2005) proved that Dickson (1801) did not cite any validly published name



FIGURE 74. Codriophorus fascicularis. — 1–6. Transverse sections of costa and leaves, sequentially from base to apex. — [1 from *Tuomikoski 5622*, H; 2 from *Jury 5962*, BCB; 3 from *Iwatsuki & Sharp 76A*, TENN; 4 from *Faurie 2873*, FH – lectotype of *Racomitrium fasciculare* var. *atroviride*; 5 from *Loof E124*, MICH; 6 from *Jardin s.n.*, 1852 – type of *Racomitrium papeetense*]. — Scale bar: 100 µm.

under *B. lutescens* which could allow "inclusion" of a type of this earlier name, based on *Trichostomum fasciculare*. Therefore this interpretation is not in accord with the provisions of Art. 52.2(c) of the current Code (Greuter *et al.* 2000) and *Bryum lutescens* is definitely legitimate. Nonetheless, Bednarek-Ochyra & Ochyra (2005) chose figure 28 on plate 47 in *Historia muscorum* of Dillenius (1741) as lectotype making *B. lutescens* a homotypic and nomenclaturally inactive synonym of *Codriophorus fascicularis*.

A similar case is provided by *Racomitrium virescens*, a species described by Lindberg (1871). This name is considered in *Index muscorum* (Wijk *et al.* 1967) to be illegitimate because it was said to include an earlier name, *Racomitrium fasciculare*. Bednarek-Ochyra & Ochyra (2005) demonstrated convincingly that this interpretation is not in accordance with Art. 52.2 of the current ICBN (Greuter *et al.* 2000) because Lindberg (1871), in his work providing critical identifications of the illustrations of bryophytes in *Flora danica*, merely quoted in one column, evidently without acceptance, the names appearing in this work, and, in the other column containing his determinations, did not include any validly published name under *R. virescens*. Therefore this name is definitely legitimate. Bednarek-Ochyra & Ochyra (2005) ensured its homotypy with *Codriophorus fascicularis* when selecting Retzius' (1779) pre-starting-date variety cited by Lindberg (1871) and based on "Dill. musc. t. 47 f. 28" as lectotype.

Outside Europe *Codriophorus fascicularis* has only been described as a separate species on three occasions. Bescherelle (1894) described *Racomitrium papeetense* from Tahiti in the Society Islands in the South Pacific and compared its habit with *Codriophorus fascicularis* and *Niphotrichum ericoides*. This species was subsequently redescribed and illustrated by Whittier (1976) but it has not been rediscovered and is still known only from the type collection which is a relatively robust but otherwise



FIGURE 75. Codriophorus fascicularis. — 1–11. Leaf apices. 12–13. Alar cells. — [1–2 from Schofield & Spence 84215, DUKE; 3 from Tuomikoski 5622, H; 4, 12–13 from Casas s.n., 3 Jul 1961, BCB; 5 from Jardin s.n., 1852 – type of Racomitrium papeetense; 6 from Iwatsuki & Sharp 76A, TENN; 7–8 from Faurie 2873, FH – lectotype of Racomitrium fasciculare var. atroviride; 9 from De Sloover 2264, BCB; 10 from Voroblev s.n., 25 Jul 1946, LE; 11 from Afonina s.n., 13 Aug 1991, KRAM]. — Scale bar: 100 µm.

typical phenotype of *C. fascicularis* and accordingly both species are here considered to be conspecific taxa.

Kindberg (1896) described *Racomitrium tenuinerve* from Alaska and British Columbia. This species is briefly discussed above in the "Variability" section and this name had already been reduced to synonymy with *Racomitrium fasciculare* by Möller (1931).

Kindberg (in Macoun & Kindberg 1892) described from Alaska *Racomitrium microcarpon* (Hedw.) Brid. var. *palmeri* which soon afterwards he elevated to species rank (Kindberg 1896). This taxon is characterised by having somewhat 'hyalinised' leaf apices as a result of living in harsh climatic conditions but otherwise it has nothing in common with *Bucklandiella microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra with which it was originally associated. As already suggested by Jones (1933), it represents *Codriophorus fascicularis* with very prominent leaf cell papillae and strongly revolute leaf margins.

In total, eight varieties and four forms have been recognised within *Codriophorus fascicularis*. Three varieties, namely *Racomitrium fasciculare* var. *brachyphyllum*, var. *erosum* and var. *perrobustum* are currently considered to be identical to *C. anomodontoides*, and *R. fasciculare* var. *hayachinense* is inseparable from *C. brevisetus*. The status of *R. fasciculare* var. *atroviride* is debatable and Noguchi (1974, 1988) associated it with *C. anomodontoides*. Here, this name is placed in synonymy with *C. fascicularis* because this variety shares its all taxonomically important


characters, including acute and entire leaf apex, elongate distal laminal cells and a costa that vanishes at three quarters of the leaf length and is flat on the ventral side.

The remaining infraspecific taxa were recognised according to the spirit of the olden epoch in bryophyte taxonomy when various habitat expressions were given taxonomic status. Such taxa as Racomitrium fasciculare var. nigricans, fo. nigrescens, var. rivulare, fo. submersum and fo. validius clearly refer to plants having a blackish colour, growing submerged in streams or in compact tufts or having stronger costae. These deviations perfectly fall within the range of variation of the species and therefore their recognition as distinct taxa is unjustified.

Chromosome number — Three chromosomal records are available for Codriophorus fascicularis, one from Finland (Vaarama 1949) and two from Great Britain (Smith & Newton 1967; Newton 1971). They show that the species is very stable cytologically and the haploid chromosome number of n = 13 has invariably been found in all the populations studied.

Habitat — Codriophorus fascicularis is a hydrophilous species which can tolerate periodic desiccation. It grows most often in shady or exposed situations on rocks, stones, boulders, cliffs and rock faces and outcrops in and close to streams, brooks and lakes that are permanently or periodically submerged or splashed with water, in seepage areas and melt-water runnels. The species is found on bare rock faces or on thin soil covering rock outcrops and in such situation tufts or patches of the moss are encrusted with silt or sand. It grows predominantly on acidic rocks, including sandstone, granite, gneiss and basalt. Occasionally, it has been collected on bark at tree bases, on logs floating at lake margins, on the shingle roof of buildings and once it was found growing on a thin sandy soil layer attached to the metal wing of a crashed aircraft.

As an acidophilous rupestral moss, Codriophorus fascicularis is considered by phytosociologists to be a characteristic species of the class Grimmio-Racomitrietea heterostichi and the order Racomitrietalia heterostichi (Hübschmann 1986; Marstaller 1993). It occurs in various associations of this class, for example in Hedwigietum ciliatae (Hübschmann 1955), Racomitrio-Andreaeetum rupestris (Hertel 1974; Hübschmann 1986), Racomitrietum lanuginose (Hübschmann 1986) and Gymnomitrietum concinnati (Philippi 1956; Hübschmann 1986) but it does not show any clear preference for a particular association. Marstaller (1982) described from Thuringia 179

in Germany a separate subassociation dominated by this species within the association Racomitrietum lanuginosi. In this subassociation C. fascicularis grows together with Racomitrium lanuginosum, Bucklandiella microcarpa, Niphotrichum ericoides and Sanionia uncinata. In the Tatras in the Western Carpathians, C. fascicularis has often been recorded in stands of the association Trifido-Distichetum salicetosum herbaceae (Balcerkiewicz 1984), and in the Sudetes it occurs in the association Cynodontio-Paraleucobryetum longifolii (Koła 1986) but with only moderate coverage.

Geographical distribution — Codriophorus fascicularis is a boreal-montane species, weakly penetrating into the Arctic, which exhibits strong affinities for an oceanic climate (Ochyra et al. 1990c; Bednarek-Ochyra 1995). It has a very dissected and disjunct range in the Holarctic, with its maximum occurrence in western and northern Europe and, additionally, it deeply penetrates into the tropics where it was once discovered in the Society Islands archipelago in the Pacific region (Fig. 77). The discovery of this species in a remote outpost in the tropics is not so extraordinary as it might at first appear as many Holarctic moss and hepatic species are known to occur at high elevations in tropical mountains (Gradstein et al. 1983; Gradstein & Váňa 1987). Tahiti is the cone of a submarine volcano reaching an altitude of 2237 m on Mt Orohena with a typical alpine zone which creates prime habitat for cool-adapted northern species.

In Europe (Fig. 78), the species is widespread and common in Iceland, the Faeröe Islands, the British Isles and Fennoscandia where it extends eastwards to the Kola Peninsula, Karelia and the Ladoga Lake region. In the European Arctic it is rare and localised on Jan Mayen, Bear Island and Spitsbergen where it reaches its extreme northernmost locality at lat. ca 81° N (Frisvoll 1983b), extending eastwards to the Polar Ural Mountains. On the mainland C. fascicularis is frequent on all European mountains, extending from the Pyrenees and Massif Central, through to the the Vosges, Ardennes, Harz and Alps, eastwards to the Ore Mountains, Sudetes, Bohemian Forest and Western Carpathians of Slovakia and Poland (Stebel & Bednarek-Ochyra 2004), with occasional occurrences in the Eastern and Southern Carpathians of Romania. Additionally, it is widely scattered as a relict on erratic blocks in northern lowlands from Brittany, France in the west (Touffet 1969), through to Germany (Düll 1994) and eastwards to the Masurian Lakeland in northeastern Poland (Ochyra et al. 1990c). The species has also been reported from the Sierra Nevada in southern Spain

FIGURE 76. Codriophorus fascicularis. - 1. Perigonium. 2-3. Outer perigonial bracts. 4-7. Inner perigonial bracts. 8. Innermost perigonial bract and antheridia. 9-13. Outer perichaetial leaves. 14-20. Inner perichaetial leaves. 21. Upper cells of innermost perichaetial leaf. 22. Basal cells of innermost perichaetial leaf. 23-28. Deoperculate capsules with well-developed or destroyed peristomes, wet. 29-30. Opercula. 31-32. Calyptrae. 33-35. Transverse sections of calyptra. 36. Transverse section of seta. 37. Epidermal cells of seta. 38. Epidermal cells of vaginula. 39. Exothecial cells at base of urn and stomata. 40. Exothecial cells in mid-urn. 41. Exothecial cells at capsule mouth, annulus, peristome and spores. --- [1-8 from Ochyra 14A; 9-13, 16-17, 27-29, 33-38 from Bauer 1071; 14, 18, 20, 32 from Limpricht 126; 15, 19, 23-24, 30, 39-41 from Krupa s.n., sine dato (Krywań); 21-22 from Tolf s.n., Apr 1888; 25-26 from Kornaś s.n., 2 Jun 1946; all in KRAM]. - Scale bars: a - 1 mm (9-20, 31-32); b - 1 mm (23-30); c - 100 µm (21–22, 33–41); d – 1 mm (1–8). (Reproduced from Fragmenta Floristica et Geobotanica Series Polonica, 2: 135, 1995, with permission).

(Höhnel 1895), north-western Spain (Reinoso & Alvarez 1984; Fernández Ordoñez 1988; Reinoso & Viera 1991; Carballal et al. 1992), the Rila Massif in Bulgaria (Petrov 1975), the Central Ural Mountains (Dyachenko et al. 2005) and the Caucasus (Savicz-Lyubitskaya & Smirnova 1970) but no voucher specimens from these areas have been available for investigation. Surprisingly, no specimens of C. fascicularis have been seen from the Shetland Islands, although the species is said to be common on this archipelago (Proctor 1992c). The altitudinal range of C. fascicularis in Europe extends from near sea level to the alpine zone at about 2400 m in the Pyrenees, Alps and Carpathians, with the highest known locality at 2663 m on the summit of Mt Lomnica in the High Tatra Mountains of Slovakia (Chałubiński 1882, 1886). In Macaronesia, the species is known only from the Azores (Sjögren 2001; Frahm 2005); the record from Madeira (Luisier 1930; Eggers 1982) is obscure and in all likelihood C. fascicularis has never been found there.

In North America (Fig. 79) Codriophorus fascicularis has two centres of distribution. In the eastern part of the continent it is widely distributed but scattered, from Labrador through to the maritime provinces of Canada, southwards to the Northern Appalachian Mountains, including the White Mountains of Maine and New Hampshire where it reaches its highest elevation of 1917 m on Mt Washington, and the Adirondack Mountains in New York where it was recorded at an altitude of 1730 m, and westwards to the Lake Superior region of Ontario, Michigan and Minnesota. In this part of the continent the species scarcely penetrates into the Arctic and it has only once been recorded on Baffin Island slightly below the Arctic Circle. In the western part of North America C. fascicularis is more frequent and abundant, extending from the Baird Mountains, Seward Peninsula, Aleutian Islands and Alaska Range in Alaska and the Olgivie and Selwyn Mountains of the Yukon, through to the coastal areas and the Rocky Mountains of British Columbia and Alberta, southwards to Washington, northern Oregon, Idaho and Montana, with highly isolated stations in Colorado, where it reaches its highest altitude of about 4100 m. As in eastern North America it has only once been recorded in the High Arctic, scarcely reaching beyond the Arctic Circle in the Baird Mountains in Alaska. In general, C. fascicularis is very rare in the Arctic. Apart from Europe and North America it is known only from the southern parts of East and West Greenland where it is common and abundant but only below the Arctic Circle which it crosses only in West Greenland, extending to lat. ca 70° N on Disko Island (Fig. 79). In Asia, it has been collected only once in Arctic Siberia on Bolshevik Island in the Severnaya Zemlya (= North Land) archipelago and several times in Chukotka (Afonina 2004). The records of C. fascicularis from Yakutia (Arnell 1913) actually refer to C. corrugatus (Bednarek-Ochyra 2004c).

Outside the Arctic, *Codriophorus fascicularis* is very rare in Asia and is known only from the Far East (Fig. 80). It has its main centre of occurrence in Japan, where it is infrequent on Hokkaido and quite widespread in northern and

central Honshu. It occurs mostly in the alpine zone, from 1700 to 3000 m on Mt Ontake, only rarely descending to 1300 m. In addition, the species is very rare and scattered on the Kuril and Komandorskiy Islands and on the mainland it is known only from southern Kamchatka and the Kolymskoe Nagorye (= Upper Kolyma Highland) in Magadan Province in the Russian Far East (Blagodatskikh 1984). Ochyra et al. (1990c) and Bednarek-Ochyra (1995) presented a wider range of Codriophorus fascicularis in Asia, covering also China, Taiwan and the Philippines but these maps were based upon the broad concept of the species, including taxa which are currently recognised as separate species, C. brevisetus and C. anomodontoides. Nonetheless, Cao (2000) and Cao et al. (2003) still recorded C. fascicularis from Yunnan and Taiwan. Examination of the voucher collection from the former area (Shevock 18224, KRAM) revealed that it actually refers to Bucklandiella subsecunda. Also, one specimen from Taiwan (Redfearn et al. 1153, MO) represents C. anomodontoides. Unfortunately, the other two vouchers [Chuang 1054 (H, NY) & 225 (NY)] have not been located in the herbaria concerned. Ching-Chang Chuang collected many specimens of Codriophorus on Taiwan, although he quoted only very few in his paper (Chuang 1973). All of them represent C. anomodontoides (see list of specimens examined, p. 216) which is the commonest species of the genus in Taiwan.

Codriophorus fascicularis was once recorded from Mexico (Crum 1994) but the voucher specimen (*Hagerová s.n.*, NY) actually represents *Bucklandiella subsecunda*. To this species belong also some collections from Colombia which were originally determined as *Racomitrium fasciculare* (Bednarek-Ochyra *et al.* 1999).

Many handbooks, floras and phytogeographical treatments (e.g., Smith 1978, 2005; Crum & Anderson 1981; Nyholm 1956, 1998; Dierßen 2001) provide information on the bipolar occurrence of Codriophorus fascicularis in New Zealand and Tasmania and southern South America, although it is not listed in separate accounts dealing with bipolar mosses (Du Rietz 1940; Schofield & Crum 1972; Schofield 1974; Ochyra 1992). However, specimens once reported by Wilson & Hooker (1847) from Hermite Island near Cape Horn as an unnamed variety of Racomitrium fasciculare were soon afterwards described by Müller (1849) as a new species, Grimmia symphyodonta Müll.Hal. (= Racomitrium symphyodontum (Müll. Hal.) A.Jaeger) which is conspecific with Bucklandiella didyma (Mont.) Bednarek-Ochyra & Ochyra (Deguchi 1984), a distinct species which has obviously nothing in common with Codriophorus fascicularis. As well, all the specimens from New Zealand and Tasmania determined as Racomitrium fasciculare (Wilson 1854, 1859; Mitten 1867) actually belong within the Bucklandiella crispula complex (Dixon 1926) which requires critical taxonomic assessment.

EXSICCATI

ALLORGE & ALLORGE – Bryophyta Azorica No. 83 (CANM, F, MO). AUSTIN – Musci Appalachiani No. 502 (BM, CANM, F, FH, NY, US, W).



FIGURE 77. Global distribution of Codriophorus fascicularis. Inadequately localised stations are indicated by asterisks.

- BARTLING & HAMPE Vegetabilia Cellularia in Germania Septentrionali Praesertim in Hercynia et in Agro Gottingensi No. 16 (UC, W).
- BAUER *Musci Europaei Exsiccati* No. **1070 & 1071** (BR, BRNM, CANM, COLO, G, hb. Frahm, JE, KRAM, M, POZG, PRC, W, WTU).
- BERGGREN Plantae in itineribus Suecorum polaribus collectae/Insulae Spetsbergenses No. 45 (s); No. 46 (s, w).
- BILLOT Flora Exsiccata De C. Billot (cont. Bavoux, Guichard, Guichard & Paillot) No. **3784** (G, JE, M).
- BLANDOW Musci Frondosi Exsiccati No. 171 (G, W).
- BREUTEL *Flora Germanica Exsiccata* No. **152** (GJO, JE, M, POZG, UC, W).
- BROTHERUS Bryotheca Fennica No. 328 (M, JE, POZG, S).
- BROTHERUS *Musci Fenniae Exsiccatae* No. 9 (Alta, G, M, S, W); No. 121 (CANM, M, S, W).
- CRUM & ANDERSON *Mosses of North America* No. **451** (Alta, BM, BR, CANM, F, H, KRAM, MICH, MO, O, POZG, UC, US).
- DELOGNE & GRAVET Les Mousses de L'Ardenne No. 67 (BR).
- DRUMMOND Musci Boreali-Americani No. 132 (BM, MICH, NY).
- FAMILLER Flora Exsiccata Bavarica: Bryophyta No. 662 (GZU, M).
- FUNCK Cryptogamische Gewächse Fichtelgebirg's No. 433 (M, W).
- GRAVET Bryotheca Belgica No. 125 (BR, G).
- GROUT North American Musci Perfecti No. 106 (CANM, CAS, FH, MICH, MO, NY, TENN, UC, US).
- HARTMAN Bryaceae Scandinaviae Exsiccatae No. 197 (COLO, W).
- HOLMEN Bryophyta Danica Exsiccata No. 186 & 187 (ALTA, BR, CANM, CAS, COLO, G, H, KRAM, O, POZG, S, UC, W).
- HOLZINGER *Musci Acrocarpi Boreali-Americani* No. 447 (BM, CANM, COLO, FH, H, MICH, MO, NY, UC, US, WTU, WVA).
- HUSNOT Musci Galliae No. 181 (BR, G, M).
- KONSTANTINOVA, BELKINA, LIKHACHEV & SHLYAKOV Bryophyta Murmanica Exsiccata No. 44 (G, MO).
- KOPSCH Bryotheca Saxonica No. 232 (HBG, JE, KRAM).

- Kryptogamae Exsiccatae No. 1081 (BR, G, GJO, HBG, JE, M, O, PRC, PRC, W).
- LIMPRICHT Bryotheca Silesiaca No. 126 (BR, HBG, KRAM, M, PRC).
- LINDGREN Musci Sueciae Exsiccati No. 88 (KRAM).
- LISOWSKI *Bryotheca Polonica* No. **69** (BR, BRNM, CANM, KRAM, M, O, POZG); No. **541** (BR, BRNM, CANM, KRAM, M); No. **807** (BR, BRNM, CANM, KRAM, M); No. **313** (BR, BRNM, CANM, KRAM, M, O, POZG); No. **787** (BR, BRNM, CANM, KRAM).
- MIGULA Kryptogamae Germaniae, Austriae et Helvetiae Exsiccatae No. 140 (G, GJO, GZU, HBG, JE, PRC, W).
- MOUGEOT & NESTLER *Stripes Cryptogamae Vogeso-Rhenanae* No. **916** (CANM, COLO, G, JE, M, W).
- MÜLLER Westfalens Laubmoose No. 39 (CANM, JE, M, POZG, W).
- Ochyra *Musci Poloniae Exsiccati* No. **631** (BCB, BR, CANM, JE, KRAM, TENN).
- Ochyra & Bednarek-Ochyra *Musci Poloniae Exsiccati* No. 737 (Alta, BCB, BR, Canm, JE, KRAM); No. 1037 (Alta, BR, BRNM, Canm, JE, KRAM, M); No. 1138 (Alta, BR, GZU, JE, KRAM, M).
- PETRAK Flora Bohemiae et Moraviae Exsiccata No. 133 (BR, PRC).
- PILOUS Musci Čechoslovenici Exsiccati No. 184 (BRNM, POZG, W); No. 1117 (POZG, W); No. 685 (BRNM, POZG, W); No. 855 (G, POZG, W); No. 1150 (G, W).
- POECH Musci Bohemici No. 33 (G, PRC, W).
- RABENHORST *Bryotheca Europaea* No. **314** (BR, CANM, G, HBG, JE, KRAM, M, POZG).
- RENAULD & CARDOT *Musci Americae Septentrionalis Exsiccati* No. **30** (BM); No. **367** (BM, PC).
- SAVICZ -LUBITZKAJA ET SAVICZ Bryotheca Rossica No. 35 (BRNM, O, POZG, S, W).
- SAVICZ-LUBITZKAJA *Hepaticae et Musci URSS Exsiccati* No. **46** (BRNM, CANM, CAS, COLO, JE, KRAM, O, POZG, W, WTU); No. **95** (COLO, KRAM, O, POZG, W, WTU).
- SILLÉN Musci Frondosi Scandinaviae Exsiccati No. 232 (W).



FIGURE 78. Distribution map for Codriophorus fascicularis in Europe. Inadequately localised stations are indicated by asterisks.

SPRUCE - Musci Pyrenaici No. 285 (G, W).

SULLIVANT - Musci Alleghanienses No. 132 (BR, BM, M, MO, NY, W).

- SULLIVANT & LESQUEREUX *Musci Boreali-Americani* No. 220 (FH, M, MICH, MO, NY, W); No. 146 (BM, COLO, FH, MICH, MO, NY).
- VERDOORN Bryophyta Arduennae Exsiccatae No. 45 (BR, DUKE, G, O, UC).
- WILSON Musci Britannici No. 166 (BR, W).
- ZETTERSTEDT Grimmiae et Andreaeae Exsiccatae No. 31a & 31b (CANM, H, M, S); No. 31c (G, H, M); No. 32 (CANM, H, M, S); No. 33 (G, H, M).

SELECTED SPECIMENS EXAMINED

ASIA. JAPAN. HOKKAIDO. Kamikawa Pref.: Mt Kaun, Mt Ponkaun – Ten'ninkyo gorge, Biei-cho, Kamikawa-gun, 1350 m, Deguchi s.n. (HIRO-12316); Mt Daisetsu, Kawakami-gun, Tsujibe (MAK-B9145 & B9227); Mt Haku'un – Mt Chubetsu, Kamikawa-cho, Kamikawagun, 1700 m, Deguchi s.n. (HIRO-12277); Mt Furano, Kamifurano-cho, Sorachi-gun, 1460 m, Deguchi s.n. (HIRO-12335). Tokachi Pref.: Mt Nipesotsu, Kami' shihoro-cho, Kato-gun, 1800 m, Deguchi s.n. (HIRO-12448). HONSHU. Aomori Pref.: Hakkoda, 1300 m, Faurie 2927 (NY - syntype of Racomitrium fasciculare var. atroviride) and Sato s.n. (MAK-B6992). Fukushima Pref.: Mt Tetsu-san, Mt Adatra-yama, Nihanmatsa City, Watanabe s.n. (MAK-B57687). Gifu Pref.: Mt Ontake, via Hidasan-cho, Sannoike Pond, Marishiten Peak, Sainokawara, Ninoike Pond, Iwatsuki & Smith J-509 (NY). Ishikawa Pref.: Ishikawa-gun, Shiramine-mura, Mt Hakusan, Maeda s.n. (MAK-B33357) and 2480 m, Fukushima s.n. (HIRO-10660). Miyagi Pref.: Mt Katta, Uematsu 872 (H). Nagano Pref.: Mt Ontake, ca 3000 m, 26 Aug 1953, Noguchi s.n. (BISH, MICH, TENN) and ca 2900 m, 26 Aug 1953, Noguchi s.n. (WTU); Shinoike (Mt Ontake), Kaitamura, Kiso-gun, 2700 m, Deguchi s.n. (HIRO-13105); Mt Kengamine in Ontake Mountains, Noguchi 32396 (NICH); Mt Yatsugatake, 2600 m, Takahashi s.n. (MAK-B13875), top of Mt Hakuba-dake, Kitaazumi-gun, Kurachi s.n. (MAK-B57689). Toyama Pref.: Midagahara, Mt Tateyama, 2000 m, Iwatsuki & Sharp 128 (TENN); Tengudaira-Jigokudani-Murodo, Mt Tateyama, 2300-2500 m, Iwatsuki & Sharp 76A (TENN). Yamanashi Pref.: Mt Kisokomogatake, Takahashi s.n. (MAK-B57686).

RUSSIA. ARCTIC. Severnaya Zemlya: Bolshevik Island, 8 km from the mouth of the Bazovaya river, 24 Jul 1992, Safronova s.n. (LE); Bolshevik Island, 25 km from Baranovo Cape, 24 Jul 1991, Safronova s.n.



FIGURE 79. Distribution map for Codriophorus fascicularis in North America and Greenland.

(H, LE). *Chukotka*: Arakamchechen Island, 16 & 19 Aug 1976, *Afonina s.n.* (KRAM, LE); lower part of Chegitun river, 13 Aug 1991, *Afonina s.n.* (KRAM, LE); lower part of Chegitun river, 13 Aug 1991, *Afonina s.n.* (KRAM, LE); vicinity of Inchoum settlement, 2 & 7 Aug 1975 and 29 & 30 Jul 1975, *Afonina s.n.* (KRAM, LE); Nunligran, 6 Jul 1970, *Afonina s.n.* (KRAM, LE). **FAR EAST. Kamchatka Province**: South Kamchatkan Nature Reserve, slope of Koschelevsky Volcano, *Czernyadjeva 16* (KRAM, PRC), 21 Jul 1990 and 3 Aug 1990, *Czernyadjewa s.n.* (s) & 38 (KRAM, LE). *Komandorskiy Islands*: Mednyy Island (between Kamchatka and Aleutians), Nov 1887, *sine collector* (H). *Magadan Province*: Magadan City, Marchekanskaya Sopka, 8 Sep 1972, *Blagodatskikh s.n.* (LE); Olskiy district, Armanskaja Highway, Oksa river, 30 Jun 1978, *Blagodatskikh s.n.* (LE). **PRIMORSKIY TERRITORY. Sakhalin Province**:

Kuril Islands, Koisosan Mt (probably Urub Island, Kolokol Mt), 866 m, Voroblev 59 (LE).

EUROPE. ANDORRA. Incles, 2400 m, 5 Jul 1984, Sotiaux 3825 (BCB).

AUSTRIA. *Carinthia*: Hoher See im Radlgraben bei Gmünd, 6 Aug 1902, *Glowacki s.n.* (GJO); Geierzipf bei Gmünd, 5 Sep 1903, *Glowacki s.n.* (GJO); Hochahnfall im Maltatal, 3 Apr 1902, *Glowacki s.n.* (GJO); Oberes Gnopnitztal bei Greifenburg, 13 Aug 1905, *Glowacki s.n.* (GJO); Ragenbach, Schlucht bei Ober-Vellach, *ca* 800 m, 30 Jul 1881, *Breidler s.n.* (GJO); Heiligenbach bei Innerkrems, 1500–1600 m, 22 Jul 1880, *Breidler s.n.* (GJO). *Niederösterreich*: Ispertale, Kl. Isper, 17 Aug 1875, Juratzka s.n. (W). Salzburg: Felbertal 1 km südl. Tauernhausspital (Hohe Tauern) Gemeinde Mittersill, Bezrik Zell am See, 9 Aug 1994, Schaffer s.n. (UC); Mittersill, Pinzgoviae, 860 m, 1865, Molendo s.n. (G, POZG); Zwölfenkogel bei Mittersill im Pinzgau, ca 2300 m, 1 Aug 1879, Breidler s.n. (GJO); Krimml, 7 Sep 1909, Suse s.n. (DUKE); Krimmler Fälle, ca 1070 m, 8 Sep 1903, Handel-Mazzetti s.n. (W-hb. Baumgartner). Steiermark: Varalpenregion, St Nikolai in der Sölk, 9 Aug 1868, Breidler s.n. (W) and 1150 m, 11 Aug 1886, Breidler s.n. (PRC); Dönneck in den Sölker Alpen, 2400 m, 29 Jul 1874, Breidler s.n. (GJO); auf der Sölkenhöhe, Sölker Alpen, 2100 m, 9 Aug 1868, Breidler s.n. (GJO); Walchergraben bei Öblarn, 11 Jul 1897 (GJO, GZU); Stubalmkessel bei Mautern, 24 Aug 1893, Glowacki s.n. (GJO); im Goltshal-Kenel am Fusse des Seckauer Zinkens, 24 Aug 1889, Glowacki s.n. (GJO); Hochgolling bei Schladming, 3 Sep 1891 Glowacki s.n. (GJO); Ramsau bei Schladming, 900 m, 28 Jul 1876, Breidler s.n. (GJO); bei Rottenmann, 2360 m, 25 Jul 1887, Breidler s.n. (GJO): Bösenstein bei Rottenmann, 30 Aug 1892, Glowacki s.n. (GJO); auf Glimmerschieferfelsen des Türkenthörls der Gleinalpe, 22 Jul 1891, Glowacki s.n. (GJO); Schiefseck bei Oberwölz, Grosse Schiefer, 2270 m, 24 Aug 1888, Breidler s.n. (GJO); Sölkfeld in den Schieferalpen bei Donnersbachwald, 1900 m, 24 Jul 1876, Breidler s.n. (GJO); Speikkogel der Koralpe, 2000 m, 5 Aug 1883, Breidler s.n. (GJO); Larnberger Alm in der Kleinsölk, 1800 m, 9 Aug 1886, Breidler s.n. (GJO); Klause bei Deutschlandsberg, 15 Aug 1876, Melling s.n. (GJO); Vetterngebirge bei Schladming, 28 Aug 1869, Breidler s.n. (GJO); "Pichelshober" in den Schieferalpen bei Schladming, 1800-1900 m, 11 Aug 1876, Breidler s.n. (GJO); Wölzer Tauern, Planneralpe über Donnersbach Bz. Liezen, ca 1600 m, 27 Jul 1972, Poelt s.n. (GZU); Kammerkogel bei Mautern (Seckauer Alpen), 24 Aug 1892, Glowacki s.n. (GJO); Bosenstein, Rottenman Alpen, 10 Aug 1892, Glowacki s.n. (G); Einachergraben bei Einach, 1220 m, 11 May 1906, Fest s.n. (GZU). Tirol: Lienz, Gandaf 252 (W); Innervillgraten, 1 Jun 1885, Gander s.n. (BRNM); St. Anton, Abting vom Galzig nach St. Christof, ca 1900 m, 20 Jul 1943, Paul s.n. (M); Oetz, zum Pipurger See, 4 Jun 1885, Hora s.n. (BRNM, CANM); Fotschertal im Sellrain, 8 Aug 1905, Handel-Mazzetti s.n. (s); Flanrlingerthal near Innsbruck, 1200 m, 15 Sep 1900, Handel-Mazzetti s.n. (BRNM).

BELGIUM. Brabant Prov.: Villers-La-Ville, 6 Oct 1968, De Zuttere 68/5274 & 68/5290 (BR). Liege Prov.: Béverée prope Malmédy, ca 380 m, Oct 1927, Toussaint s.n. (BR, DUKE, G, O, UC) [Bryoph. Arduen. Exs. No. 45]; entre Stavelot et Francorchamps, Lafreuster, Nov 1903, Cornet s.n. (BR); Stavelot, Bois de la Ville, De Sloover 4470 (BR); Jalhay, route vers la Gileppe, Mar 1919, Cornet s.n. (BR); Hoegne, De Zuttere 67/3591 (BR); valleé de la Hoegne sous Sart-station, Sladden 953 H.F (BR): Marchin, decouvert au bois Sandron (valleé du Hovoux), Oct 1928, Cornet s.n. (BR); Marchin, La-Basse, Mar 1910, Cornet s.n. (BR); Membach, lac de la Gileppe, prés du trou Malbrouck, De Sloover 5038 (BR); Château de Stavelot, Maurice-Victor 497A (BR). Luxembourg Prov.: Gerhenne près Haut-Fays, May 1873, Gravet s.n. (BR, G) [Bryoth. Belg. No. 125]; Vielsalm, Thier des Carriéres, De Sloover 3881, 4390 & 10776 (BR); Carriers du Renard, Vielsalm, De Zuttere 70/6154 (BR); Vielsalm, De Zuttere 65/1554 (BR); Roches de Hourd, Vielsalm, De Sloover 65/1519 (BR); near Vielsalm, 9 May 1970, Fabius et al. 96 (ALTA, COLO, KRAM); Ottré (comm. Bihain), De Sloover 64/B/770 (BR); Bihain, NE du Village Paroi, De Sloover 64/B/761 (BR); Grand Halleux, rochers de Hourt, De Sloover 4367 (BR). Namur Prov.: Louette-St.-Pierre, De Sloover 3320 (BR); Louette-Saint-Pierre, Bois de Louette-St-Pierre, entre la route de Willerzie et le ruisseau des Barbais, Lambinon 64/B/291 (H); Forêt de la Haute Marlagne, Floreffe, Onraedt 62.B.7776 & 62.B.7766 (BR); Malonne, 150 m, Maurice-Victor 260 (BR).

CZECH REPUBLIC. BOHEMIA. Brdy Mountains: Pilský rybník pr. Březové Hory, Pilous 283 (CANM). Děčínskě stěny: Benešov nad Ploučnicí, ca 250 m, Pospišil 71174 (BRNM). Jizerské hory: Karlov near Ještědem, ca 880 m, sine dato, Matouschek s.n. (BR, G, GJO, HGB, JE, KRAM, M, O, PRC, PRC, W) [Krypt. Exs. No. 1081]; Štolpišká silnice by Ferdinandov, 600–650 m, 14 Jul 1913, Blumrich s.n. (BR, BRNM, CANM, COLO, G, hb Frahm, JE, KRAM, M, POZG, PRC, W, WTU) [Musci Eur. Exs. No 1071] & Aug 1903, Matouschek s.n. (DUKE, G, GJO, GZU, HGB, JE, W) [Krypt. Germ., Austr. et Helv. Exs. No 140]; "Holubník", ad merid. pag. Hejnice, ca 1050 m, 16 Jul 1961, Lhotský s.n. (PRC); Malá Jizerská louka, ca 900 m, 30 Jun 1954, Smrž s.n. (BRNM); pod Sedlem Holubačka, 900 m, 22 Oct 1995, Skalická s.n. (PRC); Kristiánov, 820 m, 27 Jul 1994, Skalická s.n. (PRC); Velký Štolpich, 560 m, 7 Oct 1995, Skalická s.n. (PRC); Frýdlantské cimbuři, 870 m, 23 Aug 1995, Skalická s.n. (PRC); Bílá Smědá, 900 m, 7 Jul 1994, Skalická s.n. (PRC); Bílý Potok, 420 m, 23 Aug 1995, Skalická s.n. (PRC); Smědava, Sterneck 246, 249 & 257 (PRC); Smědá, 500-600 m, 21 Aug 1898, Schiffner s.n. (BRNM). Krkonoše: Špindlerův Mlýn, Jun 1914, Winkelmann s.n. (POZG), 29 Jun 1897, Schiffner s.n. (PRC) and Traxler 488 (PRC); Labská louka, 1346 m, Aug 1898, Vilhelm s.n. (PRC); Modrodolské boudy by Kovárna, ca 900-1000 m, 4 Oct 1899, Schiffner s.n. (PRC); Obří důl, ca 1380 m, Jul 1949, Pilous s.n. (G, POZG, W) [Musci Čech. Exs. No. 1150]; Bílé Labe, ca 1310 m, Sep 1949, Pilous s.n. (POZG, W) [Musci Čech. Exs. No. 1117]; Labský důl, Strmá stráň, 900 m, 5 Sep 1982, Šašková s.n. (PRC); Bílé Labe, Pospíšil 12536 & 12536b (BRNM); Sněžka, Sterneck 395 (PRC). Krušné Hory: Chomutov, Hora sv. Šebestiéna, 830 m, Váňa 359 (PRC); pod Ottersteinem, ca 800 m, 3 Sep 1960, Váňa s.n. (PRC). Lužické hory: Jelení skála, 675 m, Pospišil 71277 & 71276 (BRNM). Šumava Mts: Nat. Res. Povydří, S of Turnerova chata, 810 m, Kučera 125/5 (PRC); glacier cirque of the Čertovo jezero, 1195 m & 1140 m, 27 Aug 1994, Kučera s.n. (PRC); Glacier cirque at the top of the Plechý Mt, 1320 m, Oct 1992, Kučera 198 (PRC); Sušice, Srní Hill, between Čeňkova pila et Turnerova chata, 750 m, 13 May 1959, Vondráček s.n. (BRNM); 1.5 km SW of the top of Mt Velká Mokrůvka, 1180-1190 m, Kučera 82D/2 (PRC). MORAVIA. Beskydy: near Staré Hamry, ca 450 m, Podpěra 1376 (BRNM). Hrubý Jeseník: Petrův kámen, 1440 m, Podpěra 146 (BRNM); Kolštýn, ca 900 m, Jul 1947, Šmarda s.n. (BRNM); Vozka, Pospišil 4964 (BRNM); vodopád Opavice, ca 1100 m, 8 Jul 1946, Šmarda s.n. (BRNM); nad Vřesovou studánkou, ca 1300 m, 2 Jul 1946, Šmarda s.n. (BRNM); Tabulové kameny pod Pradědem, Pospišil 4382 (BRNM); Horní Branná, ca 1000-1100 m, 18 May 1953, Šmarda s.n. (BRNM); Jiříkovou chatou a Pradědem, ca 1350 m, Jul 1947, Šmarda s.n. (BRNM); Karlova Studánka, pod Kapavou skálou, ca 1000 m, 26 Sep 1964, Pokluda s.n. (BRNM); Opavice, ca 800 m, 19 Jul 1949, Šmarda s.n. (BRNM); Horní Domášov, 900 m, 16 Oct 1950, Duda s.n. (POZG); Václavov, údolí Désne by Vikýřovice, ca 600 m, 19 Aug 1912, Schenk s.n. (W).

DENMARK. JUTLAND. Nordjyllands Amt: hills at Flade near Frederikshavn, 1 Aug 1908, Hesselbo s.n. (ALTA, BR, CANM, CAS, COLO, G, H, KRAM, O, POZG, S, UC, W) [Bryo. Danica Exs. NO. 187]. Ribe Amt: Utoft, 21 Jul 1903, Jensen s.n. (ALTA, CANM, COLO, G, H, KRAM, O, POZG, S, UC, W) [Bryo. Danica Exs. NO. 186]. ZEALAND. Københavns Amt: Rude Skov, 10 Apr 1950, Martin-Jensen s.n. (C). Roskilde Amt: Ordrup Skov, 10 Apr 1949, Martin-Jensen s.n. (C); Mortenstrup-oredrev v. Hvalsö, 31 May 1883, Jensen s.n. (CANM); Stestrup Old v. Hvalsø, Jul 1881, Jensen s.n. (DUKE).

FAEROE ISLANDS. BORDOY. Gjoardalur, 200 m, Lewinsky 3601 (ALTA): Krossdalsá, 150 m. Lewinsky 4866 (BR): Giáarskard, road between Gjógv and Funningur, Lewinsky 3709 (ALTA). EYSTUROY. Slaettaratindur, ca 750 m, 7 Jul 1973, Fagerstén & Haapasaari s.n. (H, KRAM); Raktangi, Lewinsky 3749 (ALTA); Skáli, E part of Gjógvará, Lewinsky 3771 (ALTA); Neshagi, E of Fossdalsheyggjur, Lewinsky 4064 (C, H); Gøtugjógv, 210 m, 22 Jul 1961, Hansen s.n. (C); Borgín, 200 m, 21 Jul 1961, Hansen s.n. (C); Gjáarskard, road between Gjógv and Funningur, Lewinsky 3709 (KRAM); along Kvíggjará, W of Oyndarfjördur, Lewinsky 3496 (KRAM); Trogará gjógv S of Ljósá, Lewinsky 3724 (KRAM). KALSOY. Hattardalur, 200 m, Lewinsky 3687 (DUKE); Mikladalur, Lewinsky 3657 & 4299 (BR). Nólsoy, Nólsoy, central part, Lewinsky 3966 (KRAM). SANDÖ, Sand, between two lakes Sandsvatn and Gróthusvatn, 6 Jul 1973, Fagerstén & Haapasaari s.n. (H). STORE DIMON. Store Dimon, 300 m, 12 Aug 1985, Hammer s.n. (C). STREYMOY. Saksunardalur, 30 m, Crundwell 89 (s); Tjörnuvik, 150 m, Lewinsky 4256 (BR); Kaldbak, W side of Högadalsá, Lewinsky 4011 (BR); Bjargahagi, area between Dalá, Arnadalsjall and Postulakirkja, 627 m, Lewinsky 5371 (KRAM). SYDERØ. Trangisvaag, 7 May 1896, Jensen s.n. (CANM, DUKE); Prestfjall, 20 Jun 1896, Jensen s.n. (DUKE, O, WTU); Sumbø, 23 Jul 1956, Pedersen s.n. (C); Gjógvaráfjall, 3 Aug 1961, Holmen s.n. (C). VÁGAR. Oyrargjogy, Lewinsky 3920 (ALTA) & 4960 (C); Uttangardshagi, along Skardsá and in Tjörndalur, Lewinsky 4929 (C) & 3862 (KRAM). VIDOY. Dalirnir around Dalá, 100 m, Lewinsky 4319 (ALTA); between Vidareidi and Villingadalsfjall, 100 m, Lewinsky 4819 (ALTA) & 350 m, Lewinsky 5029 (C); Vidareidi, valley between Malinsfjall and Villingadalsfjall, Slack 5144 (ALTA).

FINLAND. ALANDIA. Eckerö, Signildskär, 30–31 Aug 1892, *Lindberg s.n.* (H). KARELIA AUSTRALIS. Vehkalahti, forest N of Kertunkorpi and SE of Suikkaanlahti, 14 Aug 1968, *Fagerström s.n.* (W); Vehkalahti, Pyhältö, Ämmänmäki, 12 Jun 1962, *Fagerström s.n.* (BR, O, POZG, UC, W); Vehkalahti, Onkamaa, Juurkorvenmäkis, 10 Jun 1967, *Fagerström s.n.* (s); Miehikkälä, Suur-Miehikkälä, SE om Peltola, 5 Aug 1967, *Fa*



FIGURE 80. Distribution map for Codriophorus fascicularis in the Far East.

gerström s.n. (s); Miehikkälä, Salomiehikkälä, Kirnuvuorets NW-sluttningar, 5 Aug 1967, Fagerström s.n. (o); Miehikkälä, Salomiehikkälä, W-branter E om Korvensuo, 30 Jun 1971, Fagerström s.n. (H); Vehkalahti, Turkia, Rottivuoris branta E-vägg, 23 May 1965, Fagerström s.n. (o); Virolahti, 17 Jun 1878, Blom s.n. (LE, KRAM). KARELIA BOREALIS. Havukkavaara hill, Fagerstén & Haapasaari 4122 (DUKE); Tohmajärvi, Kemie, Fagerstén & Haapasaari 4078 (ALTA, BR, CANM, DUKE); Tohmajärvi, Tohmajärvi, Hiidenvaara, Koponen 5556 (H). KUUSAMO. Posio, Korouoma-gorge SE of farm Voho, 17 Aug 1971, Ulvinen s.n. (CANM, s, w); Sodankylä, Nattaset Mts, summit of Pyhänattanen, Ahti 12095 (H); Salla, Kutsan luonnonpuisto, Pyhäkuru, 18 Jul 1934, *Tuomikoski* s.n. (H). LAPPONIA ENONTEKIENSIS. S-Haltiatunturi, 850–900 m, 11 Aug 1958, L. & H. Roivainen s.n. (POZG, PR, S, W, WTU); S-Haltia, 950 m, 30 Jul 1968, *Huuskonen & Roivainen s.n.* (ALTA, COLO): Pierfevaggi valley, 750 m, *Roivainen 341* (WTU); Halti, E-Kiedditshohka, 890–920 m, 31 Jul 1968, *Roivainen s.n.* (ALTA, CANM, W); Porojärvet, Urtasvankka, lake Lossujärvi, ca 900 m, 31 Jul 1955, *Roivainen s.n.* (CANM); Porojärvet, Ridnitsohkka Mt, ca 900 m, 24 Jul 1955, *Ollila & Roivainen s.n.* (CANM, UC); Kilpisjärvi, Salmivaara, 550 m, 9 Jul 1935, *Roivainen s.n.* (H); S-Kahperus, ca 1100 m, 1 Aug 1943, Roivainen s.n. (H); Kilpisjärvi, W-Jehkatsin, 750 m, Haapasaari 2327 (H). LAPPONIA INARENSIS. Utsjoki, Vetsikko, W slope of Veätshaknjunnis, Haapasaari 7170 (s); Laanilu, Raututuuturit, Rumahurun, 5 Aug 1933, Söyrinki s.n. (H). NYLANDIA. Par. Kyrkslätt, Loviselund, 17 Apr 1910, Brotherus s.n. (CANM, M, S, W) [Bryoth. Fenn. No. 121]; Lohia city, 7 Jun 1891, Lindberg s.n. (JE, M); Helsingfors, Jun 1871, Brotherus s.n. (ALTA, G, M, S, W) [Musci Fenn. Exs. No. 9]; Helsingfors, Tölöpark, 9 May 1875, Lindberg s.n. (CANM, G, S); City of Helsinki, N of Vuosaari about 12 km ENE of Helsinki City Center, ca 50 m, Norris & Pócs 83099 (UC); Uusimaa, Sipoo, Immersby, SW of Helgträsk, 30-60 m, Sharp et al. 26421A (TENN). Os-TROBOTNIA AUSTRALIS. Lapväärtti, Pyhävuori, 26 Oct 1965, Fagerstén s.n. (H). OSTROBOTNIA KAJANENSIS. Ala-Sathamo, Laaka, Heiuijöki, 27 Jun 1952, Kotilainen s.n. (H). OSTROBOTNIA MEDIA. Vindala, Pyhälshti, Rappukallis, 21 Jul 1903, Backman s.n. (H). REGIO ABOËNSIS. Piikkiö, between Pajavuori and Haukkavuori hills in Yltöinen village, 8 May 1973, Laine s.n. (CANM, COLO, M, POZG, W); Parainen, forest on Portnäset point, S part (Jermo) of Attu island in Attu village, 15 May 1973, Hinneri & Laine s.n. (CANM, M, W); Perniö, Ylikylä (present name Ylönkylä village), Kuukallionmäki, 19 Oct 1924, Roivainen s.n. (POZG, W): Houtskär, Berghamn Isl, 5 Jul 1965, Kärenlampi & Raudaskoski s.n. (CANM, COLO, M, POZG, W); Kustavi, Kivimaa Island, Pännäistenvuori hill, terraces at "Jeremiaan luola" cave, 17 Nov 1969, Alava, Alho & Laine s.n. (COLO, M, UC, W); Halavakoski in par. Kisko, pag Maarjarvi, 2 Jun 1935, Roivainen s.n. (ALTA); Houtskär, Skårskär vid Immaskär, 22 Jun 1933, Eklund s.n. (TENN); Raisio, Metsäkulma, 1 km SW of Palovuori hill, 19 Apr 1962, Laine s.n. (POZG, W); Lohja/Karjalohja Parish, Maila, Tamsaari, Vitt, Horton & Koponen 25119 (ALTA, CANM); Maila, 21 Jul 1974, Frahm & Koponen s.n. (BISH); Lemu, Isovallus, E side of lake Mannerjärvi, 12 May 1970, Laine s.n. (BRNM, CANM, S); Masku, Karinkylä, to W of the Kantelmäki farm, 9 May 1970, Laine s.n. (BRNM); U. Espoo., Backby, W of lake Myllyjärvi, 10 Jul 1961, Ulvinen s.n. (w); Luonnonmaa, 19 Jun 1903, Högman s.n. (M); Tenhola, Bromarv, Framnäsin luonnonsuojelualue, Laaka & Mattila 306 (H). SATAKUNTA. Vammala city, Soukko, Prihtinniemi, 11 May 1958, Roivainen s.n. (CANM); Vammala city, Humaloja, Mikola, 13 May 1961, L & H. Roivainen s.n. (POZG, s); Suodenniemi, Palojärven NW-pään NE-ranta, Pirulanvuoren laesta, 200 m, 15 Sep 1963, Suminen s.n. (H). SAVONIA AUSTRALIS. Rantasalmi, ca 1 km SE of the end of Härmäniemi cape small island (=Länsiluoto) in Haukivesi lake, Fagerstén 230 (BISH); Luumäki, Patolahti, Susvuoris E-branter, 27 Jul 1968, Fagerström s.n. (H). SAVONIA BOREALIS. Suonenjoki, Päijänteenlampi, Lampilankallio, Fagerstén 5143 (ALTA, BR, CANM, COLO, DUKE, M, S); Kuopio, Väärälahti, Hukanniemi, Haukkavuori, Haapasaari 6445 (BRNM, COLO, DUKE, S); Sonkajärvi, Jyrkkä, Uuranholi, 29 Jun 1975, Roivainen s.n. (H). TAVASTIA AUSTRALIS. Par. Asikkala, Keltaniemi, 12 Jul 1915, Brotherus s.n. (JE, M, POZG, S) [Bryoth. Fenn. No. 328]; Ruovesi, Kukonpohja, Keisanen, 13 Jun 1978, Söyrinki s.n. (CANM, s); Jaala, Ilvesvuori, 18 May 1967, Roivainen s.n. (H). TAVASTIA BO-REALIS. Virrat, Kuusijärvenperä, Koivumäki, 25 Jul 1978, Söyrinki s.n. (BR, S); Hauhuu, Jouttivuoren Nrinne, 11 Jul 1949, Söyrinki s.n. (H).

FRANCE. ALSACE. Haut-Rhin: Sentier des Roches, Hohneck bei Col de la Schlucht, ca 1150 m, Keller 1145 (G); circa lacum Rhournemer Vogesi, 20 Jun 1858, Schimper & Paris s.n. (BR, CANM, G, HBG, JE, KRAM, M, POZG) [Bryoth. Eur. No. 314]; Weissen See, ca 1060, May 1901, Herzog s.n. (JE); Lac Noir, Orbey, Bouharmont 2468, 2473 (BR). AUVERGNE. Cantal: Puy Mary, 1500 m, 21 Aug 1891, Thériot s.n. (BR); Cantal, versant nord, 1790 m, Héribaud 302 (G); Cantal - Plomb du Cantal, Pierrot 55.144 (PC) and 1800 m, Cuynet 387 (PC). Haute-Loire: Le Mézenc, 1750 m, 25 May 1952, Cuynet s.n. (PC). Puy-de Dôme: Sommet de Pierre-sur-Haute, 27 Jun 1884, Gasilien s.n. (BR) and 1400-1600 m, 1 Jul 1887, Gasilien s.n. (BR); Le Mont-Dore, sine collector (BR, G, M) [Musci Gall. No 181]; Puy de Sancy, vers 1600 m, Jelenc 3245 (BCB, BR); Pentes N du Puy-de-Sancy, 1600 m, Cuynet 387 (PC); Mont Dore, Puy de Sancy, 4 Sep 1893 & 25 Aug 1893, Thériot s.n. (GJO). BASSE NORMANDIE. Manche: Cherbourg, 29 Oct 1885, Corbière s.n. (BR); Digosville, 21 Apr 1897, Martin s.n. (BR). Bretagne: Finistère, Roc'h Trévézel, 14 Jul 1902, Dismier s.n. (BR). CHAMPAGNE-ARDENNE. Ardennes: Ravin de l'Ours, Hautes-Rivières (S of Charleville-Mézières), Bouharmont 1694 (BR). MIDI-PYRÉNÉES. Haute-Garonne: environs de Luchon, Zetterstedt 88 (0). Hautes-Pyréneés: Massif de Néouvielle, Lac d'Orédon, 1950 m, Renauld s.n. (BR); lac Orédon, Aug 1901, Douin s.n. (BR); Cauterets, vallée du Lutour, 7 Jul 1933, Leroy s.n. (BR); vallée de Lesponne, sine dato, Spruce s.n. (W). RHÔNE-ALPES. Haute-Savoie: Mont Blanc, *De Candolle 306* (DUKE); Mont Blanc, Les Contamines-Montjoie, Chalet "La Role", *ca* 1530 m, 19 Oct 1963, *Düll s.n.* (G, UC); glacier de Tré-la-Tête near Chamonix, *sine dato, Boissier s.n.* (G); Notre Dame de la Gorge, 18 Jul 1870, *Déséglise s.n.* (G); Rte de St. Gervais à Chamonix, *sine dato, Bernet s.n.* (G); Chamonix, Jul 1850, *sine collector* (G); entre Servos et les Ouches, 1850, *Müller s.n.* (G). *Loire*: Monts du Forez, pentes Est de Pierre-sur-Haute, *ca* 1500 m, *Cuynet 376* (BR) and 1300 m, *Cuynet 375* (BR);

GERMANY. BADEN-WÜRTTEMBERG. Schwarzwald: Freiburg, Hebelweg, ca 1180 m, Sep 1899, Herzog s.n. (JE); Freiburg, "Hoh-Bruck", ca 620 m, Jul 1901, Herzog s.n. (JE); Freiburg, Bärenthalstrasse, ca 1180 m, Jan 1899, Herzog s.n. (JE); Feldberg, 1500 m, Onraedt 63.A.7775 (BR); Feldberg, between Feldbergerhof et Feldsee, 1110-1300 m, De Sloover 11.373 (BR); Hornberg, Schondelhöhe, 800 m, Lüth 1428 (hb. Lüth); Belchen, "Rübgarten", 1200-1300 m, Hegewald 1719 (ALTA); Zastlertal, 900 m, Lüth 317 (hb. Lüth); Sankt Wilhelmtal, between Oberried and Notschrei, Lawalrée 20420 (G); near Schönau, 1360 m, Keller 751 (G). BAYERN. Bayerischer Wald: Spiegelau, 850 m, Aug 1906, Familler s.n. (GZU, M) [Flora Exs. Bavarica: Bryoph. No. 662(a)], between Neuwaldhaus and Zwiesel, 580 m, Jul 1904, Bauer s.n. (GZU, M) [Flora Exs. Bavarica: Bryoph. No. 662(b)] and 8 Aug 1904, Bauer s.n. (BR, BRNM, CANM, COLO, G, hb. Frahm, JE, KRAM, POZG, PRC, W, WTU) [Musci Eur. Exs. No. 1070]; Krs. Grafenau, Waldhäuser, Martinsklause, 1000 m, 25 Sep 1960, Grützmann s.n. (M). Böhmerwald: Krs. Regen, Grosser Arber, Meinunger & Schröder 20746 (JE); Krs. Regen, Bahnenischnitt E of Auerbach, Meinunger & Schröder 20790 (JE); Bayerisch Eisenstein, Jul 1925, Lorch s.n. (GZU); Gr. Arber, 31 Jun 1947, Poelt s.n. (GZU). Bayerischer Alpen: Walchen-See, 1150 m, 13 Aug 1972, Lotto s.n. (M). Fichtelgebirge: Waldstein, Meinunger & Hertel 19942 (JE); Krs. Hof, Steinbruch E of Selbitz, Meinunger & Schröder 19037 (JE); Preisdorf, Ruleberg, Meinunger & Schröder 20449 (JE). BRANDENBURG. Potsdam, Friedhof Bornstedt, Sep 1960, Benkert s.n. (B). HESSEN. Rhön: Milseburg, Aug 1905, Moenkemeyer s.n. (HBG); Milseburg, Nordab, 800 m, 3 Oct 1876, Geheeb s.n. (w). MECKLENBURG-VORPOMMERN, Parchim, Sonnenberg bei Primank, Oct 1965, Doll s.n. (JE). SACHSEN. Zittauer Gebirge: an der Lausche, 4 Jun 1922, Winter s.n. (HBG, JE, KRAM) [Bryoth. Saxon. No. 232]. Erzgebirge: Eibenstock, Carlsfeld-Wilizschhaus, Meinunger 15377 (JE). Elbsandsteingebirge: Krippengrund by Schandau, 1953, Grolle s.n. (JE). Vogtland: Markneukirchen, "Hohen Stein", 775 m, 6 May 1906, Spindler s.n. (JE); Krs. Auerbach, Schönheide - Neuheide, Meinunger 11414 (JE); Altenberg, Geisnigberg, Meinunger 11909 (JE); bei Rochsburg, Meinunger 12416 (JE). NIEDER SACHSEN. Hannover, Süntel, 15 Aug 1948, Nowak s.n. (GZU); Krs. Celle, Wiechel, 15 Aug 1948, Nowak s.n. (GZU); Krs. Celle, Wiechel S of Fassberg-Oberohe, Meinunger & Schröder 21615 (JE); Nindorf, Lüneburge Heide, 5 May 1910, Jaap s.n. (HBG); NE of Hanstedt, 23 Sep 2000, Koperski s.n. (hb. Koperski); Lohe S of Bokel, 21 Jul 1985, Koperski s.n. (hb. Koperski); Lopau SW of Wulfsode, 6 Jun 1998, Koperski s.n. (hb. Koperski); Leer, 27 Jan 1951, Klimmek s.n. (hb. Koperski); Hamburg-Cranz, 21 May 1949, Schwenker s.n. (HBG); Krs. Stade, Wingst near Dobrock, Apr 1898, Wahuschaff s.n. (HBG); Krs. Soltau, Staatsforst Garlstorf, 25 Sep 1949, Schwenker s.n. (HBG); Oldenburg, Neuenburg, 14 Jul 1893, Müller s.n. (HBG). NORD-RHEIN WESTFALEN. Sauerland, Winterberg, 28 Jun 1924, sine collector (HBG); Bruchhausen Steine, 26 Jun 1922, sine collector (HBG). SACHSEN ANHALT. Harz: Okerthale, 30 Oct 1901, Moenkemeyer s.n., (HBG); St. Andreasberg, 13 Jul 1922, Warnstorf s.n. (BRNM); between Andreasberg and Oderbrück, 11 Jul 1899, Rudolph s.n. (JE); Ilsethal, Jul 1914, Winkelmann s.n. (POZG); Brocken, 1953, Grolle s.n. (JE); Steinerne Renne, 28 May 1882, Janzen s.n. (JE); Drei-Annen-Hohne, on road to Leistenklippe, 16 May 1969, Siegel s.n. (JE); Schneeloch, 11 Aug 1885, Correns s.n. (M); Krs. Klötze, Mellin, Meinunger & Schröder 21566 (JE). SCHLEZWIG-HOLSTEIN. Kr. Flensburg, on road Sieverstedt -Kirchenholz, 20 Jul 1930, Saxen s.n. (B); Krs. Stormarn, Trittau, Forst Karnap, 24 Mar 1893, Jaap s.n. (HBG); Ahrensburg, Hoisbüttel, 25 Jan 1903, Jaap s.n. (HBG); Sachsenwald, Rev. Schadenbeck, 23 Nov 1902, Jaap s.n. (HBG); Sachsenwald, Möhnsen, 29 Apr 1899, Jaap s.n. (HBG); Trittau, Steinburg near Sprenge, 29 May 1903, Jaap s.n. (HBG); Mölln, Vorsburg, Reimers 4489 (B); Ahrensburg, Waldberg, 15 Sep 1895, Jaap s.n. (HBG); Krs. Rendsburg, Westensee near Hohenhüde, 5 May 1923, Koppe s.n. (HBG); Krs. Segeberg (Bad Segeberg), near Kaden, 1 May 1910, Timm s.n. (HBG). THÜRINGEN. Oberhof, Ranzlergrund, 16 Jun 1917, Janzen s.n. (JE); Krs. Sonneberg, Zeierdoch near Steinach, 18 Jul 1984, Marstaller s.n. (JE); Kyffhäuser, Rothenburg near Kelbra, 13 Apr

1984, Marstaller s.n. (JE); Krs. Sonneberg, Steinbach, 18 Jul 1984, Marstaller s.n. (JE); Sonneberg, Kuhtälchens, 1965, Meinunger s.n. (JE); Krs. Suhl, Schneetiegels N of Schneekopf, 7 Oct 1971, Meinunger s.n. (JE); Krs. Meinnigen, Ellenbogen N of Frankenheim, 1 May 1972, Meinunger s.n. (JE); Krs. Schleiz, Rechler Saalehang, 9 Jun 1972, Meinunger s.n. (JE); Kr. Ilmenau, Bahneinschnitz near Meyersgrund N of Steitzerbach, 8 Apr 1972, Meinunger s.n. (JE); Kr. Suhl, Lubenbach N of Zella-Mehlis, 26 Jun 1975, Meinunger s.n. (JE); Kr. Suhl, Katzenlöeher NE of Breitenbach, Meinunger 13688 (JE); Sonneberg, Alter Griffelbruch between Tierberg and Breitenberg, N of Steinbach, 20 Sep 1970, Meinunger s.n. (JE); Krs. Hildburghausen, Werrabahn near Kloster Verra, 20 Aug 1966, Meinunger s.n. (JE); Krs. Gotha, Nesselberg SW of Tambach, 15 Sep 1974, Meinunger s.n. (JE); Krs. Lobenstein, Lemnitzhammer, Meinunger 15812 (JE); Krs. Lobenstein, Heinersdorf, 9 Aug 1975, Meinunger s.n. (JE); Krs. Neuhaus, Wickersdorf, Meinunger 7241 (JE); Krs. Salzungen, Baier N of Dermbach, 17 Sep 1974, Meinunger s.n. (JE); Kr. Suhl, SE of Schmiedefeld, Meinunger 4449 (JE); Thüringer Wald, Beerberg, 1952, Grolle s.n. (JE); near Ruhla, 20 May 1902, Krieger s.n. (JE); Oberschönau, Hohe Möst, 885 m, 22 Jul 1904, Krüger s.n. (JE); Krs. Hanenau, Elgersburg, 12 Dec 1984, Marstaller s.n. (JE); Steinheid, 28 Jun 1969, Marstaller s.n. (JE); Krs. Meiningen, Kl. Steichberg near Römhild, 27 Aug 1982, Marstaller s.n. (JE).

GREAT BRITAIN. ENGLAND & WALES. Brecon (VC42): Taren yr Esgob, Brecknock, 16 Apr 1954, Hall s.n. (NMW); Craig y Fro, near Brecon-Merthyr Road, 23 Nov 1964, Harrison s.n. (M, UC). Carmarthen (VC44): Craig-y-Rhaiadr, 2 Dec 1903 & 14 Mar 1906, herb. Knight s.n. (NMW). Caernarvon (VC49): Betws-y-Coed, May 1875, Makin s.n. (E); near Betws-y-Coed, 21 Oct 1950, Ratcliffe s.n. (E); summit of Snowdon, Jun 1909, Jones & Wilson s.n. (NMW); Cwm, Glas Maur, Snowdon, 9 Jul 1952, Ratcliffe s.n. (E); Helyg, near Capel Curig, ca 330 m, 29 Sep 1950, Ratcliffe s.n. (E). Cheshire (VC 58): Ogden Clough, Hollingworth, Nov 1965, Schofield s.n. (NMW). E. Cornwall (VC 2): Cheesewring, N of Minions, 1 Apr 1966, Perry s.n. (NMW). Cumberland (VC 70): Borrowdale, Dale Head, Aug 1895, Dixon s.n. (NMW). Derby (VC 57): near Buxton, Jan 1863, Whitehead s.n. (NMW). S. Devon (VC 3): E Budleigh Common, 2 Feb 1958, Appleyard s.n. (NMW); Hay Tor, Oct 1920, Sutton s.n. (NMW). Glamorgan (VC 41): Pont-Nêdd-Fechan in the Neath valley, 8 Apr 1963, Størmer s.n. (0); Cwmdu, Maesteg, 23 Aug 1973, Wade s. n. (NMW). W. Gloucester (VC 34): Milkwall, Forest of Dean, 16 May 1914, herb. Knight s.n. (NMW). Isle of Man (VC 71): Glen Helen, 22 Apr 1903, Beesley s.n. (E) & 22 Jul 1903, Beesley s.n. (NMW). S. Lancashire (VC 59): Pendle Hill, 17 Aug 1898, Wheldon s.n. (NMW). W. Lancashire (VC 60): Dilworth Reservoir, Longridge, Nov 1898, Wheldon s.n. (NMW). Merioneth (VC 48): between Dolgellau and Penmaenpool, 28 Aug 1905, Vice s.n. (NMW); Gwynedd, Snowdonia, Beddgelert, Ogof Owain Glendwr, Jury & Rumsey J2219 (BRNM); Beddgelert, 20 Feb 1865, Hunt s.n. (H); Gwynedd, ca 4 km SSW of Dolgellau, Llyn y Gafr, 16 Jul 1984, Jury & Rumsey 5537 (BRNM); near Harlech, ca 65 m, Sep 1903, Jones s.n. (NMW); Crom Moch, Jun 1900, Jones & Horrell s.n. (G). Monmouth (VC 35): Trelleck, Aug 1903, Armitage s.n. (NMW); Aberbeeg, May 1967, Garlick s.n. (NMW). Montgomery (VC 47): Pennant Melangell, Blaen y Cwm, 9 Apr 1960, Perry s.n. (NMW); between Llanidloes and Glannant, 21 Nov 1940, Webb s.n. (NMW). N. Northumberland (VC 68): W Moor above Middleton Stale, Nov 1929, Duncan & Millar s.n. (BBSUK, NMW); Bizzlo, Cheviot North, Sep 1945, Duncan s.n. (E); Cheviot, Sep 1925, Duncan & Millar s.n. (NMW). Radnor (VC 43): Radnor Forest, 1 Jun 1927, Hyde s.n. (NMW). Shropshire (VC 40): Salop, Wrekin, at Wellington base, Sep 1892, Benson s.n. (NMW). Stafford (VC 39): Blakishall, Nov 1908, Duncan s.n. (E). N. Somerset (VC 6): near Leigh-on-Mendip, 1 Oct 1961, Appleyard s.n. (NMW). Surrey (VC 17): Chilworth, 9 Dec 1973, Wallace s.n. (NMW); Broadmoor, Wotton, 31 Mar 1953, Rose s.n. (NMW). W. Sussex (VC 13): Ebernoe near Petworth, Old School House, 25 Jun 1994, Stern & Matchars s.n. (NMW). Westmorland (VC 69): Grasmere, Aug 1948, Appleyard s.n. (NMW). N. Wiltshire (VC 8): Stourton, 165 m, 29 Jun 1993, Stern s.n. (BBSUK, NMW). Mid-West Yorkshire (VC 64): Long Gill, Kingsdale, Ingleton, 6 Apr 1956, Garlick s.n. (NMW); Ingleborough, 31 May 1926, Sherrin s.n. (E); Austwick, Dec 1915, Cheerham s.n. (E). N.W. Yorkshire (VC 65): Durham, Upper Teesdale, Aug 1899, Horrell s.n. (NMW); Teesdale, Aug 1897, Wheldon s.n. (GJO); Cronkley Fell, Aug 1883, Wheldon s.n. (NMW). S.W. Yorkshire (VC 63): Rivelin Woods, Feb 1951, Evans s.n. (NMW). SCOTLAND. S. Aberdeen (VC 92): Braemar, Jul 1905, Holmes s.n. (NMW); Glen Callater, Jul 1945, Gardnier s.n. (E). Angus (VC 90): Glen Phee, Glen Clova, Jul 1930, Duncan s.n. (NMW); near Loch Brandy, Clova, May 1940, Duncan s.n. (E) and 21 Jul 1924, Robertson s.n. (E); near Guthrie by Forfar, Oct 1945, Duncan s.n. (E); Caenlochan, Glen Isla, Aug 1954, Duncan s.n. (E); Caenlochan, Jul 1843, Gardnier s.n. (E); NW side of Whitehill, Sidlaw Hills, 8 Nov 1920, Robertson s.n. (E); Sidlaw Hills, Mar 1842, Gardnier s.n. (E); Finavon Woods, Jun 1931, Millar s.n. (BBSUK, NMW); The Long Goat, Catlaw, 20 Jul 1921, Robertson s.n. (E). Argyll (VC 98): Ben Lui, ca 610 m, 20 May 1978, Crundwell s.n. (ALTA); Tighnabruaich, 1893, Salmon s.n. (NMW). Banff (VC 94): Ben Macdhui, 4 Aug 1934, Richards s.n. (NMW). Berwick (VC 81): Lammermuirs, below Glenburnie, Whalplaw Burn, Long 61 (E). Caithness (VC 109): North Watten, Sep 1888, Lillie s.n. (WTU). Clyde Islands (VC 100): Island of Bute, Mar 1907, Meldrum s.n. (E). Dumfries (VC 72): Cove, Arkleton Hill, 21 May 1950, Milne-Redhead s.n. (NMW); Frinr's Carse, Mar/Apr 1840, Cruickshanks s.n. (E). Dunbarton (VC 99): Glen Loin, Arrochar, Apr 1915, Adam s.n. (E). N. Ebudes (VC 104): Sligachan, North, Skye, Isle of, 4 Jun 1934, Armitage s.n. (NMW); Uig area, Isle of Skye, 0-150 m, Janssens 777 (ALTA); Staffin area, Isle of Skye, 50-150 m, Janssens 607 (ALTA). S. Ebudes (VC 102): Loch Knock, Islay, 8 Mar 1898, Gilmour s.n. (NMW). Fife (VC 85): near Orr Water, Aug 1847, Evans s.n. (E); Drumcarro Craig, Dec 1850, Black s.n. (E). E. Inverness (VC 96): Badenock and Strathspey Distr., Cairn Gorm, 1090 m, Jury 5962 (BCB, BR, BRNM); Glen Feshie, 27 Jul 1956, Pettifer s.n. (NMW); Cairn Gorm, Coire an t'Sneachda, Jul 1956, Duncan s.n. (E); Cairngorm Mts, below Coire an Lochain, Schofield & Schuster 70039 (CANM, DUKE). W. Inverness (VC 97): gorge of Laudale River, on S shore of Loch Sunart, 0-75 m, Norris 51583 (UC); Glen Nevis, 8 May 1939, Størmer s.n. (O); Ben Nevis, 14 Aug 1856, Gilchrist s.n. (E); R. Callop, Glenginnan, 14 Oct 1949, Juinhead s.n. (E); Rhu, 9 Apr 1972, Ballantyne s.n. (E); Beinn Eibhinn, Ardwerikie Forest, 16 Aug 1957, Ratcliffe s.n. (E); Coire Bhealaich, Aonach Beag, ca 700 m, Long 16330 (E). Kincardine (VC 91): Strachan, 1893, Sim s.n. (NMW). Kirkcudbright (VC 73): Clonyard Hill, 5 Oct 1949, Milne-Redhead s.n. (NMW); Burnfoot Hill, New Galloway, Jul 1890, McAndrew s.n. (E). Lanark (VC 77): Auchenheath, 8 Dec 1924, Ken s.n. (NMW). Mid Lothian (VC 83): Pentlands Ihreepmuir Reservoir, 31 Oct 1908, Evans s.n. (E); Pentlands, Swanston Hill, Feb 1898, Evans s.n. (E); Ravelrig, May 1909, Evans s.n. (E); Ormiston Nood, Midcaldor, 8 May 1899, Evans s.n. (E); Corstorphine, 7 Apr 1894, Johnston s.n. (E); Corstorphine Hill, 20 Apr 1904, hb. McAndrew (E). W. Lothian (VC 84): Ochiltree Mill, Chamberlain B151 (DUKE): near Chilpstonn, Mar 1916, Adam s.n. (E): Carribber's Glen, 15 Mar 1902, Evans s.n. (E); Woodcockdale, on boulders by R. Aron, 1916, Adam s.n. (E). Moray (VC 95): Elgin, Aug 1917, Fry s.n. (NMW). Orkney (VC 111): near Round Hill and Sandy Loch, Hoy, Johnston 4893 (E) and Sinclair 182 (E); Meikle Fea, Hoy, Johnston 4847 (E); Enegares, Kame, Hoy, Sinclair 7 (E); SE side of Holm of Hinton, near Orphir in Marieland, Johnston 4893 (E); Enegares, 21 Jun 1922, Trotter s.n. (NMW). Outer Hebrides (VC 110): Barra, 1936, Watson s.n. (E); St. Kilda, Aug 1905 & Sep 1911, Evans s.n. (E). E. Perth (VC 89): Tayside Region, ca 16 km S of Braemar along A93 road to Rattray, Jury 5935 (BCB, BR, BRNM); Pitlochry Moors, Aug 1901, Cleminshaw s.n. (NMW); Sow of Atholl, 9 Jul 1888, Meldrum s.n. (E); Dunkeld, 22 Jan 1903 M'Intosh s.n. (E). Mid Perth (VC 88): Ben Lawers, ca 980 m, 1990, Long 18335 (E) and 1150 m, 25 Aug 1989, Corley s.n. (hb. Frahm); near Tyndrum, 24 May 1913, Hall s.n. (NMW); Birnam Hill, 19 Apr 1890, Meldrum s.n. (E); Broxden, Apr 1887, Medrum s.n. (E); Sma Glen, 13 Oct 1896, Meldrum s.n. (E); Stob Garbh, 7 Jul 1906, Meldrum s.n. (E); Rannoch Moor, Nov 1950, Fawrley s.n. (E); Falls of Braan, Dunkeld, 9 Apr 1966, Grierson (E). W. Perth (VC 87): Blackford, 5 Aug 1903, Meldrum s.n. (E); Dollar, 19 Apr 1899, Evans s.n. (E); Ben Ledi, May 1898, Evans s.n. (E); Stuca-Chroin, 15 Aug 1891, Meldrum s.n. (E). Renfrew (VC 76): Eaglesham, 28 Oct 1928, Catcheside s.n. (WTU). E. Ross (VC 106): above Lochluichart, 21 Jul 1978, French s.n. (NMW); Allt Nan Caorach, Vitt 34649 (ALTA). W. Ross (VC 105): Teallach, 28 Aug 1960, Pettifer s.n. (NMW); Cadha Gobhlach, above Loch Toll an Lochain, An Teallach, ca 650 m, Long 13840 (E). Selkirk (VC 79): near Galashiels, 19 Nov 1910, Evans s.n. (E). Stirling (VC 86): Rowardenan, foot of Ben Lomond, Jul 1902, Larter s.n. (NMW). E. Sutherland (VC 107): Loch Ailsh, 4 Sep 1960, Pettifer s.n. (NMW). W. Sutherland (VC 108): summit of Ben More, ca 960 m, 19 Jul 1966, Perry s.n. (NMW); ca 5 km S of Kylesku Bridge, Jury 6016 (BRNM).

ICELAND. Landmannalaugar, Lewinsky 3109 (ALTA); Kleifarvatn, below Sweifluháls, Lewinsky 3020 (ALTA) & 3224 (KRAM); SW of Reykjavik, W side of Kleifarvatn, *Crundwell 123* (s); Entre Olafvik et Búdir, 340 m, *Vanden Berghen 33* (BR); Gullbringusýsla, Krýsuvík, 100 m, 7 May 1961, *Jóhannsson s.n.* (H); Nesjavellir, *Schwabe 1/424* (IE); Hekla, 1400 m, 5 Jul 1932, *Schwabe s.n.* (JE); Breidavatn-Dofinsfjöll, *Johannsson 22464* (ICEL); Önundarfjörd, *Johannsson 26516* (ICEL); Skálmardalur, *Johannsson 33700* (ICEL); Hrollangsstadafjall, *Johannsson 28839* (ICEL); Reykjadalur, *Johannsson 33390* (ICEL); Latravik, *Johannsson 33712* (ICEL); Nupakot, *Johannsson 18489* (ICEL); Skapadalur v. Patreksfjörd, *Johannsson 25367* (ICEL); Kaldbaksvik, Strand, *Johannsson 17733* (ICEL); Trostanofjördur, *Johannsson 25513* (ICEL); Hornatar, *Johannsson 18683* (ICEL); Skötufjördur, Kalfsvik, 300–475 m, *Johannsson 28860* (ICEL); Valnsdalsfjall, *Johannsson 19301* (ICEL); Skaftafel, 0–100 m, *Aptroot 4978* (NY); Kirkjaebuklaustur, 0–100m, *Aptroot 4935* & 4947 (NY).

IRELAND. *Carlow* (VC H13): The Nine Stones, N side of Mt Leinster, 27 Aug 1975, *Perry s.n.* (NMW). *Down* (VC H38): Newcastle, Donard Lodge, Jul 1901, *Armitage s.n.* (NMW); Slieve Donard, 28 Mar 1870, *Stewart s.n.* (H). *W. Galway* (VC H16): Kylemore River above Glencorbet, *ca* 150 m, *Long 26249* (E); Twelve Bens, NE corrie of Muckanaght, *ca* 450 m, *Long 25527* (E). *Kildare* (VC H19): between Glending and Newtown, 300 m, 16 Jun 1954, *King s.n.* (NMW). *Laois* (VC H14): Dripping Old Red Sandstone rocks, The Cut, Slieve Bloom Mountains, *ca* 400 m, 26 Aug 1956, *Cridland s.n.* (UC). *Leitrim* (VC H40): Mullaghmore, Dungiven, 2 Jun 1968, *Fitzgerald s.n.* (NMW). *Longford* (VC H24): Corn Hill, Drumlish, 25 May 1965, *Middey & Fitzgerald s.n.* (NMW). *Mid Cork* (VC H4): Coomshingaun, Waterford, 25 Jul 1933, *Armitage s.n.* (NMW). *N. Tipperary* (VC H10): bog at L. Nahinch, 6 Jun 1965, *King s.n.* (NMW).

ITALY. LOMBARDIA. Monticelli di Val Malza, 5 Sep 1865, Lorentz s.n. (w). PIEMONTE. Campello-Monti, in silva Valdo editiore infi "Piano degli Abeti", 1340 m, Levier 538 (s). TRENTINO-ALTO ADIGE. Val Daone, Moazzo, 15 Aug 1863, Lorentz s.n. (M); Vallée de Rabbi near Trente, Hampe 340 (G).

LUXEMBOURG. Reuland, Lambinon 64/B/1195 (BR).

NORWAY. AKERSHUS. Ås: Åkebakkskog, 4 May 1949, Roll-Hansen s.n. (0). Asker: Vardåsen ovenfor Borgen, 19 Aug 1958, Sunding s.n. (0). Bærum: vestenden av Østernvannet, 23 May 1964, Størmer s.n. (0); Kolsås, 3 May 1940, Størmer s.n. (0); Risfjellet, 19 Sep 1952, Størmer s.n. (0). Eidsvoll: Ibdbak, 22 Jul 1912, Sørensen s.n. (0). Hurdal: Fjellsjökampen, 12 Sep 1911, Sørensen s.n. (0). Lørenskog: ved Ospetjern n.f. Lørenskog, 12 Jul 1943, Størmer s.n. (0). Nannestad: Viksvangen, 20 Sep 1962, Størmer s.n. (0); ved tjernet mellom Klofjell og Nordklofjell, 6 Sep 1969, Størmer s.n. (0); Klofjell, 600 m, 22 Sep 1962, Størmer s.n. (0); Tømte-Tangen, 26 Sep 1960, Størmer s.n. (0). Oppegård: Vassbotn, 20 May 1945, Størmer s.n. (0); Åsen, 17 May 1936, Størmer s.n. (o). Oslo: Aker, Skjærsjødammen, 26 Aug 1935, Størmer s.n. (0); Trehørningen, 24 Jul 1942, Størmer s.n. (0); Tryvasshøgda, 21 Aug 1935, Størmer s.n. (0); Hakkloa i Nordmarka, 4 Jul 1941, Størmer s.n. (0); Hakkloa, 3 Jul 1941, Størmer s.n. (0); Skjennungen, 26 Aug 1935, Størmer s.n. (0); Bomveien i Skådalen, 26 Aug 1935, Størmer s. n. (0); Kjelsås ved sydluden av Maridalsvanmet, 17 Mar 1935, Størmer s.n. (0); Kjelsåsskogen, 30 Aug 1953, Lid s.n. (0); ved Storbekken vest for Stora i Sørkedalen, 13 Sep 1959, Størmer s.n. (0); ved Lyse i Sørkedalen, 4 Sep 1959, Størmer s.n. (0); ved Sølvviken I Nordmarka (v. for Hakadoe), 3 Nov 1934, Størmer s.n. (0); Trehörningen, 30 Jul 1942, Størmer s.n. (BCB). Rælingen: ved Vesledammen vest for Narvestad, 25 Jul 1953, Størmer s.n. (0); Barlindåsen, 8 Aug 1952, Størmer s.n. (0). Ski: ved Langhus, 2 Aug 1945, Størmer s.n. (0); vest for Kringsjå, 30 Jun 1944, Størmer s.n. (0). Vestby: Linnes, 19 Jul 1958, Størmer s.n. (0). AUST-AGDER. Åmli: dalen ved Haugelandsfjell, 10 Aug 1950, Størmer s.n. (o). Birkenes: Urddalen, 5 Aug 1968, Størmer s.n. (0); Fisktjørn i Urddalen, 5 Aug 1968, Størmer s.n. (0). Bykle: Asti mot Meien, mellom Breive og Væringsvatnet, 1 Aug 1970, Baads.n.es s.n. (0). Evje: Syrtveit, 28 May 1916, Sørensen s.n. (0). Gjerstad: Höggeto, 18 Aug 1950, Størmer s.n. (o). Hornnes: Linddalen, 10 Jul 1946, Danielsen s.n. (0); Birkelandsfossen, Jun 1914, Størmer s.n. (0). Iveland: ved stasjoneft, 30 Jun 1913, Sørensen s.n. (0). Lillesand: Tune på Justøya, 29 Jul 1968, Størmer s.n. (0); berg nord for Yttre Eikeland, 7 Aug 1968, Størmer s.n. (0). Nissedal: sörsida av Fiskåheia, 14 Aug 1950, Størmer s.n. (0). BUSKERUD. Ål: ved vestenden av Bergsjøen, ca 1150 m, 9 Jun 1963, Størmer s.n. (0). Eggedal: lia vest for Engar, 27 Jul 1965, Størmer s.n. (O); Bergshamar seter, ca 900 m, 29 Jul 1965, Størmer s.n. (0); Ertesprang-Tavstjern, 30 Jul 1965, Størmer s.n. (0). Flå: Voll, 8 Jun 1963, Størmer s.n. (0); Gulsvik, 10 Apr 1954, Sunding s.n. (0). Hole: Ovenfor Steinsrud, 11 Sep 1955, Dahl s.n. (0). Hurum: Sörsida av Røskestadvann, 27 Jun 1945, Störmer s.n. (o, s); Vardeås-Gleinås, 27 Jul 1959, Størmer s.n. (0); mellom Bureås og Gleinås, 14 Aug 1945, Størmer s.n. (0); Selvik, 4 Aug 1945, Størmer s.n. (0). Krødsherad: Surtebergsete, 8 Aug 1941, I. & P. Størmer s.n. (0); 2 km N for Bjertnes, 4 Aug 1941, I. & P. Størmer s.n. (0). Lier: Dammyrdammen, 22 Jul 1944, Størmer s.n. (0); Øksnevoll, 24 Jul 1944, Størmer s.n. (0); Storsteinsfjell, 6 Aug 1944, Størmer s.n. (0); Assdöl-juvet, 19 Jul 1944, Størmer s.n. (0); Rype, 23 Jul 1946, Størmer s.n. (0). Modum: mellom Sørgruvene og Butjern, 5 Oct 1979, I. & P. Størmer s.n. (0); bekkedal ovenf, Austad, 28 Jul 1947, Størmer s.n. (0); i bekkedalen øst for Engelstad, 31 Jul 1948, Størmer s.n. (0); ved Kaggefoss, 17 Jul 1947, Størmer s.n. (0); Sønstebydalen, 6 Aug 1948, Størmer s.n. (0); Svartaosen i Finnmarka, 6 Aug 1948, Størmer s.n. (0); Ovenfor Tanberg, 18 Aug 1940, I. & P. Størmer s.n. (0); Hogstet, 27 Jul 1948, Størmer s.n. (0). Øvre Eiker: Vestby-plassen-Langtjern, 4 Aug 1949, Størmer s.n. (0); Fiskum, Hakavik, ved Eikern, 11 Aug 1947, Eknæs s.n. (o). Øvre Sandsvær: kalkberg på SØ-siden av store Mysutjern, 350 m, 14 Oct 1974, Pedersen s.n. (0); Skrimtoppen, 31 May 1940, Brusli & Hadač s.n. (0). Sigdal: lia SV for Halsteinrud, 2 Aug 1965, Størmer s.n. (0); Sigdal kirke, 28 Jun 1940, Størmer s.n. (O, TENN). FINNMARK. Hammerfest, Sep 1888, Jørgensen s.n. (0). HEDMARK. Åsnes: Skjeppåsens Shelling N for Flisa, 3 Jul 1975, Størmer s.n. (0). Elverum: Elverum kirkegård, 4 Jul 1975, Størmer s.n. (0). Folldal: Canyon ca. 1,5 km fra Myldingis utløp I Atna, 7 Jun 1964, Gjønnes s.n. (0). Sør-Odal: Svarttjernbekkens munning ved Storsjøen, 30 Sep 1978, Størmer s.n. (o). Trysil: SV-enden av Ossjøen, 7 Jul 1964, Eckblad s.n. (0). HORDALAND. Åsane: Åstveit, 19 Feb 1961, Bødtker s.n. (0). Bergen: Brennhøgda nord for Sandviken, 1 May 1965, Størmer s.n. (0); Blaamanden, 12 Aug 1906, Schellenberg s.n. (H); Blaamanden bei Bergen, 12 Aug 1906, Schellenberg s.n. (M). Bremnes: Melingsvågen, 20 Aug 1967, Størmer s.n. (O). Fitjar: Rimbareid, 16 Jun 1946, Størmer s.n. (COLO, O, W); Sørgård, 21 Jun 1946, Størmer s.n. (0). Fjell: Algeröy, 24 Apr 1961, Bødtker s.n. (0). Fusa: Kirkebygda, 11 Jun 1962, Bødtker s.n. (0). Granvin: nordvestsiden av Espelandsvann, 345 m, mellom Granvin og Ulvik, 6 Jun 1955, Jørstad s.n. (0); Nesheimshorgen, 17 Jul 1933, Havaas s.n. (DUKE); Nyadaemmo, 20 Jun 1933, Havaas s.n. (DUKE); Steinsaeterhorgi, 4 Jun 1933, Havaas s.n. (DUKE); Skålsaete, 1 Sep 1933, Havaas s.n. (DUKE); Spundsafoss, 5 Aug 1933, Havaas s.n. (DUKE); lake Nedre-Vassenden, Clarke 454 (WTU). Haüs: Kleppe, 11 May 1959, Bødtker s.n. (0). Herdla: Kjærgård på Askøy, 24 Aug 1962, Bødtker s.n. (0). Kinsarvik: Indre Kvalvik - Alsåker, på fyllitt, 22 Apr 1954, Gjærum s.n. (0). Kvam: Norheimsund, 4 Aug 1943, Størmer s.n. (0); Fosso, 26 Apr 1954, Gjærum s.n. (0). Kvinnherad: MalmangerNutens N-hell, 7 Aug 1943, Størmer s.n. (0); Håland, 11 Aug 1943, Størmer s.n. (0); Beinaviki, 10 Aug 1943, Størmer s.n. (0). Modalen: Mo, Ved Kollhaugen, 20 Oct 1957, Langedal s.n. (0). Odda: Tveit, 19 May 1953, Gjærum s.n. (0). Stord: Tveit, 19 Jun 1936, Størmer s.n. (0); Jekteviki, 11 Aug 1967, Størmer s.n. (0); Leirvik, 16 Aug 1967, Størmer s.n. (0). Süldal: Kvilldal ved Suldalsoatnet og Såta, Aug 1944, Bakka s.n. (0). Sund: Telavåg, 24 Jun 1950, Størmer s.n. (0). Sveio: Husavatn, 3 Aug 1969, Størmer s.n. (0). Tysnes: Vå, 12 Aug 1964, Bødtker s.n. (o). Ullensvang: Gamleheimen, 9 Apr 1954, Gjærum s.n. (o). Varaldsöy: Mundheim, 15 Aug 1943, Størmer s.n. (0). Voss: Selheim, 1 Aug 1959, Lid s.n. (0). MØRE OG ROMSDAL. Averøy: Averö, Jul 1867, Kiær s.n. (0). Bremsnes: Myr ved vannet nord for Hoset på Averøya, 2 Jul 1969, Baads.n.es s.n. (0); Mekknoken på Averøya, 4 Jul 1969, Baadsnes s.n. (0). Fræna: Eidem, 16 Apr 1965, Malme s.n. (0); Talstadhesten ved Talstad, ca 100 m, 12 Apr 1965, Malme s.n. (0); Talstadhesten, 10 & 13 Jul 1964, 3 Aug 1964 & 12 Apr 1965, Malme s.n. (0); Bud ved sjøen, 10 Aug 1975, Malme s.n. (0); Ersholmen nær Bud, 5 & 8 Aug 1971, Størmer s.n. (0); Malmefjord, 100 m, 24 Jun 1969, Jørstad s.n. (0). Kristiansund: Christiansund, Aug 1868, Lorentz s.n. (G, HBG, JE, M, O, S, UC). Midsund: NO-siden av Holevatnet på Otrøy, 11 Aug 1971, Størmer s.n. (0); ved Sundsbø på Otrøy, 11 Aug 1971, Størmer s.n. (o). Molde: ved Torhus på Bolsøya, 3 Aug 1971, Størmer s.n. (0); ved Lillebostad på Bolsøya, 3 Aug 1971, Størmer s.n. (0). Norddal: Bjønnhytta ved Grøndalstjønna, 970 m, 13 Aug 1951, Lid s.n. (0). Rauma: mellom Hjelvik og Hjelviksetra, 6 Aug 1971, Størmer s.n. (0); Veblungsnæs, Romsdal, 30 Jul 1869, Kiær s.n. (0); Romsdal, Stueflåten, 19 Jul 1895, Ryan s.n. (o). Sunnylven: Rindal,

15 Aug 1951, Lid s.n. (0). Ulstein: litt S for Roppe, 18 Jul 1964, Wischmann s.n. (0). Vestnes: Fiksdal, 9 Aug 1971, Størmer s.n. (0). Voll: Hovdemyrane, 100 m, 7 Aug 1951, Lid s.n. (0); Middagstind, 1100 m, 5 Aug 1951, Lid s.n. (0). NORDLAND. Bo: Tørr skogsmark rett sør for Strømsjøen, 7 Aug 1955, Jørstad 22 (0). Bodø: Nyholmen, 13 Jul 1968, Anderssen 458, 470, 471 & 478 (0); Rønvikfjell, 5 Aug 1968, Anderssen 687 (0). Hadsel: Sommerset, pr. Hanøy, 20 Sep 1954, Jørstad 91 (0). Hattfjelldal: Kjukkelvatn-Båttjern, 24-27 Aug 1951, Kierulf s.n. (0). Lodingen: Kanstadbotnmyran, 22 Aug 1957, Norang s.n. (0). Meløy: Glomvann, Glomfjord, 150 m, 630 & 750 m, 8 Jul 1954, Jørstad s.n. (0); Spilra, 6 Jul 1952, Kierulf s.n. (0). Mo-i-Rana: NE part of Burfjeldet fjeld, the mouth of an ice stream flowing from Österdalsisen i W side of Svartisvatnet lake, Alava 9657 (BR, CANM, W); Skamdal, Alava 10186 (M). Narvik: Taraldvikelva, 18 Jul 1954, Jørstad s.n. (O); 1 km S of Hauknes, Alava 10162 (BR); Skamdal, Alava 10186 (BR); Narvik, 20 Jul 1904, Vrang s.n. (G, S); Fagernesfjeldet S of Narvik, 5 Aug 1950, Ruotsalo s.n. (H); Herjangsfjord NE von Narvik, Küstenfelsen, ca 4 km N Oijord, an der Strasse Narvik-Bjerkvik, 0-20 m, 7 Aug 1980, Schriebe s.n. (GZU). Nesna: S-facing slope of Hamaröyfjellet fjeld, between Hamaröy and Sandnes villages, Alava 9912 (BR). Salten: Ölfjellet, 26 Jul 1969, Arnell s.n. (s). Sortland: vest for fjellet Galten, ca 500 m Sigerfjord, 20 Aug 1957, Jørstad s.n. (0), Vega: Vega Is., Andvågen, 25 Jun 1980, Degelius s.n. (0); hill S of Risbakken, 10 Jun 1980, Degelius s.n. (0); Eidem, Sjöby, 22 Jun 1980, Degelius s.n. (0). Lofoten Island: Odden, Clarke 643 (WTU). NORD-TRØNDELAG. Meråker: Kvernskardelvas juv øst for Stordal, 2 Aug 1974, Størmer s.n. (0). Mosvik: Mosvik, 7 Aug 1913, Kaalaas s.n. (COLO). Skei: Skei, 18 Aug 1899, Clarke s.n. (WTU). OPPLAND. Brandbu: mell. N. og s. Gulsjøen, 31 Aug 1954, Størmer s.n. (0); Velta, 17 Jun 1943, Størmer s.n. (0). Fluberg: Odden, 11 Aug 1960, Størmer s.n. (0); Högfoss ovenfor Kverndalen, 12 Aug 1960, Størmer s.n. (0). Lom: "Loflet", 21 Aug 1977, Baadsnes s.n. (0); Vassberget i Høydalen, 28 Aug 1957, Eckblad s.n. (0); Suleim, 9 Jul 1858, Zetterstedt s.n. (G, H, M) [Grim. et Andre. Exs. No. 33]. Lunner: vestsiden av Store Daltjuren, 11 Mar 1944, Størmer s.n. (0). Nordre Land: Torpa, Mell. Finni og Kinn, 2 Apr 1946, Størmer s.n. (0). Østre Toten: dalen nedenfor Leirsjøen, 6 Aug 1946, Størmer s.n. (0); mellom Stubdalen og Høgda, 9 Aug 1946, Størmer s.n. (0); Mellom Kronborg og Helgestad, 5 Aug 1946, Størmer s.n. (0); vest for Leirsjøen, 7 Aug 1946, Størmer s.n. (0). Søndre Land: Ved Vesleelva ved Skrukli st., 27 May 1946, Størmer s.n. (0). Skjåk: Svartdalsvatn, 1430 m, 22 Aug 1953, Jørstad s.n. (0); Pol. de Videseter, region de Grjotli, 1100 m, 9 Aug 1965, Onraedt 65.N13105 (BR). Sor-Fron: Harpefoss, 24 Jul 1942, Lid s.n. (0). Vang: Bitihorn, ca 1200 m, 26-28 Aug 1969, Mårtensson s.n. (S); lac Tyin, 1080 m, 6 Aug 1964, Onraedt 64.N.13106 (BR). Vestre Gausdal: Jettegrytene ved Dalbakken, 12 Aug 1957, Størmer s.n. (0); Maribu Seter, 9 Aug 1957, Størmer s.n. (0). ØSTFOLD. Idd: Holmen vest for Prestebakke, 7 Jul 1953, Størmer s.n. (0); Klo nord for Berby, 14 Jul 1953, Størmer s.n. (0); Holtet tollstasjon, 9 Jul 1953, Størmer s.n. (0); Boltjern ved Holmen, 4 Jul 1953, Størmer s.n. (0); Nypeta nord for Berby, 12 Jul 1953, Størmer s.n. (0). Fredrikstad: Onsø, Lille Fjelle, 26 Jun 1892, Ryan s.n. (0). Marker: Rødenes, Ådal, 10 Aug 1963, Størmer s.n. (0); Ved Svarttjern, 12 Aug 1963, Størmer s.n. (0). Øymark: NØenden av Store Le, 6 Aug 1963, Størmer s.n. (0). Råde: Ved Engene på halvøya i Vannsjø, 16 Jun 1969, Størmer s.n. (0). Römskog: Hagen, 26 Jun 1948, Størmer s.n. (0). Sarpsborg: Smålenene, Greaker in Tune, 1 Aug 1886, Hagen s.n. (DUKE). Trøgstad: vika overfor Flatebyvika, 5 Sep 1979, Størmer s.n. (0). Varteig: nedenfor Dalen på skogklette N-vendte berghyller næ Glåma, 16 Oct 1981, Størmer s.n. (0). ROGALAND. Årdal: Nordsiden av Jamnarhei (nord for Sandvatn), 21 Jul 1955, Jørstad 21 (0). Avaldsnes: Hndaåker, 2 Aug 1969, Størmer s.n. (0); Visnes, 2 Aug 1969, Størmer s.n. (O). Bjerkreim: Vikeså, 7 Jun 1951, Størmer s.n. (O); lia SV f. Baerland, 6 Jun 1951, Størmer s.n. (0); Midtklatte, Ørsdalsvann, 10 Aug 1953, Jørstad s.n. (0). Egersund: Varberg, 5 Jun 1951, Størmer s.n. (0); ved Fajansefabrikken, 26 Jul 1972, Størmer s.n. (0); Løyning på Søre Eigerøy, 31 Jul 1972, Størmer s.n. (0); Rotveit, 1 Aug 1972, Størmer s.n. (0); Mong, 1 Aug 1972, Størmer s.n. (0); Vestre Segleim på Nordre Eigerøy, 27 Jul 1972, Størmer s.n. (0); Skadberg på Eigerøya, 30 Jul 1972, Størmer s.n. (0); Haugane på Nordre Eigerøy, 30 Jul 1972, Størmer s.n. (0). Gjestal: Oltedal, 30 Jul 1982, Størmer s.n. (0). Hå: Nordre Ogna, mellom gården og havet, 28 Jul 1972, Størmer s.n. (0). Helleland: Lien, 15 Aug 1938, Størmer s.n. (0). Heskestad: Gya, 11 Aug 1938, I. & P. Størmer s.n. (0). Hole: Ims, 1 & 7 Jun 1948, Størmer s.n. (0); Ims, 30 May 1948, Størmer s.n. (0). Klepp: Vashus nordøst for Grudevatn, 27 Apr 1958, Størmer s.n. (0); Ved kirken, 10 Jun 1971, Størmer s.n. (0). Nærbø: Nærbø kirke, 29 Apr 1958, Størmer s.n. (0); Obrestad, 29 Apr 1958, Størmer s.n. (0); Lode, 29 Apr 1958, Størmer s.n. (0). Ryfylke: Frafjord, 15 Jul 1893, Nyman s.n. (s). Sand: Ropeid, 26 Aug 1954, Jørstad 84 (0). Sandnes: Hetland, Ullenhang, 10 Mar 1952, Størmer s.n. (0); Høyland, Sandvigen, 28 Apr 1958, Størmer s.n. (0); Figgjo - Risfjel, 11 Jun 1948, Størmer s.n. (0). Sola: Sola-vikas sørside, 27 Jul 1982, Størmer s.n. (0). Time: Søndre Kalberg øst for Frøyland, 27 Apr 1958, Størmer s.n. (0). Torvastad: Bjørgjene, 6 Aug 1969, Størmer s.n. (0). SOGN OG FJORDANE. Breumsfjeld: Nordfjord, 21 Jul 1869, Kiær s.n. (0). Davik: Förde, 24 Aug 1949, Størmer s.n. (0). Fjaler: ovenfor Tyssedal, 25 Nov 1954, Jørstad s.n. (0). Flora: Svanøy, vest for Svanøy gård, 7 Jul 1973, Størmer s.n. (0); Sørsiden av Svardalsvatnet, SØ for Osen, 9 Jul 1973, Størmer s.n. (0); Grytdalen opp til Kupevatn, 11 Jul 1973, Størmer s.n. (0); Florø, 4 Jul 1973, Størmer s.n. (0); Kinn, 5 Jul 1973, Størmer s.n. (0). Förde: Söndfjord, 18 Jul 1869, Kiær s.n. (0); Förde, 27 Aug 1948, Moss s.n. (0). Gaular: Vikumheia ved Haukedalsvann, 730 m, 18 Nov 1958, Jørstad s.n. (0). Gloppen: ved Skjardalsvatnet, 26 Jul 1948, Høeg s.n. (o). Hornindal: Grodås, 55 m, 16 Aug 1951, Lid s.n. (o). Innvik: Olden, Oldöyra, 16 Aug 1931, Lid s.n. (0). Jolster: Godtdalen, 550 m, 13 Jul 1951, Lid s.n. (0); Befring, 17 Jul 1951, 300 m, Lid s.n. (0); Vassenden, Aspehaugmyra, 230 m, 11 Jul 1951, Lid s.n. (o). Lærdal: Mellom Vindedalen gård og Hortu, 3 Aug 1970, Størmer s.n. (0). Luster: Storevatn, 1270 m, 16 Aug 1953, Jørstad s.n. (0); Nordom Liabrevatnet, 1520 m, 2 Aug 1944, Lid s.n. (0); Illvatn, 1390 m, 21 Aug 1953, Jørstad s.n. (0); Gravdalsvann, 1300 m, 20 Aug 1953, Jørstad s.n. (0); Illvassåi, 1250 m, 21 Aug 1953, Jørstad s.n. (0). Vågsöy: Kjærringnubben (= Kjerringa), 21 Aug 1949, Størmer s.n. (0); S. Oppedal, 19 Aug 1949, Størmer s.n. (O, WTU); Måløy, 18 Aug 1949, Størmer s.n. (0). Sogndal: Svartaholberget øst for Amla, ca 450 m, 6 Aug 1970, Størmer s.n. (0): Amble, 14 Jul 1936, Heiberg s.n. (0). Stryn: lia ved Visnes, 26 Aug 1949, Størmer s.n. (0); Flofjell, N Strynsvann, 1000 m, 22 Jun 1954, Jørstad s.n. (0). Sør-Trøndelag. Åfjord: Årnes, skogsvei ved Melan og Øykneset langs Stordalselva, 19 & 20 Jul 1977, Baadsnes s.n. (o). Bjugn: Jössund, Vallersund, 12 Sep 1870, Arnell s.n. (S). Hitra: Ved stein mellom Dolm og Bremnes (?), Dolmøya, Jørstad 15 (0). Nes: Duvhellarn, 1 Oct 1960, Knutsen s.n. (0). Oppdal: Kongsvoll, 1836, Blytt s.n. (0); Montis Snechæetten alpium Dovrensium, 2 Aug 1858, Zetterstedt s.n. (CANM, H, M, S) [Grim. et Andre. Exs. No. 32] and Kiær 29 (M); Dovre, Wårstien, Zetterstedt 70 (O). Rissa: Näbb, 8 May 1960, Størmer s.n. (o). Ørland: Storfosen, 11 Oct 1936, Høeg s.n. (0). Stjørna: Fiksdal, 2 Jun 1953, Jørstad s.n. (0). Trondheim: Trondheim, Ilsvikbergen, 14 May 1888, Hagen s.n. (H); Trolla Fjellvegg ved veien, 4 Oct 1936, Høeg s.n. (0). TELEMARK. Bamble: mellom Ese og Vinterdalen, 10 Jul 1955, Størmer s.n. (0). Kragerø: Landsverk sør for Øygarden, 17 Jun 1979, Størmer s.n. (0). Kviteseid: Tveit-Lundevall, 7 Sep 1980, Størmer s.n. (0); Bergsto ved Fjågesund, 8 Sep 1980, Størmer s.n. (0); N for Selsvann N for Morgedal, Jul 1960, Næss (0). Lårdal: Eirfjell, 600 m, 7 Jul 1956, Størmer s.n. (0). Mo: Nevestveit ved Børtevann, 450 m, 10 Jul 1956, Størmer s.n. (0); Barskårtveiten, 2 Jul 1956, Størmer s.n. (0). Nissedal: Fjonesund, 6 Aug 1953, Jørstad s.n. (0). Nottoden: Gransherad, Bolkesjø, 17 & 19 Aug 1942, Størmer s.n. (0); ved Dalen ø.f. Follsland, 22 Aug 1942, Størmer s.n. (0). Sannidal: Lofthaug, Sjuers, 28 Jul 1940, Lid s.n. (o). Seljord: Skorve, 1000 m, 22 Aug 1937, Störmer s.n. (POZG). Skien: Gjerpen, N-siden av Meitjern, 28 Jul 1966, Størmer s.n. (0). Solum: Rugla, 22 Jun 1949, Størmer s.n. (0); bukt s.f. Spiredalen, 22 Jun 1946, Størmer s.n. (o). Tinn: Hovdestøl SV for Dal kapell, 600 m, 26 Sep 1980, Størmer s.n. (0); Mal, 25 Aug 1942, Størmer s.n. (0); Bergstølnut SV for Krokan, 26 Aug 1942, Størmer s.n. (0). Vinje: Hangaksla, 12 Jul 1891, Størmer s.n. (0). TROMS. Lyngen: Skibotn, Falsnes, 27 Jun 1955, Roivainen s.n. (BR, H); Mellan Koutovanka och Lyngen, 20 Aug 1867, Norrlin s.n. (H). Nordreisa: Snefonnfjell ved Siilibahta, 28 Jul 1933, Mejland s.n. (0); Nordreisen, 23 Aug 1891, Arnell s.n. (s). Skånland: Astafjord, Fornes, 12 Jun 1953, Jørstad s.n. (0). Tromsö: Kvalöy, Straumhella, 16 Aug 1967, Fagerstén s.n. (H). Vesterålen: Sortland, Nyksund, Haapasaari 8198 (BRNM, H, S). VEST-AGDER. Bakke: Strandeli, 9 Aug 1938, I. & P. Størmer s.n. (0). Eiken: 1 km Ø f. kirken, 15 Aug 1939, Størmer s.n. (0). Feda: Nordvestvendt li øst for brua ved Feda, 18 Jul 1977, Størmer s.n. (0). Fjotland: Solhom, ca 575 m, 13 Jul 1964, Jørstad s.n. (0); Lindefjell, Kvinesdalen, 11 Jun 1954, Jørstad s.n. (0). Flekkefjord: Mellom bygrensen og Sveiga, 15 Jul 1977, Størmer s.n. (0); Hidra, mellom Veisdal og Langeland, 25 Jul 1977, Størmer s.n. (0); Mellom Øvstefjellså og Langevatnet, 20 Jul

1977, Størmer s.n. (0); Flekkefjord, 5 Aug 1939, I. & P. Størmer s.n. (0). Greipstad: Bertelsödegård - Trobbevann, 11 Aug 1959, Størmer s.n. (0). Hægeland: Röiknes, 14 May 1918, Sørensen s.n. (0). Hagebostad: Tingvatn, 15 Aug 1939, Størmer s.n. (0). Halse og Harkm: Ekebrek, 26 Aug 1939, Størmer s.n. (0); Skjernøya, 24 Jun 1947, Størmer s.n. (0); Risøbank, 28 Jun 1947, Størmer s.n. (0). Hidra: Berefjord, 9 Aug 1939, Størmer s.n. (0); Midbö, 11 Jun 1951, Størmer s.n. (0). Holum: Sodeland, 22 Aug 1939, Størmer s.n. (o). Kvinesdal: 2.5 km E of Knaben gruver, Hedenäs 11973 (s). Lista: Udal, 2 Aug 1954, Størmer s.n. (o); Sigersvoll, 6 Aug 1954, Størmer s.n. (0). Lyngdal: Fleseland, 7 Aug 1971, Skofteland s.n. (o). Nes: Fjellså, 5 Aug 1939, Størmer s.n. (o). Oddernes: mell. Mosby og Mestad, 8 Aug 1959, Størmer s.n. (0). Randesund: Børresvåg ved Dvergsnes, 9 Aug 1959, Størmer s.n. (0). Øvre Sirdal: Rauå ved Tjørhom, 12 Aug 1938, I. & P. Størmer s.n. (0). Sirdal: Tonstad, 8 Aug 1938, I. & P. Størmer s.n. (0). Søgne: Lastad-Ålo, 14 Aug 1959, Størmer s.n. (0); Vige, 14 Aug 1959, Størmer s.n. (0); Skarvøya, 23 Jun 1947, Størmer s.n. (0). Spangereid: Våge, 19 Aug 1939, Størmer s.n. (0). VESTFOLD. Hedrum: Solberg til Litjern, 28 Sep 1890, Jørgensen s.n. (0). Sandeherad: Hanan ved Sandefjord, 27 Apr 1891, Jørgensen s.n. (0); Hjertås n.f. Sandefjord, 1 May 1890, Jørgensen s.n. (0); Fjellvik ved Sandefjord, 11 Sep 1889, Jørgensen s.n. (0). JAN MAYEN. 1892, Martin s.n. (BM); ved Vestbreen, 5 Aug 1930, Lid s.n. (O); base of Bluffs W of Radio Station, Oosting 434 (DUKE). SVALBARD. Bjørnøya: Hambergfjell on the S end, 390 m, 16 Aug 1983, Dunfjeld & Engelskjøn s.n. (s); NE coast: 27 m, Haabethvatn, 10 Aug 1983, Engelskjøn s.n. (s); Mount Misery, Berggren 45 (H, s). Spitsbergen: Smeerenberg, Berggren 46 (BR, H, S, W); Nordkap, Berggren 456 (S); Hornsund, between Torellbreen and Hornbreen, 18 Aug 1959, Kuc s.n. (KRAM); Daudbjørnpynten, 250 m, 12 Aug 1962, Birkenmajer s.n. (KRAM); SE of Claus-Andersenfjellet, 12 Aug 1962, Birkenmajer s.n. (KRAM).

POLAND. Beskid Śląski: Kościelec, Skałki Forest, 1 Aug 1996, Stebel s.n. (KRAM). Góry Izerskie: Orle, 820 m, 12 May 1957, Lisowski s.n. (BR, CANM, M) [Bryoth. Pol. No. 541]; Jarzębnik stream near Hala Izerska, ca 840 m, 26 Sep 1981, Ochyra s.n. (ALTA, BCB, BR, CANM, JE, KRAM, TENN, UC) [Musci Pol Exs. No. 631]; N slopes of Mt Łużec above Świeradów Zdrój, ca 800 m, 26 Sep 1981, Ochyra s.n. (ALTA, BCB, BR, CANM, JE, KRAM, UC) [Musci Pol Exs. No. 737]. Góry Stołowe: N of Mały Szczeliniec, 17 Aug 1957, Lisowski & Szweykowski s.n. (BR, BRNM, CANM, KRAM) [Bryoth. Pol. No. 787]. Karkonosze: Kopa, Bornmüller 50 (JE); Czarcia Ambona near Duży Śnieżny Kocioł, 1500 m, 2 Sep 1907, Cypers s.n. (GJO); Śnieżka, 18 Apr 1883, Timm s.n. (HBG) and 30 Jun 1884, Janzen s.n. (JE); Wielki Śnieżny Kocioł, 930 m, 20 Sep 1867, Limpricht s.n. (BR, HBG, JE, KRAM, M, PRC) [Bryoth. Siles. No. 126], Fudali 244/2001 & 243/2001 (KRAM) and 1400 m, Lambinon 63/P/990 (BR); by tourist route from Szklarska Poręba to Łabski Szczyt, 1000 m, 11 Jul 1956, Lisowski s.n. (BR, BRNM, CANM, KRAM, M, O, POZG) [Bryoth. Pol. No. 313]; Szklarska Poręba, 6 Jun 1953, Lisowski 1983 (BRNM); Mały Śnieżny Kocioł, 12 Sep 2000, Fudali 182/2000 (KRAM) and 18 Aug 1899, Reichenberg 424 (PRC) [Musci Bohem. No. 424]; Mały Staw, 1183 m, 16 Sep 2002, Żarnowiec s.n. (KRAM); NW slope of Szrenica, 952 m, Szmajda 3822 (POZG); Łomniczka River valley near Karpacz, 9 Jul 1969, Marstaller s.n. (JE). Pobrzeże Szczecińskie: Szczecin-Glinki). May 1896. Winkelmann s.n. (POZG). Poiezierze Bytowskie: Leśnictwo Płótowa w Ndl. Sierżno, 8 Jul 1953, Lisowski s.n. (CANM, BR, BRNM, KRAM, M, O, POZG) [Bryoth. Pol. No. 69]. Pojezierze Kartuskie: between Kartuzy and Chmielno, 10 Jul 1934, Krawiec s.n. (POZG); N of Kosy, Rusińska 2397 (POZG); Kamienna Góra near Lubygość Lake, Rusińska 1004 (POZG). Pojezierze Krajeńskie: Mochle, 28 Sep 1932, Krawiec s.n. (POZG). Tatry Wysokie: Czarny Staw Gasienicowy towards Zmarzly Staw, ca 1620-1700 m, 25 Jun 1959, Boros s.n. (BP); Dolina Gasienicowa, at foot of Mały Kościelec Crag by tourist route from the hut "Murowaniec" to Czarny Staw Gąsienicowy, 1550 m, Bednarek-Ochyra & Ochyra 103/90 (ALTA, BR, GZU, JE, KRAM, M) [Musci Pol. Exs. No 1138]; Mt Beskid, ca 2010 m, 7 Aug 1986, Wójcicki s.n. (ALTA, BR, BRNM, CANM, JE, KRAM) [Musci Pol. Exs. No. 1037]; Dolina Roztoki, under Świstówka, 1490 m, 8 Jun 1956, Lisowski s.n. (BR, BRNM, CANM, M) [Bryoth. Pol. fasc. 31 No. 807]; Morskie Oko, 1600-1700 m, De Sloover 16823 (BR).

ROMANIA. *Rodnei Mts*: under Pietrosul Borșei peak, 2300 m, *Ștefureac s.n. B1489* (BUCA); Județ Bistrița – Năsăud), Ineu near Valea Vinului, *ca* 2100–2280 m, 27 Jul 1942, *Boros s.n.* (BP). *Retezat Mts*: Galeș Lake, *Wallfisch s.n.* (hb.Wallfisch).

RUSSIA. MURMANSK PROV. Lapponia Imandrae: Chuna Tundra Mts, Jul 1885, Brotherus s.n. (LE, KRAM); Chibiny, vallis Kukisvum, in ripa glareosa fl. Kukisjok, 14 Sep 1956, Schljakov s.n. (CANM, COLO, KRAM, POZG, O, W, WTU) [Hep. Musci URSS Exs. No. 95]; Ponoj village, 30 Jul 1972, sine collector (KPABG, KRAM); Kirowsk region, S part of Chibiny Mts, Ajkuajvenchjok river valley, Lisowski 6934 (POZG); Khibiny Mts, Kukisvumchorr Plateau, Snezhnyj Cirque, 27 Jul 2003, Filin s.n. (KRAM, MW); Khibiny Mts, Takhtarvumchorr river, 27 Aug 1969, Ramenskaya s.n. (KPABG, KRAM); Chiltald Mts, NW slope of Malaya Konya Mt (E of Verkhnetulomskoe Lake), ca 500 m, 30 Jun 1988, Belkina s.n. (G, MO) [Bryoph. Murm. No. 44]; Yuksporlak Pass, Shlyakov 2035 (KPABG); Teribarka, 7 Jul 1872, Brotherus s.n. (H). Lapponia Petsamoënsis: litus sinus Petschengaënsis prope Liinahamari, 17 Aug 1955, Shlvakov s.n. (BRNM, CANM, CAS, COLO, JE, KRABG, KRAM, O, POZG, W, WTU) [Hep. Musci URSS Exs. No. 46]. Lapponia tulomensis: Biological Station near Polyarnyy, 19 Aug 1927, Savicz s.n. (BRNM, O, POZG, S, W) [Bryoth. Rossica No. 35]; Insula Kildin, Savicz 486 (LE). Lapponia murmanica: Gavrilovo, Savicz 722 (LE); Lica river, Savicz 403 (LE); Porchnikha, Savicz 4140 (LE); Ionn-Njuygoajv Mts, creek of SSE of Rieppjavr, Likhachev 18/6 (KPABG, KRAM); Barents Sea shore, Voronja river, E lower course of Vornja river and Primorskiye lakes, near Gavrilovo, Belkina 107-3-01 (KPABG, KRAM); Barents Sea shore, vicinity of the Dalniye Zelency, W part of Zelenetskoe lake, Belkina 34-19-01 (KPABG, KRAM); Dalniye Zelentsy, Belkina 3-1-01 (KPABG, KRAM); Laplandskiy Reservoir, Salnye tundry, Wuim Mt, 460 m, Belkina 25-2-03 (KPABG, KRAM) and 990 m, Belkina 5-04 (KPABG, KRAM); Lovozerskye Mts, Ivniak stream, Belkina 86-2084 (KPABG, KRAM); Lovozerskye Mts, N side of Karnasurt Mt, Kromka stream, 550 m, Belkina & Likhachev 101/12 (KPABG, KRAM); Lovozerskye Mts, Elmarajok Pass, Belkina 89/5 (KPABG, KRAM); Lovozerskye Mts, Ilmanok, 650 m, Belkina & Likhachev 73/37 (KPABG, KRAM); Lovozerskye Mts, second Raslak cirque, 900 m, Lichathey 72/13 (KPABG, KRAM): Lovozerskye Mts, Murnuai creek, 600 m. Belkina 67/22 (KPABG, KRAM); Chiltald Mts, Malaja Konya Mt, E slope of Malaja Konya, Belkina 181-1-88 (KPABG, KRAM); Kandalaksha Bay, 5.5 km WE of Kolvica, between Okatyeva Mt and Klyuchihinskaya Mt (Domashnye tundry, Zeleznye Vorota), Belkina 24-1-02 (KPABG, KRAM); region between Lotta and Nota rivers, Lavnatundra Mts, Lavnatundra Mt, 640 m, Belkina & Likhachev 153/2 (KPABG, KRAM); Lavnatundra Mt, Jumos river, Belkina 221-1-87 (KPABG, KRAM); Griemiaha-Vyrmes Massif, 45 km SSW of Murmansk and 5 km SSE of Vyrmes lake, Belkina 106-19-02 (KPABG, KRAM); Dolgava Shchel Bay, Likhachev 184-1-81 (KPABG, KRAM); Rybachiy Penninsula, Kiekurskiy Cape, Likhachev 78/1 (KPABG, KRAM). KARELIA. Karelia Ladogensis: N corner of Ladoga Lake, 23 Jul 1935, Huuskonen s.n. (ALTA, CANM, LE, PRC); Salmi, Käsnäselkä, 2 Jul 1936, Huuskonen s.n. (BR); Salmi, Retsu, Kalliolampi, Jul 1937, Tuomikoski s.n. (H); Kurkijoksi Region, vicinity of Kolkhoz, 1950, Kozłova s.n. (LE, KRAM); White Sea shore, Kandalaksha Bay, Kindo Peninsula, 23 Aug 1993, Notov s.n. (KRAM, MW); Kirenapa, Korpikylan, 6 Jul 1936, Tuomikoski s.n. (H). NENETZKIY AUTONOMOUS OKRUG. Terra Samoyedorum (NE part of Archangielsk Prov.), sine dato, Schrenck s.n. (LE). URALS. Polarniy Ural, Mt Pendirma-Paj, 1150 m, 20 Jul 1987, Klimeš s.n. (BRNM). Komi Republic: Sverdlovskaya Oblast', Denezkin Kamen Reserve, 1492 m, 28 Jul 1996, Dyachenko s.n. (KRAM);

SLOVAKIA. Liptovské Hole: near hut Na Zverovce, ca 1200 m, Aug 1935, Šmarda s.n. (BRNM). Nízké Tatry: Lazisko, Krížská dolina (part of dolina Chabenec), ca 1600 m, 11 Jul 1990, Váňa s.n. (PRC); Ďumbier, Krupová hola, ca 1800 m, De Sloover 6119 (BR); Vajskovská dolina, ca 1700 m, 30 Aug 1987, Váňa s.n. (PRC); Kráľova hola (1948), ca 1700 m, Pokluda 3986 (BRNM); Vel' Vápenica (1961), ca 1500 m, Pokluda 3985 (BRNM); Liptovský Ján, Ludárová dolina, Ďumbierov kotál, ca 1650 m, Pokluda 3983 (BRNM). Roháče: Roháčká dolina near Zuberec, 1100-1400 m, 18 Aug 1962, Boros s.n. (BP). Vysoké Tatry: dolina Mlynica, Skok, ca 1810 m, Aug 1948, Pilous s.n. (BRNM, CANM, G, POZG, W) [Musci Čech. Exs. No 855] and Krajina 907 & 912 (PRC); dolina Mlynica, Kozie plesa, 1950 m, Krajina 174 (PRC); Slavkovský štít, ca 1890 m, Aug 1948, Pilous s.n. (BRNM, W) [Musci Čech. Exs. No 685]; Pod Zeleným plesem u Kriváně, 1900-2000 m, Vilhelm 243(920) (BRNM, PRC); Malá Studená dolina, ca 1800 m, 20 Aug 1951, Šmarda s.n. (BRNM); Studené Sedlo, ca 2380 m, 8 Sep 1975, Dvořák s.n. (BRNM); Tatranská Lomnica, v údolí Zeleného potoka pod Brnčálovým plesom, ca 1400 m, 21 Jun 1969, Pokluda s.n. (BRNM); Lomnický štít, 2345 m, 12 Aug 1957, Hadač s.n. (BRNM); Temnosmrečinová dolina, ca 1700 m, Aug 1947, Šmarda s.n. (BRNM); Východná Vysoká, ca 2400 m, 7 Sep

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1975, Dvořák s.n. (BRNM); Mengusovská dolina, ca 1600 m, 2 Jul 1937, Šmarda s.n. (BRNM); Štrbské Pleso, Vel'ké Hincovo pleso, ca 1750 m, 2 Sep 1950, Jedlička s.n. (BRNM); ústie Tomanové do Tiché doliny, ca 1180 m, 14 Jul 1959, Šmarda s.n. (BRNM); Špania dolina, ústie do doliny Tiché, ca 1120 m, 19 Jul 1959, Šmarda s.n. (BRNM); Velké Svišťovky, ca 1950 m, 5 Oct 1976, Dvořák s.n. (BRNM); Polany – Závory (v Zadní Tiché), ca 1700 m, 6 Jul 1959, Šmarda s.n. (BRNM); Bielovodská dolina, nad Hviezdoslavovým vodopádom, 1550 m, 8 Aug 1974, Pokluda s.n. (BRNM); Zlomisko, ca 1900 m, 13 Jul 1937, Šmarda s.n. (BRNM); Spišské pleso, ca 2000 m, 24 Jul 1938, Šmarda s.n. (BRNM); Vel'ké Hincovo pleso, ca 1800 m, 13 Sep 1940, Boros s.n. (BP); Osterva - Popradské pleso, ca 1700-1800 m, 12 Sep 1962, Boros s.n. (BP); Velické pleso, Velická dolina, 1900 m, 14 Aug 1962, Boros s.n. (BP, KRAM); Päť Spišských plies, Malá Studená dolina, ca 2000 m, 1 Sep 1940, Boros s.n. (BP); Vel'ká Svišťovka, ca 1800-2000 m, 14 Jul 1958, Boros s.n. (BP, KRAM).

SLOVENIA. Komen Mt near Gornij Grad, 13 Aug 1898, *Glowacki* s.n. (BR, GZU)

SPAIN. Lleida: Pallars Sobirá supra Estany Gerber, hacia Estany Negre de Baix, ca 2200 m, 7 Jul 1990, Muñoz s.n. (hb. Frahm); Estanys Gerber, 27 Jul 1961, Casas s.n. (BCB); Vall d'Aneu, Gerber lake, 7 Jul 1990, Brugués s.n. (BCB); Vall d'Espot, pr. estany Maurici, 2300 m, 13 Jun 1956, Casas s.n. (hb. Frahm); Sant Maurici lake, 13 Jun 1956, Casas s.n. (BCB); Tredós, Arán, Beńos de Tredos, Aigoamog, ca 1800 m, 8 Jul 1990, Muñoz s.n. (hb. Frahm); Vall d'Arán, Aigoamog, towards Major of Colomer lake, ca 1900 m, Jul 1966, Casas s.n. (BCB, hb. Frahm); Pica d'Estats, 31 Jul 1986, Vives s.n. (BCB); San Nicolau valley, Aubada of Llong lake, 2000 m, 1 Jul 1959, Casas s.n. (BCB, O, VIT); Ribera de Sant Nicolau, Boí, hermitage of the Sant Esperit, 30 Jul 1961, Casas s.n. (BCB, hb. Frahm); Salardu, Vall de Ruda, 1850 m, 5 Sep 1988, Casas s.n. (BCB); Boí, Aigüestortes, over Llebreta lake, 29 Oct 1994, Casas & Carrillo s.n. (BCB); Salardú, Mig of Saboredo lake, 2250 m, 5 Sep 1988, Casas et al. s.n. (BCB). Huesca: Gistaín, Circo de la Pez, siliceous boulder of the Montó, 1700 m, 15 May 1969, Monserrat et al. (BCB).

SWEDEN. ÅNGERMANLAND. Säbrå: Säbrå, Jul 1868, Arnell s.n. (s). Sattnä: Rösåsberget, Sep 1891, Tärnlund s.n. (ALTA). Skog: Sandsberget, Jul 1872, Arnell s.n. (H, S). ÅSELE LAPPMARK. Dorotea: Hemberget, 2 Jul 1914, Möller s.n. (DUKE). Vilhelmina: Marsfjällen, 1200 m, 20 Jul 1926, Möller s.n. (H, S) and 1300 m, 22 Jul 1914 Möller s.n. (H, S); Borka, 11 Jul 1916, Möller s.n. (s). BOHUSLÄN. Hogdals: Svinesund, sine dato & collector (H). Jörlanda: Sävelycke, 19 Jun 1926, Stenholm s.n. (S). Kville: Homborgsund, 23 Jul 1922, Möller s.n. (H). Ljung: Ljungskile, vid Lyckorna, 16 Nov 1934, Krusenstjerna s.n. (s). Stenkyrka: Nötesäter, 26 Sep 1945, Selling 81 (s); Djupvik, 26 Sep 1945, Selling 226 (s). DALARNA. Ål: Oxberg, 28 May 1914, Möller s.n. (H). Enviken: Vockelberget, 15 Aug 1894, Hellsing s.n. (CANM). Gafet: Mockfjärd, 9 Jul 1955, Fries s.n. (s). Grangärde: Trollberget, 11 Sep 1952, Pettersson s.n. (s). Idre: Storvätteshågna, 5 Aug 1928, Halle s.n. (s); Nipfjället, 28 Jul 1964, Hakelier s.n. (s). Stora Tuna: Rephacken, 20 Aug 1911, Möller s.n. (H). Sundborn: Ryggen, 24 Apr 1910, Möller s.n. (s); Logären, 25 May 1913, Möller s.n. KRAM). Transtrand: Hemfjället, 22 Jul 1909, Möller s.n. (САNM). Vika: Ryggen, 24 Apr 1910, Möller s.n. (H, M); Vika, 11 Sep 1913, Möller s.n. (H, S). DALSLAND. Åmål: Stora Berga, 16 Oct 1929, Larsson s.n. (WTU). Bäcke: Kårud, berg vid Lysesjön, 28 May 1917, Larsson s.n. (S): Torpane, 12 Jul 1914, Bergström s.n. (BR, H), Dalskogs: Famshed, 31 Jul 1913, Larsson s.n. (s). Edsleskogs: Kyrkoherdebostället, vid torpet Presterud, 1 Jul 1915, Larsson s.n. (s). Fargelanda: Norra Spångerud, berg vid Djurvattnet, 27 Aug 1916, Bergström s.n. (G). Frändefors: Djupedalen, berg vid Venern, 7 Sep 1916, Larsson s.n. (s). Mo: Byn vestre, på Otterberget, 19 May 1915, Larsson s.n. (s); Öjersbyn, 24 May 1913, Larsson s.n. (s). Ödeborgs: Bråten, till Torp, 29 Jun 1920, Larsson s.n. (s). Råggärds: Hugeryr, 5 Aug 1917, Larsson s.n. (s). Rölanda: Hökesäter, berg vid Skottbackatjärnet, 22 Aug 1920, Larsson s.n. (s). Torrskogs: Nästegård, 22 Sep 1929, Larsson s.n. (s). Torps: Ellenö, 20 Jun 1915, Larsson s.n. (s). Valbo-Ryrs: Vågsäter, 28 Aug 1913, Larsson s.n. (s). GÄSTRIKLAND. Hille: Edskön, 7 Jul 1835, Thedenius s.n. (H). HALLAND. Hishult: Ågård, 6 Jun 1926, Stenholm s.n. (S). Lindome: Råsjön E of Dunsered), 27 Jul 1922, Johansson s.n. (DUKE). HÄLSINGLAND. Enånger: Barkhälla, 21 Jul 1951, Säfverstam s.n. (s). HÄRJEDALEN. Linsells: Linsellknätten, 27 Jul 1974, Danielsson s.n. (S). Storsjö: Tandådörren, 1050 m, 8 Jul 1931, Florin s.n. (ALTA, BR, S); Dunsjöfjällets, ca 700 m, 16 Jul 1931, Florin s.n. (s); Gråsjöns, 1106-1122 m, 7 Jul 1931, Florin s.n. (s); Vålåsjöfjället, 100-1300 m, 8 Jul 1931, Florin s.n. (s); Ljungdalen, 600-650 m, 27 Jun 1931, Florin s.n. (H, s); Isengelda, ca 1100-1200 m, 11 Aug 1936, Halle s.n. (s); Mittåstötarna, 1183 m, 8 Aug 1936, Halle s.n. (s). Sveg: NE slope of Mt Grövsjöberget, 16 Jul 1989, Hedenäs s.n. (s); WSW of the Lake Stortjärnen, 13 Jul 1989, Hedenäs s.n. (s); vid foten av Kläppen, ca 800 m, 5 Jul 1931, Florin s.n. (s). Tännäs: Anåfjällen, Anåfjället, 1000-1300 m, 4 Aug 1936, Halle s.n. (s); Rutfjället, ca 900 m, 17 Jul 1910, Möller s.n. (DUKE). JÄMTLAND. Åre: Ånn, 1 km N of Landverk, 16 Jul 1980, Hedenäs s.n. (s); Handöl, NW escarpment of N Tväråklumpen, 1250 m, 27 May 1981, Hedenäs 11969 (s); Enafors, Aug 1922, Hülphers s.n. (s); Åreskutan, 28 Jul 1895, Ahlfrengren s.n. (H); Åreskutan, Aug 1894, Nyman s.n. (H). Frostviken: Gäddede, 5 Aug 1914, Möller s.n. (BR). Hallen: Bydalen, Drommskåran, 13 Aug 1904, Arnell s.n. (s). Hotagens: Höbergsfjäll, ca 450-600 m, 2 Aug 1932, Florin s.n. (s); Furuviksklumpen, ca 340 m, 30 Jul 1932, Florin s.n. (s); Penningkejsen, ca 1020 m, 28 Jul 1932, Florin s.n. (s). Kall: Rutsdalen, 500-700 m, 30 Jul 1924, Halle s.n. (s); Storvallen vid Rutälven, 400-450 m, 1 Aug 1924, Halle s.n. (s); Strådalen, 30 Jul 1924, Halle s.n. (s); Sösjöfjällen, Mälkantjokko, 1000-1246 m, 25 Jul 1924, Halle s.n. (H, S); Sösjöfjällen, Gettegaise 800-1000 m, 26 Jul 1924, Halle s.n. (s); Manshögarna, 800-1100 m, 29 Jul 1924, Halle s.n. (H, s); Skäckerfjällen, 550-700 m, 31 Jul 1924, Halle s.n. (H, S). Storsjö: near Pfad between Sylhyddan and Helagshyddan, 19 Jul 1914, Halle s.n. (KRAM). Ström: Löfberga, 30 Jun 1914, Möller s.n. (DUKE, H). Undersåkers: Sylarna, 1300 m, 1 Jul 1937, Krusenstjerna s.n. (s); Sylarne, 12 Aug 1915, Möller s.n. (H); Ottfjället, 19 Jul 1936, Krusenstjerna s.n. (s); Neadalen, Skardörrlåset, slope towards Biskopsån, 840 m, 14 Aug 1950, Mårtensson s.n. (G, S). LULE LAPPMARK. Gällivare: Atjektjåkko, 1000-1200 m, 28 Jul 1934, Halle s.n. (s); dalen mellan Sitasjaure och sjön ö. om Stuor-Ritatjåkko, 24 Jul 1934, Halle s.n. (s); Suorva, 425-500 m, 15 Jul 1934, Halle s.n. (s); Pautetjåkko, 1000-1300 m, 20 Jul 1934, Halle s.n. (s); fjället Pierka, 750-945 m, 23 Jul 1934, Halle s.n. (S, DUKE). Kvikkjokk: Tarra, 750 m, 20 Jul 1923, Möller s.n. (s); Njuonjes, 350 m, 12 Jul 1921, Möller s.n. (ALTA, H, S), 650 m, 11 Jul 1921, Möller s.n. (S) and 1000 m, 7 Jul 1921, Möller s.n. (H). LYCKSELE LAPPMARK. Sorsele: Häggås, ca 400 m, 20 Jul 1925, Möller s.n. (H, S). Tärna: Brantfjället, 16 Jul 1937, Hülphers s.n. (s); Mietjafjäll, 12 Jul 1937, Hülphers s.n. (s). NÄRKE. Askersund: Älmedalen, 30 May 1981, Hakelier s.n. (s). Hidinge: S of Våtsjön, 20 Aug 1966, Koponen s.n. (H). Kil: Ullaviklint, 24 Jul 1902, Svedberg s.n. (DUKE). Tysslinge: Felkasjön, 22 Jun 1933, Waldheim s.n. (s). Viby: Tystingsberget, Zetterstedt s.n. (CANM, G, H, M, W) [Grim. et Andre. Exs. No. 31a]. ÖSTERGÖTLAND. Blåviks: Lycköhål, 22 Jul 1933, Florin s.n. (S). Kvillinge: Granstorpet, 24 Jul 1878, Olsson s.n. (DUKE), Motala: Lemna, Jan 1842, Holmgren s.n. (H). PITE LAPPMARK. Arjeplog: Tjapkatjåkko, 700-900 m, 5 Aug 1929, Florin s.n. (CANM, S); Vuoggatjålmejaur, Revs, 650 m, 23 Jul 1918, Möller s.n. (s); Vuoggatjålmejaure, 3 Jul 1933, Hülphers s.n. (s); Merkenes, 1000 m, 1 Aug 1918, Möller s.n. (s); Merkenes, Rattes, 1000 m, 29 Jul 1918, Möller s.n. (s); Rånekjokks dalgång Storselet, 645-700 m, 28 Jul 1929, Florin s.n. (s); Smuolejaure, ca 700 m, 28 Jul 1929, Florin s.n. (s); Ferras, 900-1100 m, 31 Jul 1929, Florin s.n. (s); Rebneskaise, 800-1100 m, 23 Jul 1929, Florin s.n. (s); Godepakie (Godepakte), 1000-1300 m, 4 Aug 1929, Florin s.n. (DUKE, O, S). SKÅNE. Riseberga: Skäralid, Aug 1884, Thedenius s.n. (S). Bösarp: Bösarp, 10 Jul 1886, Grönvall s.n. (DUKE, H). SMÅLAND. Hestra: vid Kyrkan, 18 Jul 1938, Stenholm s.n. (s). Huskvarna: Huskvarna, 15 Aug 1896, Arvén s.n. (s). Jönköping: Tenhult, Jul 1890, Arvén s.n. (o, s, uc). Madesjö: Otteskruv, 21 Jun 1913, Medelius s.n. (H). Svennarums: Hook, 26 Jun 1927, Florin s.n. (CANM, H, S). SÖDERMANLAND. Hölö: Djupviksberget, 12 Jul 1911, Arnell s.n. (H). Huddinge: Lissma, Nytorp, 18 Oct 1981, Hedenäs 11972 (s). Nacka: Saltsjö-Duvnäs, 15 Aug 1933, Tärnlund s.n. (ALTA); Nackaåsen, 5 Jun 1922, Tärnlund s.n. (s) and 20 Aug 1926, Tärnlund s.n. (BR, H). Ornö: Ornö, 13 Jun 1941, Persson s.n. (S). Östertälje: Getan, 5 Jul 1958, Krusenstjerna 68 (s). Överjärna: Charlottenborg, 15 May 1957, Krusenstjerna 21 (s). STOCKHOLM. Sväria: Svärtagård, 1 Sep 1929, Florin s.n. (s). Tveta: Agdala, 2 Sep 1928, Florin s.n. (s). Tyresta: ca 0.5 km SW of Lake Bylsjön, Hedenäs 11971 (s). Ytterjärna: Gerstaberg, 12 May 1959, Krusenstjerna 51 (s). TORNA LAPPMARK. Jukkasjärvi: Nuolja, 20 Jul 1910, Jäderholm s.n. (ALTA) and 3 Aug 1917, Jäderholm s.n. (POZG); Nuolja, Jul 1944, Hülphers s.n. (S); Abisko nationalpark, 7 Aug 1954, Een et al. s.n. (s); Abisko nationalpark, Slåttatjåkko, 11 Aug 1944 & 15 Aug 1944, Persson s.n. (s); Nuoljal, 31 Jul 1944, Persson s.n. (GZU, S); Abisko, Arvén 385 (BR);

Kårsavaggejåkk, 29 Jul 1944, Arnell & Persson s.n. (s); Kedketjårro, 17 Jul 1946, Nyholm s.n. (s); Lake Tornetrask area, SE of Laktatjakka along Laktatjakka stream, W of Laktatjakkastugan, 900-1100 m, Vitt, Horton & Slack 26315 (ALTA, COLO); Wassitjokko, 11 Aug 1902, Möller s.n. (S); Tuoptevarajok, 28 Jul 1910, Jäderholm s.n. (DUKE); Lullikatjårro, 26 Jul 1912, Jäderholm s.n. (H). Karesuando: Peldsa, ca 1000 m, 18 Jul 1912, Möller s.n. (H, S). Kiruna: Riksgränsen, 520-900 m, 9 Aug 1980, Schriebl s.n. (GZU); Luopakte, 13 Aug 1953, Nyholm s.n. (CANM). UPP-LAND. Blidö: Yxlan, 10 Jul 1945, Jansson s.n. (s). Bromma: Johannelund, 22 Jun 1954, Krusenstjerna s.n. (s); Nockeby, 30 Sep 1901, Möller s.n. (H). Djurö: Skarpö, Runmarö, 16 May 1921, Möller s.n. (ALTA, H). Färentuna: Klippan, 24 Sep 1963, Krusenstjerna s.n. (s). Fresta: Skällnora, 11 Sep 1927, Florin s.n. (H, s). Frösunda: Berg, 13 May 1928, Florin s.n. (s). Gustavsbergs: Skeviks klyfta, 17 Sep 1933, Florin s.n. (s); Skeviks Schlucht, 17 Sep 1933, Florin s.n. (DUKE). Kårsta: nära Kårsta, 25 Sep 1927, Florin s.n. (BR, KRAM, S). Lidingö: Kyrkviken, 7 Jun 1928, Möller s.n. (s); Grönsta, 7 Jun 1928, Möller s.n. (H, s). Ljusterö: Särsö, Aug 1913, Hülphers s.n. (s). Lovö: Kungshattsön, 7 Apr 1927, Florin s.n. (S). Sollentuna: Edsberg, Sep 1921, Möller s.n. (DUKE, H). Solna: Solnadal, 31 Aug 1927, Florin s.n. (H, S). Stockholm, 1841, Thedenius s.n. (CANM); Stockholms-Näs, Hedersberg, 30 Jun 1929, Florin s.n. (s); Stockholm, norra Djurgården, Ö om Ugglevikskällan, 19 Jun 1954, Krusenstjerna s.n. (s). Täby: Rostock, 17 May 1928, Florin s.n. (s). Värmdö: Värmdö, Jun 1889, Thedenius s.n. (H, W); Grinda, 10 Aug 1917, Möller s.n. (H). VÄRMLAND. Gåsborns: westlich Mögreven, ca 210 m, 30 Sep 1927, Åberg s.n. (H). Nyed: berg vid Stormossen, 9 Aug 1920, Arnell s.n. (s). Sunne: Åråsberget, 17 Jun 1923, Åberg s.n. (ALTA). VÄSTERBOTTEN. Lövånger: Kallviken, 29 Jul 1938, Malmström s.n. (s). VÄSTERGÖTLAND. Angered: Hjellbo, 27 Apr 1926, Stenholm s.n. (s); Lerjeholm, 14 Jul 1926, Stenholm s.n. (s). Billingen: Simsjön, Jun 1930, Hülphers s.n. (s). Hössne: Åtran, 12 Aug 1927, Halle s.n. (s); Rönnåsen, 22 Sep 1933. Halle s.n. (s). Kalv: övre Backa vid Fegen, 28 Aug 1938. Halle s.n. (s). Öglunda: Billingen, 19 Jun 1891, Arnell s.n. (s). Partille: Göteborg, 20 Apr 1918, Stenholm s.n. (BRNM, CAS, JE, H, S); Göteborg, Högen, 26 Sep 1931, Stenholm s.n. (H); Göteborg, 1821, Wahlberg s.n. (H). Undenäs: öster om Trehörningen, Stenkälla-reservatet, 11 Aug 1943, Krusenstjerna 196 (s). Vest. Frölunda: Önneröd, 10 Apr 1922, Stenholm s.n. (s). VÄSTMANLAND. Ljusnarsbergs: Hörken, 12 May 1928, Tärnlund s.n. (S); Finnfall, Jämmerdalen, Koponen 10612 (H). Nora: Hammarby, V om Svarttjärnen, 17 May 1986, Hakelier s.n. (s). Vikers: Älvhyttan, 25 Jun 1924, Tärnlund s.n. (s).

SWITZERLAND. BERN. Guttannen, 1360 m, 27 Sep 1995, *Maier* 10561 (G) & 1300 m, 29 Sep 1995, *Maier* 10596 (G); La Châtelard, 1000 m, 20 Jul 1956, *De Sloover s.n.* (BR). GRAUBÜNDEN. Alpes des Grisons, Schlucht bei Vals, 1650 m, Aug 1880, *Culmann s.n.* (G); Lavin, Val Fernina, 1740 m, 30 Jun 1996, *Maier* 10679 (G); Davos, *sine dato*, *Herter s.n.* (CANM, POZG). URI. Andermatt, 19 Jul 1954, *Casas s.n.* (BCB). VALAIS. Barberine, 1900 m, 13 Jul 1951, *Bonner* 782 (G); Vallon d'Orug, 1709 m, 31 Aug 1889, *Bernet s.n.* (G).

MACARONESIA. AZORES. Sine loco, Watson 357 (E). Pico Island: between 1500 m and the top, 1937, Persson s.n. (s); Pico, summit, 2352 m, 9 May 1937, Persson s.n. (H, S). Saint Jorge Island: between Calheta and Topas, 15 May 1937, Persson s.n. (s). Saint Miguel Island: Pico da Vara, ca 850 m, 8 Jun 1937, Allorge s.n. (CANM, COLO, F, MO) [Bryo. Azor. No. 83].

NORTH AMERICA. CANADA. ALBERTA. Jasper National Park, Mt Edith Cavell, beside Lake Cavell, ca 1675 m, Bird 5133 (ALTA, CANM); Tonquin Valley, 28 Jul 1926, McFadden s.n. (WVA); trail to Angel Glacier, along Cavell Creek, Mt Edith Cavell, 12 km S of Jasper, 2000 m, 21 Jul 1959, Weber s.n. (CANM, COLO). BRITISH COLUMBIA. Wadhams, near mouth of Johnston Creek, Schofield 85958 (CANM, DUKE); Garibaldi Park, Sentinel Glacier foreland, Spence & Dubeski 689 & 873 (CANM); S end of Garibaldi Lake, near Barrier, Schofield & Mueller 32690 (DUKE); Mt Matier, E of Pemberton, Schofield 56848 (ALTA, CANM, DUKE); ridge W of confluence of Alsek and Tatshenshini River, Schofield & Godfrey 98343 (ALTA, DUKE, MO); Little Alp Camp, Mt Waddington, 2500 m, Aug 1934, Munday s.n. (MICH); Lausmann Creek, head of Queen's Reach, Jervis Inlet, Schofield 38288 & 63867 (DUKE); Calvert Island, Mt Buxton, Schofield 27994 (CANM, DUKE); Kwakshua Channel, Keith Anchorage Area, Schofield & Williams 27001 (CANM, DUKE); S of Surf Islets, Schofield 86133 (ALTA, CANM, DUKE); Penrose Island, Finn Bay, Schofield 85990 (ALTA, CANM, DUKE); Pitt Island, Holmes Lake,

Schofield, Vitt & Horton 72655 (CANM, DUKE); Prince Rupert, Mac-Fadden 4099 (CANM, MO, TENN); Wyndham Lake, 130-650 m, Vitt 24586 (ALTA, CANM); Prudhomme Lake, ca 15 km E of Prince Rupert, Schofield 87145 (DUKE); Princess Royal Island, Evinrude Inlet, Schofield 86492 (ALTA, CANM, DUKE); Hecate Starit, Bonilla Island, Schofield 41938 (ALTA, CANM, DUKE, MO); Larsen Island, Larsen Harbour, Schofield 41798 (ALTA, CANM, DUKE); near Silverton, 11 May 1927, MacFadden s.n. (CANM, CAS, FH, MICH, MO, NY, UC, US) [N. Am. Musci Perf. No. 106]; summit of Whistler Mt. above Alta Lake. Ireland 69-91 (CANM): Airv Creek, W of Passmore near Slocan Park, 700 m, Tan & Ensing 77-546 (CANM, MICH); Mt Arrowsmith, trail leaving Cameron Lake, ca 1525 m, Halbert 3894 (CANM, DUKE) & 3895 (DUKE, MO); Slocan Lake, Ten Mile Creek, MacFadden 4109 (BM, CANM, MO, TENN); Lake O'Hara, Yoho National Park, Bailey 4108 (MO). Selkirk Mountains: Upper Sheep River Valley around "Billings Creek", SE Salmo, 980-1000 m, Duell 681 (MO); Kootenay Belle Mine Trail, Salmo distr., MacFadden 17167 (CANM, MO); Prince George Area, Ralston Creek, 4.8 km S of Bijoux Falls Park, 760 m, Vitt 25003 (ALTA). Hudson Bay Mountains: Smithers area, Glacier Gulch Trail, from branching at Twin Falls Trail, 610-1100 m, Vitt 24928 (ALTA); Pierce Lake Trail, Chilliwack Valley area, Schofield & Taylor 57226 (0); trail to Lindeman and Greendrop Lakes, S of Chilliwack Lake, Schofield 57918 (DUKE); Old Glacier House site, Mac-Fadden 17959 (MICH, NY); Bridal Veil Falls, Popkum, Schofield & Harrison 81757 (DUKE); Manning Park, Ahti 15428 (H); Wells Gray Park, Battle Mt, Fight Lake Meadow, Ahti 15050 (H). Cassiar Mountains: Glacial Lake, Schofield, Donovan & Cienes 76605 (ALTA, CANM, DUKE); Atsulta Range, headwaters of Kahan Creek, flowing into Jennings R., Schofield 65831 (CANM, DUKE); Horn-Glacial Mt area, SW end of Glacial Lake, ca 40 km SE of Dease Lake, 1500 m, Vitt 19356 & 9415 (ALTA). Omineca Mountains: Peak Range, above Peak Lake, ca 1130 m, Ireland 18703 & Ireland & Bellolio-Trucco 18731 (CANM, COLO); Swannell Range, S side of Sustut Lake, 1300-1520 m, Ireland & Bellolio-Trucco 18439 (ALTA, CANM, MICH, NY); Peak Range, Mt Hartley, SE of Katherine Lake, 1525-2000 m, Ireland & Bellolio-Trucco 18676 (CANM, DUKE, F. FH. H. MO. TENN, US. WTU). OUEEN CHARLOTTE ISLANDS. Bolkus Island: Sincuttle Inlet, Schofield 34730 (CANM, DUKE). Frederick Island: NE side, Schofield 34195 (DUKE). Graham Island: head of Dawson Inlet, Schofield 15897 (CANM) and Schofield & Vaarama 24658 (CANM, DUKE); Gudal Bay, near Gudal Creek, Schofield 33552 (CANM); Athlow Bay Goose Cove, Schofield 64434 (CANM, DUKE); Lander Lake, Seal Inlet, Schofield 33842 (CANM, DUKE); Naden Harbour, Schofield 34380 (CANM, DUKE); Tana Bay, Schofield 100775 (ALTA, DUKE); Gospel Point, N Rennell Sound, Schofield 33870 (DUKE); Eden Lake, Schofield 35232 (DUKE); Mt Brown, Schofield & Spence 84215 (DUKE). Hippa Island: W side, Schofield 33952 (CANM, DUKE). Langara Island: Henslung Harbour, Schofield 34276 (CANM, DUKE). Lihou Island: Schofield 15384 (CANM, DUKE). Louise Island: N of Mt Carl, lakes at head of Skedans Creek, Schofield & Spence 83567 (DUKE); S end of Mathers Lake, Schofield 37345 (DUKE). Moresby Island: Alliford Bay, Schofield 15182 (CANM, DUKE, NY, TENN, WTU); E of Deena River Mouth, Schofield 30821 (CANM); Bigsby Inlet, Schofield & Vaarama 24159 (CANM, DUKE); Skidegate Channel, entrance to East Narrows, Schofield 14018 (CANM, DUKE); above Tasu, Mine Mt, Schofield & Schofield 73313 (DUKE); Fairfax Inlet, Tasu Sound, Schofield & Schofield 73604 (ALTA, CANM, DUKE); Botany Inlet, Schofield 37673 (CANM, DUKE); Jedway area, Schofield 34621 (CANM, DUKE); Moresby Mt, Schofield & Spence 83730 (CANM, DUKE); Onward Point, Schofield 30162 (DUKE); unnamed lake, E of Antiquary Bay, Schofield & Krajina 39429 (DUKE); NE cove Moresby Lake, 95 m, Horton 1387 (ALTA) and Vitt 12247 (ALTA); "Blue Heron" Cove, N of Sunday Inlet, Schofield 31392 (DUKE); Lagoon Inlet, Schofield 31972 (DUKE); E end of Takakia Lake, Schofield 25189 (DUKE); Upper Victoria Lake, 31-46 m, Horton 1683 (ALTA, O); Cumshewa Head, Schofield 44580 (E, US). Tuft Island: of Lvell Island. Schofield & Vaarama 24022 (DUKE). VANCOUVER ISLAND. Brooks Peninsula, above Cape Cook, Schofield 68543 (DUKE); Ucluclet, Macoun 459 (BM, E, FH, H, MICH, MO, NY, US); Cape Vancouver, Macoun 319 (FH); Robson Bight, Tsitika River mouth, Schofield 85626 (DUKE); Awatsino Provincial Forest, near mouth of the Stranby River, Halbert 5773 (DUKE); Port Hardy area, Fort Rupert, Schofield & Williams 26783 (DUKE); Forbidden Plateau, near top of Albert Edward Mt, ca 2070 m, Boas 1646 (DUKE); Nissen Bight, Halbert 8577 (DUKE); Coast Mills Peninsula near Bamfield, Halbert 4093 (FH, DUKE); Robinson Island, Brandon Point, mouth of Blunden Harbour, Schofield 41165 (DUKE). NOVA SCOTIA. Inverness Co.: Lone Shieling,

Erskine 4503 (CANM); Big Southwest Brook, Schofield 4893 (CANM). Victoria Co.: trail to South Point, Ireland 11928 (CANM); S of Black Brook Campground, Ireland 11655 (CANM, MICH); Jigging Cove Lake, Ireland 11758 (ALTA, CANM, H, MICH, NY, US); Indian Brook, Schofield 6030 (CANM, DUKE, NY, POZG); Corney Brook, 250-300 m, Schofield, Belland & Moniz de Sa 96410 & 96414 (CANM); MacGregor Brook, Belland & Schofield 10509 (CANM); Fishing Cove River, Belland 15229 (ALTA, CANM, DUKE); North Aspy River, 12 km SW of Cape North, Allen 2259 (MO); Indian Brook, Schofield 6008 (CANM); Cape Breton Island, Smokey, Nichols 76A, 729, 1813 & 1814 (NY); Breton Island, Macoun 1616 (CANM). NEW BRUNSWICK. Albert Co.: Fundy National Park, Kinney Brook canyon, Belland & Schofield 97634 (CANM, DUKE); at the junction of the Point Wolf and East Branch rivers, Belland & Schofield 18349 (CANM). Charlotte Co.: Leely Cove, Erskine 4236 (CANM). NEW-FOUNDLAND. Avalon Peninsula: Doctor's Hill, St. Barbe, Tuomikoski 4522 (CANM, MICH, UC); Biscay Bay, Ferryland, Tuomikoski 348 (CANM, H, MICH, UC); near Logy Bay, Norris 3522 (BR, UC); Black Ridge, Holyrood, Harbour Main-Bell Island, Tuomikoski 697 (CANM, H); Conception Bay, 2 km SE of Bauline, Brassard 7127 (ALTA, BR, CANM); Back River, Biscay Bay, Brassard 10069 (CANM); Cataracts Provincial Park, 5 km WNW of Colinet, Brassard, Hancock & Mitchell 7395 (CANM, MICH, NY); Little Chance Cove, Trinity Bay, Brassard 10005 (hb. Frahm); Big Bull Arm, Macoun 943 (CANM). Central & Northeastern: Hampden, White Bay, Tuomikoski 3066 (CANM, H); Gambo, Bonavista North, Tuomikoski 5910 (CANM, H); Notre Dame Bay, E of Norris Arm, Norris 3977 (UC); Gaff Topsail, Humber, Tuomikoski 5619 (CANM, H); Kitty's Brook, Humber, Tuomikoski 5530 & 5539 (CANM, H); Blue Hills, S of Terra Nova Park, Schofield 58548 (CANM, DUKE); Norris Arm, Grand Falls, Tuomikoski 5764 (CANM, H); Wesleyville area, SE of Lumsden, Belland 210 (H); Bonavista North Disrict, 5 km NE of Middle Brook, ca 30 m, Brassard 7061 (ALTA, BR); ca 7.5 km S of Sops Arm, Norris 4206 (UC). N Coast: Gros Morne National Park, Alpine Plateau, Centennial Peak, Belland 1009 (ALTA); along Lomond River, Norris 4606 (UC); White Bay North District, Bartlett's River, Fife 1883 (MICH, NY); Ha-Ha Bay, White Bay, Tuomikoski 3699 (H); St. Anthony, White Bay, Tuomikoski 3283 & 3284 (H); Williamsport, White Bay, Tuomikoski 3168 (H); Harbor Deep, White Bay, Tuomikoski 3123 (H). S Coast: Pushthrough, Fortune Bay and Hermitage, Tuomikoski 1550 (CANM, H); Rose Blanche, Burgeo-La Poile, Tuomikoski 821 (CANM, H); Table Mountain near Cape Ray, Tuomikoski 2053, 2056 & 2060 (H); N of Port Aux Basques, Cain 5975 (CANM); Cheeseman Provincial Park near Port Aux Basques, Norris 3077 (UC); Harbor Breton, Huronian rocks, Long 159 (FH); Burin Peninsula, 3 km E of Lawn, Hancock & Butler 296 (CANM, MICH, NY); Pass Island, Tuomikoski 1632 (CANM, H). W Coast: Steady Brook, Humber River, Tuomikoski 2858 (CANM, H); Benoit's River, Humber Arm, Tuomikoski 5311 (H); Bonne Bay area, ENE of Trout River, 300 m, Brassard, Hancock & Mitchell 7564 (ALTA, CANM); Hawke Hill, W of Holyroad, Schofield 58620 (CANM, DUKE). LABRADOR. Chateau Bay area, Henley Harbour, Belland 2636 (CANM); Mealy Mountains, 1100 m, Damman 60-43 (CANM); Crater Lake, WSW of Hebron, 700 m, Gillett 9428 & 8911 (CANM); Grand Lake, Cape Caribou, 18 Jul 1963, Kallio s.n. (CANM); Grand Lake, 25 Jul 1938, Wickes s.n. (FH, NY, US); Torngat Mountains, Nachvak Fjord, Kogarsok River, ca 700 m, Hedderson 5159 (KRAM). NORTHWEST TERRITORIES. Mackenzie Mountains, Liard Range, NW of Sawmill Mt, Vitt 20549 (ALTA, CANM, NY) and Horton 10777 (ALTA); Nahanni National Park, Tlogotsho Range, Talbot T5099 (CANM, NY); Flat River and Nahanni River Region, 1540 m, Scotter 13563 (CANM); Baffin Island, Kingnelling Fiord, Cumberland Peninsula, ca 215 m, LaFarge 49461 (COLO, H, NY). QUEBEC. Nouveau-Quebec Co.: Ile Atkinson, Lac à l'Eau Claire, Ireland 21024 (ALTA, CANM, DUKE, F, FH, H, MICH, MO, NY, TENN, US, WTU); Lac Guillaume-Delisle, Richmond Gulf, near University of Laval Base Camp, Ireland 21084 (CANM): Nastapoka Sound, 3 km S of Pointe Sivraaluk, Ireland 21356 (CANM); Ungava Bay, Weber 1396 (ALTA, H); Poste-De-La-Baleine, Great Whale River, Ireland 21454 (CANM); E coast of Hudson Bay, Port Harrison, Kucyniak & Tuomikoski 1755 (CANM); E coast of James Bay, Goose Bay, Kucyniak & Tuomikoski 592 (CANM, WTU); Territoire de la Baie de James, Lethiecq 4309 (CANM). Charlevoix Quest Co.: Mont du Lac des Cygnes, Parc des Laurentides, 935 m, 21 Jul 1983, Bergeron s. n. (CANM). Gaspe Co.: W edge of Tabletop Mountain, East Fork River Ste. Anne, 1110 m, Collins 4300 (FH); Mt Albert, 845 m, Collins 4222 (FH, NY) and 1110 m, Collins 4300 (NY). Matane Co.: Mont Blanc, LePage 3222 (DUKE, KRAM, WTU); Mont Blanc, 1200 m, Fabius 6025

(NY, PC) and ca 1130 m, Fabius 6009 (BRNM, NY, PC). Pontiac Co.: Parc de la Vérendrye, near Poulter Lake, Ireland & Koponen 16164 (CANM). Rimouski Co.: Bic, LePage 3434 & 3437 (WTU). Sherbrooke Co.: Mont Oxford, 392 m, Nuyt 9323 AM8 (CANM). ONTARIO. Algoma Co.: NE of Wawa, Ireland 24457 (CANM, POZG, TENN); Aubrey Falls, ca 60 km W of Thessalon, Ireland 15652 (BISH, CANM, F); Lake Superior Provincial Park, Old Woman Bay, Ireland 15118 (ALTA, BISH, COLO, CANM, DUKE, F, FH, H, MICH, MO, NY, TENN, US, WTU); Montreal River, E shore of Lake Superior, Schofield 14759 (CANM); Towab Hiking Trail along Agawa River to Agawa Falls, Ireland 24373 (CANM, DUKE, F, WTU); Lake Superior, Agawa Bay, Ireland 4809 (CANM). Nipissing Co.: Lake Temagami, Gull Lake Portage, 21 Aug 1945, Cain s.n. (ALTA, DUKE); Lake Temagami, Cattle Island, 24 Jul 1939, Cain s.n. (CANM, F, MICH) & Cain 1686 (WTU). Thunder Bay Co.: Spur Bay at NW corner of Ombabika Bay, Lake Nipigon, Garton 20895 (CANM, MO, NY); Mt McKay, S of Fort William, Garton 5435 (CANM, DUKE, NY): Little Pic River, ca 35 km W of Marathon, Ireland 15228 (ALTA, CANM, DUKE, FH, H, MICH, NY, US). YUKON TERRITORY. Southern Olgivie Mountains: Tombstone Mt, Vitt 8117 (ALTA, CANM); 6 km N of Tombstone Mt, 1400 m, Vitt 16749 (ALTA, CANM, NY); lakes 10 km NE of Tombstone Mt, 1700 m, Vitt 8038 (ALTA) & 8039 (ALTA, MO, NY): N of Tombstone River, 6 km NNE of Tombstone Mt, 1400-1430 m, Horton 6325 & 6440 (ALTA). Selvyn Mountains: S of Fuller Lake, Itsi Range, Schofield, Vitt & Horton 70204 (ALTA, CANM, DUKE); Kinbasket Lake, along Ptarmigan Creek, about 45 km S of beginning of Canoe Lake Road, 975 m, Vitt, Goffinet & Hastings 35832 (ALTA); Kinbasket Lake, 2040-2100 m, Vitt 34337 (CANM); S of Horse Creek, 2040-2100 m, Vitt 34405 (ALTA); Hess Mountains, Keele Peak, Keele Lake, 1040-1430 m, Vitt 15767 (ALTA) and Horton 5465 (ALTA); Rouge Range, Emerald Lake, 1150 m, Vitt 23442 (ALTA); Sheep Camp, Williams 605 (F); Lake Lindeman, Williams 605 (F, MO).

GREENLAND. Angmagssalik Distr.: Ikasaulaq fjord, 15 m, Molenaar 527A (ALTA, hb. Frahm, H); Ikâsaulaq, Lewinsky 1157 (ALTA); Angmagssalik area, Kong Oscars Ham, 20 m, Daniëls & Molenaar 68294C (FLAS); W. Somandsfjeld, 200 m, Molenaar 68269D (C); Mitdluaglat at Sermilik, Jul 1958, Holmen s.n. (c); Angmagssalik, Holmen 69-532 (C); Ikáteq, Lewinsky 71-254 (NY); Sieraq, Lewinsky 1028 (ALTA, C, hb. Frahm), 70-858 & 70-1560 (C, DUKE); Akorninarmiut, Finnsbu, 11 Aug 1931, Bjørlykke s.n. (0); Kulusuk, Kap Dan, Holmen 69-076, 69-081 & 69-091 (C); Qårtuluk, Lewinsky 70-890 (C, NY); Tasilâlik, Holmen 69-005, 69-006 & 69-007 (C); Isertoq, Lewinsky 71-636 (ALTA, C); Tâsilaq, Lewinsky 70-1312 (C, H); Ikàsagtivaq, E of Paornartivartik, Hamann 69-752, 69-774 (C); Ilivtiartik, Torssukàtak (Tûnok), Holmen 69-366 (С, DUKE, Н); Paornakajît, Lewinsky 71-54 (С, Н); Ikâsaulaq, Lewinsky 1154 (C, DUKE); Qinqertivaq, Holmen 69-599 & 69-789 (C, COLO, F); Kitermit, Holmen 69-151 (C). Disko Island: Godhavn, Holmen & Mogensen 71-889 & 71-1464 (c), Holmen 71-333, 14.303, 14.557 & 14.558 (C) and Mogensen & Brassard 77-163a (C, NY). Fiskenæsset Distr.: Majoraríssap ilua, Damsholt 71-860 & 71-869 (C); Equalult, Bjørnesund, Damsholt 71-753 & 71-1060 (C); Mississippi, head of Bjørnesund, Damsholt 71-1085 (C); Naujât, Fiskenæsfjorden, Andersen & Feilberg 72-407 (C, DUKE); Tasiussarssuaq, Damsholt 71-721 & 65-0620 (c); Quvnigdlip, Damsholt 71-617 (c); Perserajôrssuaq, 750 m, Damsholt 71-901 (C). Godthåb Distr.: Qingua, Buksefjorden, Lewinsky 73-34 (BR, C, DUKE); Eqalugialik, Itivdleq, Lewinsky 73-586 & 73-212 (C); Godthaab, Holmen 3046 (C), 75 m, Holmen 3010a (C); Qasigiangult, Ameralik, Lewinsky 73-356 (C); Kilaersarfik, Ameragdla, Lewinsky 73-497 (C, NY); Præstefjord, Lewinsky 73-767 (C). Julianehåb Distr.: Pamiagdluk, Anordliuitsoq, Jacobsen 3070 (C); Qagssiarssuk, Jacobsen 7020 (c); Imerdlugtoq, Jacobsen 2999 (c); Puiatoq (Prins Christian Sund), Jacobsen 6034 (C); Kangikitsoq, Tupaussat, Jacobsen 3057 (C); Tasermiut, 1250 m, 13 Aug 1959, Holmen s.n. (C); Narssaq, Jacobsen 3091 (C); Angnikitsoq, Angnikitsup nuå, Jacobsen 4066 (C); Kangersuneq qingordleq, Igdlorssuit, Jacobsen 5043 (c). Skjoldungen Distr.: Siorartussoq Island, Lewinsky 70-626 (C); Itivdlerssuaq, Lange næs, Lewinsky 70-399 (C). Umivik Distr.: Kulasuk (Gerners Ø), Lewinsky 70-1582, 70-1583 & 70-1592 (C); Tre Løvers Ø, Lewinsky 70-826 & 70-1613 (с) & 70-798 (с, н).

USA. ALASKA. Aleutians East Co.: Izembek National Wildlife Reserve, Swan Lake, Cold Bay area, Schofield & Talbot 99483 (ALTA, DUKE); Frosty Peak, Schofield & Talbot 99410 (ALTA, DUKE); E Moffet Lagoon area, Schofield & Talbot 99263A (ALTA, DUKE); Russell Creek, Flock FB-1077 (COLO, KRAM, NY). Kiska Island, above Trout Lagoon, 135 m, Darigo 30 (MO); Shumagin Islands, Simeonof Island, Schofield 106108 (MO). Aleutians West Co.: Adak Island, Mitt Lake, Smith 3614 (ALTA); Mt Reed, Schofield et al. 101319 (ALTA, DUKE); Razorback Mt, 457 m, Talbot 86-110 (OSC); Clam Lagoon, Smith 3646 & 3654 (TENN); Andrew Lake, W side of Mt Moffat, Smith 3509a (TENN); Amaknak Island, Dutch Harbor, Bunker Hill, Schofield 104469 (DUKE); Amchitka Island, Infantry Road, Persson 7373 (MICH); Atka Island, Eyerdam 536 (BM, FH, WTU); Attu Island, Hultén 6046 (FH); Massacre Bay, Nees Peak, Gilbert Ridge, ca 35 m, Bell Howard 960 (MICH, US); Unalaska Island, Captains Harbour, Hultén 5216 (FH); Pribilof Islands, sine dato, Palmer s.n. (PC); St Paul Island, 3 Jul 1892, Macoun s.n. (s - lectotype of Racomitrium tenuinerve) and Palmer 169 (CANM, US - type of Racomitrium microcarpon var. palmeri); St George Island, Kincaid 50 (WTU) and Bailey 12 (PC). Anchorage Co.: Girdwood, 15-30 m, Viereck 1928 (COLO); Chugach State Park, Table Mt, Schofield 99227 (ALTA). Bethel Co.: St Matthew Island, Trelease 1885 (MO, NY) & 2169 (MO); Sea Lion Point, Schofield 108489 (MO). Bristol Bay Co.: Raspberry Island, Port Vita, Raspberry Strait, Eyerdam 918 (CANM); King Salmon, Schofield 2303 (CANM, NY). Haines Co.: Chilkat Peninsula, along Mud Bay, near Haines, Worley 12012 (KRAM) & 12013 (BR). Juneau Co.: Mendenhall Glacier, Vitt 12547 (ALTA); Juneau Ice Field, 1220 m, Ward 8-27-49-26 (KRAM, NY) and Welch 20531 (KRAM, NY); Juneau Quadrangle, Roberts Peak, 1065 m, Hermann 22000 (NY). Kenai Peninsula Co.: Chugash National Forest, Ptarmigan Creek Campground, Vitt 18399 (ALTA); Chisik Island, ca 549 m, Schofield & Talbot 98816 (ALTA). Ketchikan Gateway Co.: Ketchikan, Eyerdam 687 (CANM, F, MICH, MO) & 689 (F, MO, WTU) and Welch 19473 (NY); 27 km WNW of Ketchikan, along Clover Passage, Hermann 22169 (BR, FH, WTU); Springy, Hermann 22169 (MICH); along East Channel, Hermann 22206 (G, KRAM, NY, S); Ketchikan, opposite Guard Island, Hermann 22199 (NY). Kodiak Island Co.: Cannery Station, Olga Bay, 660 m, Looff & Looff E242 (CANM, FH, MICH); Alitak, Looff & Looff E124 (CANM, FH, MICH,); Pillar Mt, 150-300 m, 14 Jun 1973, Bishop s.n. (ALTA, BISH, KRAM); road to Pillar Mt from Kodiak, 30-400 m, Sharp 152 (NY, TENN); Sitkalidak Island, Eyerdam 9 (BM, F, FH, MO, WTU). Lake & Peninsula Co.: Newhalen, on Lake Iliamna, Thomas 51-52 (WTU); Aniakchak National Monument, Aniakchak Caldera, Surprise Lake, 330 m, Jul 1993, Hasselbach s.n. (OSC). Matanuska-Susitna Co.: Little Susitna River headwaters, vicinity of Snow Bird and Independence Mines, near Fishhook, Talkeetna Mountains, N of Matanuska River, Steere 12264 (NY). Nome Co.: Seward Peninsula, Kigluaik Mt, Steere 13471, 13491& 13522 (NY); Cape Prince of Wales, ca 700 m, Flock FB-315 (COLO); Cape Mt, Flock FB-314 (NY); St. Lawrence Island, Mt Sevuokok, near Gambell, Steere 13692 & 13632 (NY). Northwest Arctic Co.: Upper Ambler River, source of "Cooper Creek", Lewis 2397 (BR, F) & 2411(F); "Kowalski Mt" ca 6 km S of Ulaneak Creek, 530 m, Lewis 1858A (F). Prince of Wales Island-Outer Ketchikan Co.: Cape Fox, Trelease 2377 (MO); Augustine Bay, Frye 570 (WTU); Prince of Wales Island, Kasaan, Looff & Looff E4 (OSC). Sitka Co.: Baranof Island, on Harbor Mt, above Sitka, Worley & Boas 10120 (CANM, NY, PC); NE of Davidof Lake, Mt Yanouski, Worley & Hamilton 9864 (O); Hot Springs, Trelease 2350 (MO, NY); Sitka, Townsend 47 (US). Skagway Hoonah-Angoon Co.: Glacier Bay, Trelease 1871 & 2455 (MO); Idaho Inlet, Stephens 361 (M, UC) Skagway, Williams 605 (BM, NY, US); Clifton Station, Skagway, Boas 10 (DUKE); Yakobi Island, Little Lake Iakanis, ca 655 m, Shacklette 3950 & 3964 (MICH); near mouth of Bohemia Creek, ca 2 m, Shacklette 3982A & 3983 (MICH); Bohemia Creek, ca 85 m, Shacklette 4000 & 4147 (MICH). Valdez-Cordova Co.: Passage Canal, Whittier, Harvill 484, 505 & 512 (MICH); Icy Bay, Stair Mozaika 5223 (MICH); Evans Island, Port San Juan, Eyerdam 5102 (CANM, DUKE, F, WTU); Port San Juan, Eyerdam 163 (NY) & 5054 (MO, WTU); Knight Island, Thum Bay, Prince William Sound, Eyerdam 818 (CANM, MO) & Eyerdam 823 (DUKE, F, WTU); Latouche Island, Prince William Sound, 50 m, Shacklette 4631 (MICH); Prince William Sound, College Fjord, Viereck 2424A (COLO). Wrangell-Petersburg Co.: Coronation Island, Egg Harbour, Foster 2452 (US); Coronation Island, 9 Dec 1965, Lambert s.n. (DUKE); Etolin Island, W of Kunk Lake, E Ridge of Bessie Peak, Worley & Hamilton 8156 (E); Kuiu Island, Washington Bay, Eyerdam 988 (BM, CANM, DUKE, MICH, NY, TENN); Mitko Island, Petersburg, on the Panhandle, Horton 1833 (ALTA); Wrangel Island, Trout Lake Campsite, Worley 7937 (CANM, DUKE). Yakutat Co.: Gulf of Alaska, Yakutat Bay, E of Yakutat, Steere 14186 (NY); Yakutat, De Monti Bay, Stair 4833, 4921, 4922 & 4992 (MICH); Yakutat Bay, Trelease 2322 (MO, NY). COLORADO. Clear Creek Co.: 35 km SSW of Idaho Springs, Mt Evans, ca 3660 m, Weber 7772 (duke, mo, ny, tenn, wtu), ca 3900 m, Hermann 27454 (ALTA, COLO, F, MICH, MO, TENN, UC, US, WTU) and ca 4100 m, 15 Aug 1960, Weber, Porsild & Holmen s.n. (CANM, COLO, NY, UC, US) and 15 Jul 1970, Weber & Bujakiewicz s.n. (CANM, MICH, MO, US). IDAHO. Boundary Co.: Smith Falls, 18 km NW of Copeland, Anderson 22.685 (DUKE, E, H). MAINE. Hancock Co.: Mt Desert Island, Sargent Mt, 16 Jun 1890, Rand s.n. (NY). Piscataquis Co.: Mt Katahdin, along Hamlin Ridge trail, Crane 577 (CANM, DUKE, NY, TENN); Chimney Pond, ca 1300 m, Hermann 19246 (CANM); Mt Katahdin, South Basin, Collins 2332 (FH, MICH, US); Mt Katahdin, Great Basin Trail, Habeeb 2036 (F); Mt Coe, Richards & Cooper 511 (DUKE); Baxter Peak, 1400 m, Hermann 19590 (BR, MICH); Pamola Peak, Richards & Cooper 193 (COLO); 22 km N of Millinocket Baxter State Park, Helen Taylor Trail, Holcombe 419 (DUKE). MICHIGAN. Keweenaw Co.: Lake Superior, E Copper Harbor, along Fanny Hooe River, Allen 13277 (hb. Frahm, MO). MINNESOTA. Cook Co.: Grand Marais, 7 Aug 1902, Holzinger s.n. (BM, CANM, COLO, FH, H, MICH, MO, NY, UC, WTU, WVA) [Musci Acr. Bor.-Am. No. 447], Wood 123 (NY) and Novell 60 (US). MONTANA. Flathead Co.: MacDonald Lake, Williams 313 (BM, CANM, COLO, F, H, MO, NY, UC). NEW HAMP-SHIRE. Carroll Co.: White Mountains, Franconia Notch, Aug 1851, James (F). Coos Co.: Mt Washington, SW of Gorham, ca 1220 m, Hermann 19334 (CANM, MICH), ca 1525 m, Hermann 19327 (BM, COLO, DUKE, F, US) and 1917 m, Githens 2917 (CANM) & 2920 (TENN, US); Mt Clay, ca 1685 m, 11 Aug 1939, Wickes s.n. (NY, WVA); Mt Jefferson, ca 1740 m, 12-13 Aug 1939, Wickes s.n. (NY). Grafton Co.: North Slide, Tripyramid, Goodrich 293 (DUKE, TENN, WTU); Mt Lafayette, 1000 m, Faxon 137 (NY), 1065 m, 18 Aug 1910, Kaiser s.n. (BM, DUKE, F, FH, H) and ca 1600 m, Jul 1895, Farlow s.n. (F, OSC). NEW YORK. Essex Co.: summit of Mt McIntyre, Winne & Smith 2809 (CANM); White Face Mt, Adirondack Mountains, Hand 63-146 (CANM) and ca 1430 m, Smith, Christofferson & French 40454 (ALTA, BM, BR, CANM, COLO, F, H, MICH, MO, O, POZG, TENN, UC, US) [Moss. N Am. No. 451]; North Elba, Indian Pass Brook near Rocky Falls, 700 m, Hermann 14777 (CANM, NY); Indian Pass, Smith & Dunbar 18754 (FH) and Phelps & Dunbar 146 (MICH); along Feldspar Brook, WNW of Lake Tear, ca 1150 m, Norris 78594 (TENN, UC); Mt Marcy, ca 1730 m, Ketchledge 575 (MICH, NY); Mt Skylight, ca 1490 m, Ketchledge 600 (MICH, NY); Town of Keene, Haystack Mt, 1600 m, 14 Jun 1976, Slack s.n. (DUKE, F, hb. Frahm) & 1355 (MO); Mt Wright, Smith 36056 (MICH); Lake Placid, Cobble Hill, 2 Sep 1898, Britton s.n. (MICH). Orange Co.: Florida, Lelmert 312 (US). OR-EGON. Hood River Co.: Mt Hood, along Timberline Trail, 2000-2400 m, Ireland 7086 (CANM): Mt Hood, trail from Cloud Cap Inn to Elliot Glacier, Lawton 4422 (WTU). Multnomah Co.: Cloud Cap Inn, near Mt Hood, ca 1980 m, Schofield 19669 (CANM). Tillamook Co.: Mt Hebo, Schofield 72374 (ALTA, CANM, DUKE, MO, OSC) and Lyford 2196 (OSC). VERMONT. Chittendent Co.: Mt Mansfield, ca 610 m, 2-3 Jul 1896, Grout s.n. (NY). Windsor Co.: Mt Horrid, Rochester, 12 Jun 1910, Kirk & Dutton s.n. (FH). WASHINGTON. Chelan Co.: Cascade Mountains, Glacier Basin, Sep 1925, Grant s.n. (NY); Stevens Pass, ca 1200 m, Sandberg & Leiberg 863 (DUKE, US) and Leiberg 353 (US). King Co.: 7.5 km SE of North Bend, Ireland 5835 (CANM). Pierce Co.: Mt Rainier, 1980 m, Piper 241 (NY, WTU); N slope of Tattoush Range, Paradise Park, Foster 1031 (NY). Snohomish Co.: above Heather Lake, Mt Pilchuck, Eyerdam 905 (BM). Whatcom Co.: Austin Pass, Mt Baker, Schofield 57214 (O); Mt Baker, summit of Table Mountain, ca 490 m, Spence 828 (CANM); Dailey Prairie, Schofield 103177 (DUKE).

OCEANIA. SOCIETY ISLANDS. *Tahiti*: Papéete, 1852, *Jardin s.n.* (BM, PC – type of *Racomitrium papeetense*).

Codriophorus brevisetus (Lindb.) Bednarek-Ochyra & Ochyra (Figs 81–83)

Codriophorus brevisetus (Lindb.) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. ≡ Racomitrium brevisetum Lindb., Acta Soc. Sc. Fennica 10: 244: 1872. — TYPE CITATION: In promontorio Lamoricière, o et fr., medio Julii 1860, Schmidt; ad Dui, fertile Aug. 1861, Glehn. [Lectotype (selected here): "Ex herbario S. O. Lindberg Rhacomitrium brevisetum Lindb. nsp. Sachalin, Dui Aug 1861 Glehn" – H-SOLindberg!; isolectotypes: BM!, PC!; syntype: "Rhacomitrium brevisetum n. sp. Lindb. o, fr. Sachalin, pr. Lamoricière, med. Julii 1860 F. Schmidt." – H-SOLindberg!]. Racomitrium fasciculare (Hedw.) Brid. var. orientale Cardot, Bull. Herb. Boissier Sér. 2, 8: 334. 1908. = R. orientale (Cardot) Sakurai, Bot. Mag. Tokyo 51: 109. 1937. - TYPE CITATION: Japon: Iwagisan (n. 321); Ichifusa (n. 1407); Miyadzu (n. 1532); Kattasan, à 1900 m. (n. 2594); Iwakisan (n. 2640); Ubayu, à 1500 m. (n. 2837); Hakkoda, à pierres et rochers à 1100 m. (n. 2917, 2923, 2955); Jizogatake, à 2000 m. (n. 2383, 2384, 2520, 2538); Ochiai (n. 3025); Ontake, troncs de conifères, à 2300 m. (3305); Komagatake, à 2400 m. (n. 3385); Norikusa, troncs de conifères, à 2000 m. (n. 3392). Corée: Ouen-San (n. 23, rapportée à tort au R. varium; n. 183); île Quelpaert, à 2000 m. (n. 604, 624). [Lectotype (selected here): "Herbarium of Edwin B. Bartram Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. orientale Card. sp. nova. Japon: Jizogatake. Leg. Faurie, 1903. nº 2384" - FH-Bartram!; syntypes: (1) "Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. orientale Card. (e specim. origin.) Japon: Ochiai. Leg. Faurie, 1904. nº 3025." - NY!, s-Roth!; (2) "Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. orientale Card. Japon: Iwagisan. Leg. Faurie, nº 321 (ser. 2)." - PC!; (3) "Herb. J. Cardot. Rhacomitrium varium L. & J. fasciculare Brid. var. orientale Card. forma epilosa Corée: Ouen-San. Aout 1901. Leg. Faurie, nº 23." – PC! = Codriophorus anomodontoides!; (4) "Herb. J. Cardot. R. fasciculare Brid. var. orientale Card. nov. var. Japon: Hakkoda, 1100 m. Leg. Faurie, 1904, nº 2917." - PC! = Codriophorus anomodontoides!], syn. nov.

R. sawadae Cardot, Bull. Soc. Bot. Genève Sér. 2, 1: 122. 1909 ['sawadai']. — TYPE CITATION: Japon: mont Hayachine (Sawada). [Lecto-type (*selected here*): "No. 90. Racomitrium Sawadai Cardot. sp. nov. Mt Hayachine. June 16. 1906. K. Sawada." – TNS!], *syn. nov.*

R. papillosum Sakurai, Bot. Mag. Tokyo 51: 108, *f. 67A–B.* 1937, *hom. illeg.* [*non* Kindb. 1881]. \equiv *R. frigidum* Sakurai, Musc. Jap.: 64. 1954. — TYPE CITATION: Honshiu: Prov. Shimotsuke. Berg Akanagi (Leg. K. Sakurai Nr. 850 Typus Aug. 1922). [Holotype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai. 850. Rh. papillos. Mt Akanagi, Nikko City, Tochigi Pref., leg. Kyuichi Sakurai, 18.8.1922" – MAK-Sakurai!; isotype: H-Brotherus!], *syn. nov.*

R. hypnoides Lindb. fo. *chrysophyllum* Sakurai, Bot. Mag. Tokyo 51: 136. 1937. — TYPE CITATION: Hokkaido: Prov. Ishikari, Berg Daisetsu, in alpiner Lage (Leg. M. Tsujibe in Herb. K. Sakurai Nr. 9224 Juli 1936). [Lectotype (*selected here*): Entirely epilose mixed with piliferous plants of *Racomitrium lanuginosum* in the envelope bearing the label "Makino Herbarium. Herb. Dr. K. Sakurai Nr. 9224 Rh, hypnoides, var. chrysophyllum Sak. var. Typus. Mt. Daisetsu, Kawakami-gun, Hokkaido, leg. Masanobu Tsujibe" – MAK-Sakurai!], *syn. nov.*

R. canescens (Hedw.) Brid. var. *yezoalpinum* Sakurai, Bot. Mag. Tokyo 51: 141. 1937 ['yezo-alpinum']. – TYPE CITATION: Hokkaido: prov. Ishikari, Berg Daisetsu, in alpiner Lage (Leg. M. Tsujibe in Herb. K. Sakurai Nr. 9217, Nr. 9229 Juli 1936). [Lectotype (*selected here*): "Makino Herbarium. Herb. Dr. K. Sakurai. Nr. 9217. Rh. canescens var.<u>Tsuibei</u> yezo-alpinum Sak. (Typus) Mt. Daisetsu, Kawakami-gun, Hokkaido, leg. Masanobu Tsujibe, 1936.7.14" – MAK-Sakurai!], *syn. nov.*

R. fasciculare var. hayachinense Nog., J. Hattori Bot. Lab. 38: 356, *f. 7.22–29.* 1974. — TYPE CITATION: [Japan] Honshu. Iwate Pref., Mt. Hayachine, summit, Oct. 1954, leg. K. Hosoi, herb. Nog. 65522. [Holotype: NICH, not found; lectotype (*selected here*): [icon in] Noguchi (1974): *f. 7.22–29.*], *syn. nov.*

Plants small to medium-sized, usually relatively gracile, sometimes coarser, rather stiff and rigid, in dull, dense or loose tufts or patches, yellow- or olive-green, yellow-brown, yellow, green, sometimes golden-brown to golden with a rusty tinge above, brown, blackish-brown to blackish below, sometimes brown, blackish-brown or blackish throughout. *Stems* erect to ascending,

(1.0-)3.0-5.5(-8.5) cm long, sparsely fasciculate-branched to freely and irregularly branched, occasionally almost unbranched or subpinnately branched, without or sometimes with a few short, tuft-like lateral branchlets, in transverse section circular, lacking a central strand, with 6-8 layers of large, yellowish-hyaline, thick-walled medullary cells and a 3-4-layered cortex of small stereid cells with small lumina and brown, incrassate walls; rhizoids mostly sparse at the base or scattered in clusters in the lower part of the stem, reddish-brown, branching, smooth, lustrous; axillary hairs short, filiform, composed of 7-9 cells, with 1-2 short, quadrate, brownish basal cells and hyaline, elongate median and distal cells. Leaves crowded, straight, lanceolate to narrowly lanceolate, loosely erect-appressed to erecto-patent, sometimes subsecund when dry, erect-spreading to spreading when wet, 2-3 mm long, 0.6-0.8(-0.9) mm wide, from a lanceolate or oblong- to ovate-lanceolate, fairly narrowly canaliculate-concave, non-plicate base gradually tapering to a narrow or broader, canaliculate acumen, acute to narrowly rounded-obtuse, epilose, sinuose-denticulate, papillose-crenulate or notched-serrate apex; margins narrowly to broadly recurved on both sides from the base almost to the apex, occasionally to 5% of the way up the leaf, entire except for the apex, bistratose in 1-2(-3) rows of cells and forming bulging thickenings in the distal half or rarely extending nearly to the base on one or both sides, less often with extensive unistratose patches on one or both sides distally or entirely unistratose throughout; costa single, yellowish-brown, sharply delimited from the laminal cells, occasionally imperceptibly merging with the bistratose laminal cells and less distinct at the apex, 60-75(-85) µm wide at the base, gradually tapering upwards, ending at least 3/4 of the way up the leaf to subpercurrent, entire throughout or very seldom with occasional spurs above, situated at the bottom of a fairly shallow, wide-angled groove, in transverse section bistratose almost throughout with occasional tristratose patches at the extreme base, flat on the ventral side, not prominently convex, lunate to flattened on the dorsal side, with ventral and dorsal cells of similar size, 2-3 above, 3-4 in mid-leaf, and 4-7 below; laminal cells unistratose throughout, except for the bistratose margins or, occasionally, variously bistratose near the apex, with thick and sinuose walls, transparent, shortly rectangular to isodiametric, quadrate, irregularly angular to transversely rectangular, 5–15 µm long, 7-8 µm wide, becoming elongate in mid-leaf and below, (12-)15-20(-25) µm long, 7-8 µm wide, and long-rectangular at the base, (17-)25-35(-50) µm long, $7-9 \,\mu\text{m}$ wide, longer and wider at and above the insertion, 35-50 µm long, 7-12 µm wide, with strongly thickened, nodulose and porose walls, forming a distinct, yellowbrown strip of 2–3 layers of cells along the insertion; *alar cells* quadrate to short-rectangular, with sinuose or straight, moderately thickened walls, forming flat, rather indistinct, not or shortly decurrent auricles; supra-alar cells quadrate to short-rectangular, 10-27 µm long, (5-)7-10(-12) µm wide, mostly straight- walled, forming pellucid marginal borders composed of (8-)10-20(-27) cells, occasionally

with a second shorter row of about 8 cells, sometimes basal marginal border indistinct, consisting of 3-10 subquadrate cells with thick and sinuose walls. Dioicous. Perigonia gemmiform, to 2 mm long; outer perigonial bracts lanceolate, to 2 mm long, similar to the vegetative leaves; inner perigonial bracts oblong-ovate to oblonglanceolate, short-acuminate, with a narrow, subpercurrent costa; innermost perigonial bracts broadly ovate, abruptly acute, deeply concave, with 15-20 pale brown antheridia intermixed with a few filiform, pale yellowish-brown paraphyses, reaching half the length of the antheridia. Outer and median perichaetial leaves lanceolate, similar to the cauline leaves, 1.8-2.6 mm long, 0.9-1.0 mm wide, with a thin, subpercurrent costa; innermost perichaetial leaves oblong, to 2 mm long, 0.8 mm wide, hyaline throughout or sometimes with a few thicker-walled, chlorophyllous cells at the extreme tip, exceptionally with chlorophyllous distal cells. Setae single per perichaetium or occasionally geminate, straight, exserted, (2-)4-6(-8) mm long, brown, smooth, twisted once to the left immediately below the urn, dextrorse below; vaginula dark brown, to 1 mm long, with thick- and longitudinally sinuose-walled epidermal cells. Capsules erect, straight, ovoid, obloid to obloid-cylindrical, gradually or abruptly narrowed to the seta, (1.0-)1.2-1.5(-2.0) mm long, 0.7-0.8 mm wide, light to dark brown, lustrous, fairly leptodermous; operculum long-rostrate, with a straight rostrum, nearly as long as the urn; annulus separating, 2-3-seriate, consisting of yellow- or reddish-brown, vesiculose cells with strongly incrassate walls; exothecial cells mostly oblong or rectangular, mixed with irregular, $(20-)25-55(-60) \mu m$ long, (10-)15-25(-35) µm wide, thin- to firm-walled, becoming shorter, dark brown in 2-3 tiers at the mouth; stomata 6–16 at the neck of the urn, arranged in 2–3 rows, ca 25 µm wide, superficial, bicellular, with rounded pori; peristome teeth 16, lanceolate, 350-450(-580) µm long, reddish-brown, cleft nearly to the base into 2 filiform branches, with a short basal membrane, 40-50 µm tall, densely low papillose throughout; preperistome distinct, narrow, 3-4 rows of cells high. Spores spherical, pale brownish, finely papillose, (10-)13-15(-18) μm in diameter. Calyptra conical-mitrate, about 1.5 mm long, lobed at the base, light to dark brown and distinctly roughened at the tip, non-plicate, naked.

Etymology — The specific name refers to the short setae and is derived from the Latin *brevis* = short and *seta* = the stalk which supports the fruit in mosses.

Diagnostic characters and differentiation — Codriophorus brevisetus has not been universally recognised as a species in its own right and quite often it has been considered merely a variety, var. brachyphyllum, within the broadly circumscribed Racomitrium fasciculare (Cardot 1908a; Noguchi 1974, 1988). On the other hand, in recent Chinese taxonomic treatments C. brevisetus has been accepted as a distinct species (Cao 2000; Cao et al. 1998, 2003). Notwithstanding its taxonomic status, C. brevisetus has been one of the most confused and poorly understood taxa within the genus as is evidenced by great number of misdetermined specimens, not only as other species of the genus Codriophorus itself, but also as some species of the genera Bucklandiella, Racomitrium and Niphotrichum. The main cause was lack of care in examining the original type collections of the taxa concerned and attaching great importance in their evaluation to such characters as the branching pattern and leaf shape, which are of less taxonomic value, and underestimating some stable structural characters of the costa, leaf margins, apex, and areolation which appear to be of great taxonomic importance. In addition, in the absence of a precise definition of C. fascicularis, the central species of this complex, it was impossible to describe accurately the taxonomic concept of the satellite taxa and to establish the true status of numerous taxa described by Lindberg (1872), Macoun & Kindberg (1892), Kindberg (1893, 1896), Bescherelle (1894), Cardot (1908a, 1909), Brotherus (1927), Sakurai 1937a, b, 1939, 1942, 1954) and Noguchi (1974) from East Asia and the Pacific region. Lectotypification of C. fascicularis (Bednarek-Ochyra & Ochyra 2005) made possible the exact circumscription of this core species of sect. Fascicularia and subsect. Fasciformes and a redefinition of other species in this complex.

As presently conceived, Codriophorus brevisetus is characterised as follows: (1) plants generally small and slender; (2) stems erect or ascending, variously branching but, with a few exceptions, lacking short, lateral, tuftlike branchlets; (3) leaves loosely erect-appressed to erecto-patent on drying, lanceolate, gradually acuminate, straight, narrowly canaliculate above, canaliculate-concave below, non-plicate, not or slightly decurrent; (4) *leaf apex always lacking a hair-point*, acute to narrowly rounded-obtuse, sinuose-denticulate, papillose-crenulate or notched-serrate; (5) margins variously recurved on both sides from the base almost to the apex, mostly bistratose distally in 1-2(-5) rows of cells and forming bulging marginal thickenings, frequently extending nearly to the base as a uniseriate thickening, rarely with extensive unistratose patches to entirely unistratose throughout; (6) costa extending to three quarters of the leaf length or subpercurrent, bistratose throughout, except for some tristratose spots at the base, flat on the ventral side, lunate to flattened and scarcely convex on the dorsal side; (7) laminal cells unistratose throughout, except for the

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FIGURE 81. Codriophorus brevisetus. — 1. Habit. 2. Portion of branch, dry. 3. Portion of stem section. 4–6. Axillary hairs. 7–18. Leaves. 19–23. Leaf apices. 24. Upper leaf cells at margin. 25. Mid-leaf cells. 26–28. Alar and supra-basal leaf cells. 29. Basal juxtacostal cells. — [1–2 from *Deguchi 12436*, HIRO; 3 from *Vorobjev 56*, KRAM; 4–6, 19 from *Alanko 32059*, H; 7–8, 23 from *Faurie 2384*, FH (lectotype of *Racomitrium fasciculare var. orientale*); 9–11 from *Gao & Chang 9212* (ALTA); 12–14, 21–22, 24–25, 28–29 from *Glehn s.n.*, H (lectotype of *Racomitrium brevisetum*); 15–16, 20 from *Faurie 3025*, s (syntype of *Racomitrium fasciculare var. orientale*); 17 from *Hattori 389* (H); 18 from *Deguchi 12614* (HIRO); 26–27 from unknown collector, MAK-B57636)]. — Scale bars: a – 1 cm (2); b – 1 cm (1) and 2 mm (7–18); c – 100 µm (3, 19–29); d – 100 µm (4–6).



margins, very rarely bistratose near the apex, quadrate to short-rectangular above, elongate in mid-leaf and at the base; (8) angular cells consisting of a dozen or so quadrate to short-rectangular cells with straight or sinuose walls, forming a scarcely differentiated, weakly decurrent group; (9) supra-alar cells usually forming a pellucid marginal border, composed of (8-)10-20(-27) straight-walled cells, occasionally the marginal border scarcely distinct; (10) innermost perichaetial leaves oblong and hyaline throughout, only sometimes with a few chlorophyllous apical cells and exceptionally with an areolation of chlorophyllous cells in the whole distal portion of the bracts; (11) setae short, (2-)4-6(-8) mm long, twisted once to the left immediately below the urn and to the right below; (12) capsules small, ovoid, obloid to obloid-cylindrical, (1.0-)1.2-1.5(-2.0) mm long; (13) peristome teeth fairly short, 350-450(-580) µm long, with or without a low basal membrane, split nearly to the base into two filamentous branches, papillose throughout.

Codriophorus brevisetus can be correctly and faultlessly identified by the combination of the following three essential diagnostic characters, namely (1) the long costa, usually vanishing below the apex or extending to at least three quarters of the leaf length, in transverse section flat on the ventral side; (2) epilose, dentate, serrate, cristate or papillose-crenate leaf apex; and (3) short, isodiametric to shortly rectangular distal leaf cells. A very important and helpful auxilliary character enabling recognition of C. brevisetus is the bistratosity of the leaf margins which is really unique in sect. Fascicularia. It is found only in C. brevisetus although occasional bistratose spots are known in just a very few plants of C. fascicularis. Although the bistratosity of the leaf margins is very variable in this species, all plants with variously bistratose leaf margins clearly belong within C. brevisetus. Plants with entirely unistratose leaf margins are also included in this species on the basis of the combination of costa length, form of the leaf apex and areolation of the distal laminal cells. In general, the combination of the aforementioned characters is unknown in any other species of subsect. Fasciformes and should ensure the safe recognition of C. brevisetus.

Codriophorus fascicularis shares with C. brevisetus a long and subpercurrent costa but is at once distinct in its entire leaf apex, entirely unistratose leaf margins and elongate upper laminal cells. C. anomodontoides is similar to C. brevisetus in having a dentate and cristate leaf apex, but it differs immediately in having unistratose leaf margins, elongate cells throughout the leaf lamina, and costae ending $\frac{3}{4}$ of the way up the leaf that are distinctly convex on the ventral side. Finally, C. corrugatus has a similar dentate-cristate to denticulate leaf apex but, when typically developed, is very distinct from C. brevisetus in its corrugate and wavy leaf acumen. In addition, its shoots often have a nodose appearance due to the common presence of short, tuft-like lateral branchlets and the costa vanishes mostly in mid-leaf.

Sakurai (1937*a*) confused *Codriophorus brevisetus* with *C. carinatus* and considered them to be conspecific

taxa, the former having priority. Indeed the two species are likely to be confused since they share lanceolate leaves, short and isodiametric upper laminal cells and often bistratose leaf margins. However, the leaves in *C. carinatus* are usually terminated with a short, hyaline and denticulate leaf tip and the costa is strongly convex on the dorsal surface, 2–3-stratose in the lower half with a distinct stereid band on the dorsal side and markedly enlarged ventral epidermal cells.

Confusion of *Codriophorus brevisetus* (and any other species of this genus) with species of other segregates of the former genus *Racomitrium* is in practice impossible if the specimens are carefully studied microscopically. The genus *Bucklandiella* is diagnosed by its smooth or pseudopapillose laminal cells and this character markedly contrasts with the papillose laminal cells with character-istic large and flat papillae covering nearly the whole cell lumina in *Codriophorus*. Nonetheless, even in the recently published *Moss Flora of China* (Cao *et al.* 2003), some specimens determined as *C. brevisetus* evidently represent species of *Bucklandiella*, namely *B. nitidula* (Cardot) Bednarek-Ochyra & Ochyra (*Gao & Zhang 9212*, KRAM) and *B. subsecunda* (Hook. & Grev.) Bednarek-Ochyra & Ochyra (*Gao et al.* 19369, ALTA).

Sakurai (1937b) described from Japan *Racomitrium* canescens var. yezoalpinum and this variety evidently fits the concept of *C. brevisetus*. Nonetheless *R. canescens* itself is now classified in the genus *Niphotrichum* which is distinct from all other genera of the Racomitrioideae, among others, in having tall conical papillae situated over the cell lumina which markedly contrast with large and flat papillae in *Codriophorus* distributed primarily over the cell walls and lateral parts of the lumina.

Codriophorus shares a similar papillosity of the laminal cells with Racomitrium but the latter is at once distinct in its leaves having long, strongly papillose, eroso-dentate and hyaline hair-points. In some stunted and depauperate plants the hair-point may sometimes be reduced and this may pose some identification problems. They can be safely distinguished on the anatomical structure of the costa which in the median and lower parts have markedly larger ventral epidermal cells and a 2-3-stratose dorsal band of much smaller, stereid cells. Sakurai (1937b) described from Japan Racomitrium hypnoides (= R. lanuginosum) fo. chrysophyllum which was considered to be identical to R. fasciculare var. fasciculare by Noguchi (1974). The type material consists of a mixture of true Racomitrium lanuginosum with piliferous leaves and Codriophorus brevisetus with epilose leaves. Putting to one side the leaf apex, the plants of the two species in this collection share a quite similar habit and the same slightly yellow colour of the leaves which is the only diagnostic character stressed by Sakurai (1937b) in the protologue. In order to retain the hitherto existing synonymy proposed by Noguchi (1974), the epilose plants which represent C. brevisetus are here selected as the lectotype of this form name.

Variability — *Codriophorus brevisetus* is one of the most variable species within the genus and it is this which



FIGURE 82. *Codriophorus brevisetus.* — 1–8. Transverse sections of costa and leaves, sequentially from base to apex. — [1 from unknown collector (MAK-B57640); 2 from *Gao & Chang 9212* (ALTA); 3 from *Faurie 3025*, s (syntype of *Racomitrium fasciculare* var. *orientale*); 4 from *Alanko 32059* (H); 5 from *Hattori 389* (H); 6 from *Glehn s.n.*, H (lectotype of *Racomitrium brevisetum*); 7 from *Faurie 2384*, FH – lectotype of *Racomitrium fasciculare* var. *orientale*; 8 from *Hasegawa s.n.*, 10 Aug 1954, H].]. — Scale bar: 100 µm.

has probably caused so much confusion and hindered its correct interpretation and circumscription. Additionally the problems have been compounded by a lack of care when examining the relevant type collections of the taxa concerned. The plants of C. brevisetus exhibit a quite remarkable morphological plasticity with regard to size, robustness, colour and branching pattern, all of which are certainly induced by environmental conditions. Most plants are gracile and small, 3-4 cm long but, occasionally, some are fairly robust and coarser, reaching to 8.5 cm (e.g., Higuchi 2711, MAK). Most are freely and irregularly branched, although some, especially those growing in compact tufts, are almost unbranched (e.g., Deguchi s.n., HIRO-12614; Uematsu 601, H). Short, lateral branchlets are absent in the vast majority of populations of C. brevisetus and they have been observed in only a very few plants (e.g., Shcherbakov s.n., 24 Sep 1947, KRAM, LE). Likewise, the coloration of the plants is subject to considerable variation, although plants green, yellow and yellow-green in the upper part definitely predominate. Rarely the plants are golden-brown or golden with a rusty hue (e.g., Sakurai 9224, MAK, type of Racomitrium hypnoides fo. chrysophyllum).

Of the structural characters of Codriophorus brevisetus, the stratosity of the leaf margins appears to be the most variable and it ranges between two extremes. In most populations examined (85–90%) they are variously bistratose in 1-2 rows of cells on one or both sides from the leaf apex nearly to the base, forming distinctly bulging thickenings. Such a phenotype is represented by the type of the species from Sakhalin (Fig. 82.6). At the opposite extreme the leaf margins may be entirely unistratose throughout and such phenotypes are represented, for example, by the type of *Racomitrium fasciculare* var. orientale (Fig. 82.7). These extremes are linked by numerous intermediates which differ from one another in the extent of the unistratose patches. Also, on the same plant it is possible to find leaves with perfectly unistratose margins and others with variously bistratose ones.

The leaf areolation is relatively stable in *Codriophorus brevisetus*, especially in the distal part, and therefore the cell size in this part of the leaf is of great importance as a diagnostic character. The cells are uniformly short, $8-15 \mu m$ long, and are the shortest in sect. *Fascicularia*. Their size is often decisive for the determination of some critical specimens if other diagnostic characters, especially the length of the costa, are difficult to interpret. The laminal cells are consistently unistratose throughout, except for those on the margins. Very rarely, in two populations from Japan and China, they are variously bistratose in the

distal half, especially near the apex (unknown collector, MAK-B57640; *Gao & Chang 9212*, ALTA) (Fig. 82.1–2).

The length of the costa is also somewhat variable in *Codriophorus brevisetus*. In general (in 95% of plants examined) it was subpercurrent and ended a few cells below the apex or vanished $\frac{3}{4}$ of the way up the leaf. Very seldom, in some leaves, the costa ceased at two thirds of the leaf length or somewhat below, but never below mid-leaf, and in this respect the leaves resembled those of *C. corrugatus* and *C. anomodontoides*. However, in other leaves the costa extended much higher way up the leaf and this character coupled with the leaf areolation of short distal cells clearly suggested that the true identity of such plants was *C. brevisetus*.

Although *Codriophorus brevisetus* produces sporophytes in great abundance, it varies only little in sporophyte characters. Some variation was observed in seta length and in the shape and size of the capsule but generally this variation was within limits typical for other species of the genus. One remarkable deviation was observed in the form of the innermost perichaetial leaves. These were hyaline throughout in all plants, occasionally with a few thicker-walled chlorophyllous cells at the extreme tip, but in a single specimen from Kamchatka (*Czernyadjeva 26*, KRAM, LE) the innermost perichaetial leaves were chlorophyllous almost throughout, with areolation similar to that on the vegetative leaves.

Reproduction — Codriophorus brevisetus is a very prolific species and commonly produces sporophytes in great profusion. Over 90% of specimens examined during the present work proved to be fertile.

Taxonomic and nomenclatural notes — Codriophorus brevisetus was described by Lindberg (1872) as Racomitrium brevisetum from two specimens collected on Sakhalin in the Far East. This author showed the close affinity of his new species to C. fascicularis, although in habit it was similar to Bucklandiella microcarpa. For a long time C. brevisetus remained a poorly known and obscure species. Sakurai (1937a) reported it from Hokkaido and Honshu in Japan and considered Racomitrium carinatum (\equiv Codriophorus carinatus), a species described by Cardot (1909) from Korea, to be conspecific with it. C. brevisetus was accepted by Savicz-Ljubitskaya & Smirnova (1970) in the Flora of the acrocarpous mosses of the Soviet Union, but without taxonomic discussion.

Noguchi (1974) reduced *Racomitrium brevisetum* to synonymy with *R. fasciculare* var. *brachyphyllum*, along with *R. nipponicum* and *R. papillosum*. The concept of

FIGURE 83. *Codriophorus brevisetus.* — 1. Portion of branch with mature capsule, wet. 2. Perigonium. 3. Innermost perigonial bract and antheridia. 4. Inner perigonial bract. 5. Outer perigonial bract. 6–9. Perichaetial leaves, a sequence from outermost to innermost. 10–12. Apices of innermost perichaetial leaves. 13. Epidermal cells of vaginula. 14. Transverse section of seta. 15. Capsule with calyptra, wet. 16. Capsule with operculum, wet. 17–18. Deoperculate capsules with well-developed peristome, wet. 19–23. Deoperculate capsules with peristomes destroyed, wet. 24. Calyptra. 25. Transverse section of calyptra. 26. Exothecial cells at base of urn and stomata. 27. Exothecial cells in mid-urn. 28. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 24 from *Deguchi 12436*, HIRO; 2–5 from *Alanko 32059*, H; 6–11 from *Glehn s.n.*, H (lectotype of *Racomitrium brevisetum*); 13–14 from *Voroblev 56*, PR; 12, 5–18, 26–28 from *Czernyadjeva 26*, KRAM; 19–23 from *Deguchi 12085*, HIRO]. — Scale bars: a – 100 µm (14), 200 µm (28) and 2 mm (2); b – 0.25 cm (1) and 2 mm (15–24); c – 100 µm (10–13, 25) and 1 mm (3–9); d – 100 µm (26–27).



this taxon presented by Noguchi (1974) is quite obscure because in its circumscription he mostly referred to the size and branching of the plants and the leaf shape. This variety was described by Cardot (1908a) from five specimens from Korea. Of these, only two syntypes have been located and examined and both represent Codriophorus anomodontoides as evidenced by the anatomical structure of the costa which is clearly convex on the ventral side. Also having the same status is Racomitrium nipponicum which was placed by Noguchi (1974) in synonymy with Racomitrium fasciculare var. brachyphyllum. On the other hand, the third synonymous name of the latter varietal name, R. papillosum, is correctly a synonym of Codriophorus brevisetus, although Noguchi (1974) introduced here some confusion. R. papillosum was described by Sakurai (1937a) but this name proved to be a younger homonym of R. papillosum of Kindberg (in Warnstorf 1881). Therefore, Sakurai (1954) replaced it by R. frigidum and Noguchi (1974) placed this homotypic name in synonymy with *Racomitrium fasciculare* var. *fasciculare*.

Additionally, Noguchi (1974) described a new variety, *Racomitrium fasciculare* var. *hayachinense*, which was diagnosed by having bistratose leaf margins in the upper part. Unfortunately, the holotype of this varietal name has not been located at NICH and is probably lost, but the description and a good illustration, here selected as lectotype under Art. 9.2 of the Code (Greuter *et al.* 2000), clearly indicate that this variety is identical to *Codriophorus brevisetus*. Interestingly, the type locality of this variety is situated on Mt Hayachine in Iwate Prefecture on Honshu from whence Cardot (1909) described *Racomitrium sawadae*. Although Noguchi (1974) considered this species to be conspecific with *R. fasciculare* var. *atroviride*, it is actually identical to *Codriophorus brevisetus*.

Apart from the synonyms of Codriophorus brevisetus discussed above, three additional new synonyms of this name are proposed here. Racomitrium fasciculare var. orientale was described by Cardot (1908a) on the basis of specimens from Japan and Korea and Sakurai (1937a) raised it subsequently to species rank. In total, 21 specimens are cited in the protologue, only five of which have been located during the course of the present study. Two of them represent C. anomodontoides and the other three C. brevisetus. Cardot (1908a) described this variety as very polymorphous, but in his brief description he stated that it was characterised by having exceptionally short upper laminal cells and this character is diagnostic for C. brevisetus, not C. anomodontoides. Because the specimen from Ochiai situated south-west of Otaru city in Shiribeshi Prefecture best fits the description of the variety, it is here selected as lectotype. It represents a typical expression of C. brevisetus, automatically making Racomitrium fascicu*lare* var. *orientale* a synonym of this name.

The identity of the other two taxa, *Racomitrium canescens* var. *yezoalpinum* and *R. hypnoides* fo. *chrysophyllum*, described by Sakurai (1937b) are briefly discussed above in the "Diagnostic characters and differentiation" section (p. 198) and their names complement a list of synonyms of *Codriophorus brevisetus*.

Chromosome number --- Not available.

Habitat — The habitat data for *Codriophorus brevisetus* available on the herbarium labels are scanty and not very informative and therefore prevent a detailed ecological characterisation of the species from being made. They indicate that it is a saxicolous species associated with moist or wet habitats. It grows on boulders and stones on the banks of rivers and streams, on cliffs, and on soil and stony ground in montane tundra. In volcanic areas on Kamchatka *C. brevisetus* has been found on boulders at the edge of fumaroles.

Geographical distribution — Codriophorus brevisetus is a Far East Asian species (Fig. 84). It has maximum occurrence in Japan where it occurs in the mountains from Hokkaido to Honshu, mostly at elevations of 1000-2600 m, rarely descending to 400-800 m. In mainland Asia it is scattered in the Russian Far East, ranging from the Southern Primorye through to the Kuril Islands, Khabarovsk Territory and Sakhalin northward to southern Kamchatka, occurring at elevations of 590-1550 m. In addition, it is known from a single locality in north-easternmost China in Heilongjiang Province. Cao et al. (2003) indicate C. brevisetus to be more frequent in south-east and north central China. Alas, the specimens from the Chinese herbaria at IFSBH and SHM have not been available for investigation, while of four specimens which have been located in foreign herbaria, two were misnamings of Bucklandiella nitidula and B. subsecunda (see above in the "Diagnostic characters and differentiation" section, p. 196), one was Codriophorus anomodontoides (Hong & Liu 179, ALTA), and only one (Gao & Zhang 9212, ALTA) was correctly determined.

Racomitrium brevisetum has once been reported from Ellesmere Island in the Canadian Arctic Archipelago (Bryhn 1906; Steere 1947*b*) but the voucher material proved to be *Orthotrichum killiasii* Müll.Hal. (Persson 1947).

SPECIMENS EXAMINED

ASIA. CHINA. HEILONGJIANG PROV. Ning-an Co.: Da-hai-lin, Gao & Zhang 9212 (ALTA).

JAPAN. HOKKAIDO Abashiri Pref .: Mt Shari, Kamishari-mura, Shari-gun, 650 m, Deguchi s.n. (HIRO-12491). Ishikari Pref.: Ibari, Mt Eniwa, Takachi 2099 (H). Kamikawa Pref.: Mt Hokkai - Mt Haku'un, Kamikawa-cho, Kamikawa-gun, 2100 m, Deguchi s.n. (HIRO-12244); Mt Daisetsu, Kawakami-gun, 14 Jul 1936, Tsujibe s.n. (MAK- lectotype of Racomitrium canescens var. yezoalpinum) and 14 Jul 1936, Tsujibe s.n. (MAK - lectotype of Racomitrium hypnoides fo. chrysophyllum). Shiribeshi Pref .: Mt Yôtei, Kutchan, Abuta-gun, 1800 m, Deguchi s.n. (HIRO-12614); Ochiai (SW of Otaru city), Faurie 3025 (NY, s - syntype of Racomitrium fasciculare var. orientale). Sôya Pref.: Mt Rebun, Rebun-cho, Rebun-gun, Rebun I., 680 m, Deguchi s.n. (HIRO-11999) and 400 m, Deguchi s.n. (HIRO-11991); Mt Rishiri, Higashi-Rishiri-cho, Rishiri-gun, 560 m, Deguchi s.n. (HIRO-12083) and 670 m, Deguchi s.n. (HIRO-12085); Rishiri I., Mt Rishiri, 1400 m, Hasegawa 15901 (H). Tokachi Pref.: near Tomuraushi spa, Shintoku-cho, Kamikawa-gun, 500 m, Deguchi s.n. (HIRO-11862); Mt Haku'un, lakeside of Shikaribetsu, Shikaoi-cho, Kato-gun, 1000 m, Deguchi s.n. (HIRO-12442) and 800 m, Deguchi s.n. (HIRO-12436). HONSHU. Aomori Pref.: Hakkoda, Faurie 311 (PC) and 13 Aug 1897, Faurie s.n. (PC); Mt Hakkoda, ca



FIGURE 84. Global distribution of Codriophorus brevisetus. Inadequately localised stations are indicated by asterisks.

1200 m, 3 Aug 1954, *Noguchi s.n.* (WTU) and Jul 1934, *Sato s.n.* (MAK-B6994); Iwagisan (= Mt Iwaki), *Faurie 321* (PC – syntype of *Racomitrium fasciculare* var. *orientale*). *Fukushima Pref.*: Mt Azuma, *Higuchi s.n.* (MAK-B57684) & *2711* (MAK); Mt Adatara, 1700 m, *Watanabe 1633* (NICH). *Gifu Pref.*: Mt Ontake, trail to Sennin-taki, *ca* 1850 m, *Iwatsuki & Smith J-543* (NY); Mt Ontake, via Hidasan-cho, Sannoike Pond, Marishiten Peak, Sainokawara, Ninoike Pond, *Iwatsuki & Smith J-503* (NY). *Gunma Pref.*: Mt Tanigawa, July 1956, *Inoue s.n.* (TNS); Oze, Tone-gun, *Narita s.n.* (MAK-B20414); Oshimizu-goya – Ozenuma, Katashina-mura, Tone-gun, *Sakurai s.n.* (MAK-B57635). *Ishikawa Pref.*: Shiramine-mura,

"Shakashindo", Mt Hakusan, Akiyama 3626 (KYO). Iwate Pref.: Nodamura, Kunohe-gun, Murai s.n. (MAK-B57609); Mt Ganju (= Mt Iwate), Uematsu 281 (H); Mt Iwate, 27 Jul 1927, Toba s.n. (H); Mt Ikawa (= Ikawa town near Ofunato city), Uematsu 86 (H); Mt Hayachine, Sawada 90 (TNS – lectotype of Racomitrium sawadae). Miyagi Pref.: Mt Katta, Uematsu 877 (H) & 1069 (H); Matsushima (Sendai city), Hattori 389 (H); Mt Omae, Rikuzen, 7 Jun 1908, Jishiba s.n. (BM) & 722 (H); Omaetake, Rikuzen, Uematsu 589A & 601 (H). Nagano Pref.: Mt Ontake, Tonohara, 2200 m, Manago 206 (NICH); Mt Ontake, Okamura 911 (H); Mt Yatsugatake, Sasaoka 3701 (H, MICH); Shinano, Mt Yatsugatake, Uematsu 741 (H) & 736 (H); Mt Ootenjo-dake, Minamiazumi-gun, Sugiuchi s.n. (MAK-B57636); Nishihodakasawa, Kamikochi, Minamiazumigun, sine collector (MAK-B57747); Mt Yoko-dake, Mt Yatsugatake, sine collector (MAK-B57681); Mt Hakuba, Kitaazumi-gun, Sakurai s.n. (MAK-B893); foot of Mt Kirigamine, Suwa-gun, Takaki s.n. (MAK-B57623); Mt Kinpuzan, Sasaoka 5348 (BM); Mt Togakushi, Kamiya 163 (H); Mt Tsubakuro - Mt Otensho, Hotaka-cho, Minami-azumi-gun, 2600 m, Deguchi s.n. (HIRO-12897); Mt Surikogi-yama, Iida city, 2100 m, Nishimura s.n. (HIRO-5649 & 5621); Mt Shirouma, Takaki s.n. (MAK-B16372). Nara Pref .: en route from Yôjigayado mountain hut to Zenki, Yoshino-gun, 1790 m, Deguchi s.n. (HIRO-6776). Niigata Pref.: Mt Iide, Higashikanbara-gun, Sakurai s.n. (MAK-B57640 & B57641); Mt lide-san, Yama-gun, Ikegami s.n. (MAK-B57688). Saitama Pref .: Chichibu-gun, Mt Kobushi, 2280 m, Jinno s.n. (HIRO-14700) and 2480 m, Jinno s.n. (HIRO-14693); Chichibu, 2300 m, Nagano 4319 (NICH). Shimane Pref.: Fusigama (= Ushigama), Aug 1888, Miyoshi s.n. (H). Shizouka Pref./Nagano Pref.: Mt Akaishidake, Takaki s.n. (MAK-B57752). Tochigi Pref.: Nikko, Kamiji 127 (F, FH) and June 1898, Faurie s.n. (PC); Nikko, Mt Shirane, Gono 62 (H) & 64 (H); Yumoto, Nikko City, Tsujibe (MAK-B7472); Nikko City, Osada s.n. (MAK-B6080); Mt Nantaizan, Bisset 39 (BM); Mt Nyobo (Mt Nyoho), Iishiba 929 (H); Mt Akanagi, Nikko City, 18 Aug 1922, Sakurai s.n. (H, MAK - isotype of Racomitrium papillosum). Yamagata Pref.: Mt Gassan, ca 1750 m, 6 Oct 1955, Yuhki s.n. (WTU); Mt Gassan, Midagahara, 4 Oct 1971, Arakane s.n. (WTU); Yamagata City, Mt Zao, Ikegami s.n. (MAK-B57742); Mt Tsao (=Mt Zao), Oct 1907, Jishiba s.n. (w). Yamanashi Pref .: Nakakuma-gun, Mt Kita, 2500 m, Osada 67372 (NICH). SHIKOKU. Ehime Pref.: Mt Ishizuchi, between Omogo Valley and the summit, Iwatsuki 44818 (NICH); Mt Ishizuchi, Kono 229 (H). Tokushima Pref.: Mt Tsurugi, ca 1900 m, 12 Aug 1955, Nakajima s.n. (WTU) and 1700 m, Koponen 36486 (H). Not localised: Jizogatake, Faurie 2384 (FH - lectotype Racomitrium fasciculare var. orientale).

RUSSIA. FAR EAST. Amurskaya Prov.: basin of the Zeja River, Prokhorov & Kuzeneva 110 (KRAM, LE). Kamchatka Prov.: South Kamchatkan Nature Reserve, slope of the Koschelevsky volcano, Czernyadjeva N26 & N563 (KRAM, LE); basin Left Kikhchik river, Czernyadjeva 116A (KRAM, LE). KHABAROVSK TERRITORY. Ul'chskiy Distr.: S slope of Mt Shaman-Tiul, 15 km SE of Sofijsk, 900 m, Alanko 32059 & 32059A (H). Verkhnebureinskij Distr.: Bureya Res., 590 m, Khasanov 89-M-194 (KRAM) and 1420 m, 24 Aug 1987, Petelin s.n. (KRAM); Bureinskiy State Reserve, Dusse-Alin Range, ca 1 km S of Medvezh'e Lake, 1550 m, Ignatov 97-2003 (KRAM, MHA) and 1500 m, Ignatov 97-2000 (KRAM, MHA); Dusse-Alin Range, Kuraigagna Creek 1-2 km S from the upper cabin, 950 m, Ignatov 97-2009 (KRAM, MHA); Kuraigagna Creek valley (Levaya Bureya river tributary), 19 Jul 1994, Petelin s.n. (KRAM, MW). PRI-MORSKIY TERRITORY. Sokołowskij Distr.: Lysaja Bielievienaja Mt E of Nakhodka), 24 Sep 1947, Shcherbakov s.n. (KRAM, LE). Sakhalin Prov.: Kuril Islands, Ostrov Kampaniejskij (probably Urub Island), Koiso-san (=Kolokol Mt), 866 m, Voroblev 56 (KRAM, LE, PR); Sakhalin Island, Due, Aug 1861, Glehn s.n. (BM, H, PC, S - lectotype of Racomitrium brevisetum); Lamoricière (not precisely localised), Jul 1860, Schmidt s.n. (H, LE, S – syntype of Racomitrium brevisetum).

12. *Codriophorus anomodontoides* (Cardot) Bednarek-Ochyra & Ochyra (Figs 85–88)

Codriophorus anomodontoides (Cardot) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. \equiv Racomitrium anomodontoides Cardot, Bull. Herb. Boissier Sér. 2, 8: 335. 1908. — TYPE CITATION: Japon: Ubayu, rochers (n. 2810); Jimba, rochers (n. 3388). Corée: montagne des Diamants (n. 366, 510); d'île Quelpaert, à 2000 m. (n. 625) [Lectotype (*selected here*): "Herb. J. Cardot. Racomitrium anomodontoides Card. <u>sp. nova.</u> Japon: Jimba, rochers Ig. Faurie 1905. n°. 3888" – PC-Cardot!; syntypes: (1) "Herb. J. Cardot. Racomitrium anomodontoides Card. <u>sp. nova.</u> Corée: montagne des Diamants. Lg. Faurie, 1906. nº 366." – H-Brotherus!, NY!; (2) " "Herb. J. Cardot. Racomitrium anomodontoides Card. (<u>e specim. origin.</u>). Japon: Ubayu, rochers. Leg. Faurie, 1904. n. 2810" – s-Roth!].

Racomitrium brevipes Müll.Hal. *in* A.Jaeger, Ber. Thät. S. Gall. Naturw. Ges. 1877–1878: 419. 1880, *nom. nud.* — ORIGINAL MA-TERIAL: Japonia, <u>Niko</u> trans Yokohama (Schaal) [Chirotype: "Rhacomitrium brevipes C. Müll. n. sp. Japonia: Niko trans Yokohama I. F. Schaal 1875 hb. Jäger 1877 c. Sauerbeck, 1879" – BM-Bescherelle!], *syn. nov.*

R. canaliculatum Mitt. *ex* Cardot, Beih. Bot. Centralbl. Abt. 2, 19: 103. 1905. \equiv *R. hedwigioides* Sakurai var. *canaliculatum* (Cardot) Sakurai, Bot. Mag. Tokyo 51: 134. 1937, *nom. illeg. prior ut spec.* — TYPE CITATION: Japon: Nikko. Leg. Bisset. [Lectotype (*selected here*): "Grimmia (Rhacomitrium) canaliculatum Mitt. Japon, Nikko, Sept. 1886 J. Bisset" – PC-Renauld!; isotype: BM!], *syn. nov.*

R. fasciculare (Hedw.) Brid. var. *brachyphyllum* Cardot, Bull. Herb. Boissier Sér. 2, 8: 334. 1908. — TYPE CITATION: Corée: Tjyang– Tjyen (n. 343); montagne des Diamants (n. 681); île Quelpaert, 1200–1500 m. (n. 92, 95. 96) [Lectotype (*selected here*): "Herb. J. Cardot. R. fasciculare var. brachyphyllum Card. var. nova Corée: Tyyang-Tyjen leg. Faurie 1906 No. 343" – PC-Cardot!; isolectotype: NY!; syntype: "Herb. J. Cardot. Rhacomitrium fasciculare Brid. var. brachyphyllum Card. (e specim. origin.). Corée: île Quelpaert, 1200 m. leg. Faurie 1905. n. 92" – s-Roth!]. First synonymised with *Racomitrium brevisetum* by Cao (2000: p. 62).

R. fasciculare var. *erosum* Broth., Bishop Mus. Bull. 40: 13. 1927 [*R. erosum* Broth., Bull. Soc. Bot. Ital. 1904: 22. 1904, *nom. nud.*]. — TYPE CITATION: Maui: on rocks (B) [Holotype: "Bryotheca E. Levier. 1192 Racomitr. erosum Broth. n.sp. = Rh. fasciculare v. erosum (Broth.) Archipelag. Hawaii in insula Maui legit D. D. Baldwin, sine no" – H-Brotherus!]. First synonymised with *Racomitrium anomodontoides* by Lawton (1972: p. 254).

R. fasciculare var. *perrobustum* Broth., Bishop Mus. Bull. 40: 13. 1927 [*R. perrobustum* Broth., *nom. nud.*, Bull. Soc. Bot. Ital. 1904: 22. 1904, *nom. nud.*]. — TYPE CITATION: West Maui, on rocks, elevation 1,065 m (B.78) [Holotype: "Bryotheca E. Levier. 573 Racomitr. perrobustum Broth. = Rh. fasciculare v. perrobustum (B.) Insulae Hawaiicae in rupibus faucium insulae Maui occid. 3500 p. 1875 legit D. D. Baldwin. "Racomitrium fasciculare" ... Baldwin in scheda (gedrückt)" – H-Brotherus!; isotype: NY!], *syn. nov.*

R. fasciculare var. robustum Broth., Bishop Mus. Bull. 40: 37. 1927, nom. inval. err. pro. R. faciculare var. perrobustum.

R. bandaiense Sakurai, Bot. Mag. Tokyo 51: 106, f. 5. 1937. — TYPE CITATION: Honshiu: Prov. Iwashiro, Berg Bandai in alpiner Lage (Leg. K. Sakurai Nr 1641 Typus Juli 1927) [Holotype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai. 1641 Rhacomitrium bandaiense sp. nov. Juli – 1927 Leg. K. Sakurai. Mt. Bandai, Mt. Akahani, Inawashiro-machi, Yama-gun, Fukushima Pref." – MAK-Sakurai!], *syn. nov.*

Racomitrium nipponicum Sakurai, Bot. Mag. Tokyo 51: 107, f. 6. 1937. — TYPE CITATION: Honshiu: Prov. Kotsuke, Berg Akagi (Leg. G. Takahashi in Herb. K. Sakurai Nr. 7938 Typus Mai 1936) [Holotype: "Herb. Dr. K. Sakurai Nr. 7938. Rhacomitrium fasciculare nipponicum Sak. 60_9 Herb. Genzo Takahashi Typus Onuma Lake side, Mt. Akagi, Fuji-mura, Seta-gun, Gunma Pref.; May 23, 1936, coll. Genzo Takahashi" – MAK-Sakurai!], *syn. nov.*

FIGURE 85. *Codriophorus anomodontoides.* — 1. Habit. 2. Portion of branch, wet. 3. Portion of branch, dry. 4. Portion of stem section. 5–7. Axillary hairs. 8–16. Leaves. 17–18. Leaf apices. 19. Mid-leaf cells. 20. Supra-basal leaf cells. 21. Alar cells. 22. Basal juxtacostal cells. 23–35. Transverse sections of costa and leaves, sequentially from base to apex. — [1-3 from Kuwahara 637, NY; 4, 8–9, 19–20, 23–30 from Chuang 1412, ALTA; 5–7, 12–13, 17 from*Deguchi s.n.*, HIRO-8718; 10–11 from*Faurie 366*, PC (syntype of*Racomitrium anomodontoides*); 14 from*Sakurai s.n.*, 15.04.1909, H; 15–16, 18, 21, 31–35 from*Faurie 3388*, PC (lectotype of*Racomitrium anomodontoides*)]. — Scale bars a – 1 mm (3, 8–16) and 50 µm (5–7, 17–35); b – 100 µm (4); c – 1 cm (1); d – 0.5 cm (2).



R. hedwigioides Sakurai, Bot. Mag. Tokyo 51: 133, f. 8. 1937. — TYPE CITATION: Honshiu: Prov. Shimotsuke, Nikko, Kirifuri (Leg. K. Sakurai Nr. 16 Typus Juli 1911) [Holotype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai. 16. Rh. hedwigioides! Nikko, Nikko City, Tochigi Pref., leg. Kyuichi Sakurai, VII – 1911" – MAK-Sakurai!], *syn. nov.*

R. formosicum Sakurai, Bot. Mag. Tokyo 51: 134, f. 9. 1937. — TYPE CITATION: Formosa: Prov. Taichu, Berg Nokô (Leg. Suzuki in Herb. K. Sakurai Nr. 7037 Typus Aug. 1926) [Holotype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai Nr. 7037. No. 1727. Herb. H. Sasaoka. R. No. 2679. Mosses of Formosa, Japan. Rhacomitrium fasciculare, var. formosicum (Broth.) Sak. Prov. Taityn: Mt. Noko, 5th Aug. 1926, Coll. S. Suzuki. L. No. 73.II" – MAK-Sakurai!; isotype: BM-Dixon!]. First synonymised with *Racomitrium anomodontoides* by Cao (2000: p. 64).

R. yakushimense Sakurai, Bot. Mag. Tokyo 51: 135, f. 10. 1937. — TYPE CITATION: Kiushiu: Prov. Ohsumi, Insula Yakushima (Leg. N. Takaki in Herb. K. Sakurai Typus Nr. 7939, Nr. 7940 Juli 1936) [Paratype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai. Nr. 7940. Herb. Noriwo Takaki No. 360. Rh. yakushimense Locality: Hananoe gawa, upper stream of Anbo river, Isl. Yakushima, Pref. Kagoshima, Southern Kyushu, Japan (on wet rock.) Date 1936.8.4." – MAK-Sakurai!]. First synonymised with *Racomitrium anomodontoides* by Cao (2000: p. 64).

R. bandaiense var. *ramosum* Sakurai, Bot. Mag. Tokyo 53: 288. 1939. — TYPE CITATION: Honsyu: Prov. Settu, Berg Rokko (Leg. K. Uno comm. N. Ui in Herb. K. Sakurai Nr. 11657 3 Nov. 1935) [Holotype: "Makino Herbarium. The collection of Dr. Kyuichi Sakurai. 3409 Rhacomitrium Unoi n.sp. bandaiense var. ramosum Sak. Herb. Dr. K. Sakurai 11657. Mt. Rokko, Kobe City, Hyogo Pref. Coll. Kakuo Uno, 1935.11.3; communicavit Ui" – MAK-Sakurai!], *syn. nov.*

R. hedwigioides var. *chrysophyllum* Sakurai, Bot. Mag. Tokyo 65: 221. 1942. — TYPE CITATION: Honsyu: Prov. Sado, Saru-hati (Leg. Y. Ikegami Typus in Herb. K. Sakurai Nr. 13338 30. April 1939) [Holotype: "Makino Herbarium. Herb. Dr. K. Sakurai Nr. 13338 Rh. (Ikegamii n.sp.) hedwigioides, var. chrysophylla Sak. (879) Typus. Saruhachi, Hatano-cho, Sado-gun, Niigata Pref. IV.30.1939, leg. Yoshinobu Ikegami" – MAK-Sakurai!; isotype: MICH!], *syn. nov.*

Plants large and robust, rarely medium-sized and fairly slender, rigid, stiff and coarse, in dull, loose tufts or extensive patches, yellow-green, olivaceous, dirty or dark green, dirty yellow, yellow-brown to brownish- or olivegreen above, brown to blackish-brown below. Stems erect or ascending, less often prostrate, often ascending from a creeping, denuded primary shoot, (3-)6-13 or, occasionally, up to 20 cm long, sparingly, irregularly or dichotomously, less often freely branched, rarely with some short, tuft-like lateral branchlets, in transverse section circular, without a central strand and with a 6-8-layered medulla of large, yellowish-hyaline, thick-walled cells grading into a multistratose cortex of 5-6 rows of stereid cells with very small lumina and strongly incrassate, brown walls; rhizoids sparse or fairly abundant near the base or scattered in clusters throughout the creeping stems, reddish-brown, lustrous, smooth, branching; axillary hairs filiform, hyaline throughout, 7–9 cells long, usually with short basal cells and elongate distal cells. Leaves densely set, straight to slightly curved, shortly decurrent, erect-appressed to loosely erect, often with recurved, homomallous apices, occasionally crispate when dry, erecto-patent to spreading when wet, narrowly lanceolate to ovate-lanceolate, from a broadly ovate or ovate-lanceolate, broadly canaliculateconcave, slightly plicate base short-acuminate or from a lanceolate base gradually tapering to a long subulate, canaliculate acumen, 3.0-4.0(-4.5) mm long, 1.0-1.3 mm wide; *leaf apex* epilose, finely acute, subacute to narrowly rounded-obtuse, denticulate-cristate, dentate or papillosecrenulate; margins unistratose throughout, narrowly or broadly recurved on both sides from the base nearly to the apex, entire except for the apex; costa single, yellowish-brown, sharply delimited from the laminal cells, situated at the bottom of a deep, wide-angled channel, gradually narrowed upwards, usually spurred in the distal portion, (50-)55-75(-85) µm wide at the base, extending to 3/4, rarely to 5/6 of the way up the leaf, occasionally to mid-leaf only, in transverse section weakly protruding on the dorsal side, mostly bistratose throughout, distinctly convex on the ventral side with 4-8 enlarged epidermal cells, flattened or canaliculate dorsally, very seldom distinctly convex on the dorsal side with 2-3 layers of small stereid cells; laminal cells unistratose and elongate throughout, sometimes somewhat shorter near the apex, (15-)30-50(-60) µm long, 8-10 µm wide, with moderately thick to incrassate and strongly sinuose longitudinal walls; cells at the insertion rectangular, 35-55(-70) µm long, 5-8 µm wide, with strongly thickened, nodulose walls, forming a brown to yellow-brown strip of 2(-3)rows of cells; alar cells differentiated, short-rectangular to subquadrate, 15-30 µm long, 10-15 µm wide, moderately thick- or thin-walled, forming brown to yellow-brown, pellucid, swollen, somewhat decurrent auricles; supraalar cells short-rectangular, 30-45 µm long, 7-8 µm wide, with straight, thin to moderately thickened walls, forming a distinct, pellucid marginal border consisting of (7-)11-18(-24) cells, sometimes with a second row, consisting of up to 8 pellucid cells. Dioicous. Perigonia bud-like, about 2 mm long; outer perigonial bracts lanceolate, 1.8-2.0 mm long, similar to the cauline leaves but smaller; innermost perigonial bracts broadly ovate, shortly acute, 0.9-1.0 mm long, deeply concave, with about 20 club-shaped, brownish antheridia intermixed with a few, hyaline paraphyses, much shorter than the antheridia. Outer perichaetial leaves lanceolate, similar to the vegetative leaves, 3.0-3.1 mm long, 1.1-1.2 mm wide; innermost perichaetial leaves sheathing the seta, oblong-lanceolate to oblong, shortly acuminate, subacute at the apex, 1.9-2.2 mm long, 1.2-1.3 mm wide, hyaline thoughout. Setae single in the perichaetium or quite often geminate, straight, (4-)5-12(-20) mm long, brown, smooth, slightly glistening, with one torsion to the left immediately below the urn, dextrorse below; vaginula dark brown, 1.0-1.2 mm long, with sinuose and thickwalled epidermal cells. Capsules obloid to cylindrical, (1.5-)1.8-2.2(-2.5) mm long, 0.8-1.0 mm wide, often sulcate when dry, brown, lustrous, moderately pachydermous; operculum long-rostrate with a straight rostrum, somewhat shorter than the urn; annulus deciduous, 2-3seriate, composed of thick-walled, vesiculose cells; exothecial cells rectangular, thick-walled, 50-90 µm long, 13–20 µm wide, in regular longitudinal rows, becoming



FIGURE 86. Codriophorus anomodontoides. — 1–8. Leaves. 9–14. Leaf apices. — $[1-2 \text{ from Higuchi s.n., MAK-B33022; 3–4, 14 from Faurie 343, PC (lectotype of Racomitrium fasciculare var. brachyphyllum); 5–6 from Sakurai 1641, MAK (type of R. bandaiense); 7–8 from Kuwahara 667, NY; 9 from Frank s.n., Jul 1981, PRC; 10 from Iwatsuki & Sharp 15352, TENN; 11 from Faurie 3388, PC (lectotype of R. anomodontoides); 12 from Takaki s.n., 4 Aug 1936 (paratype of R. yakushimense); 13 from Baldwin 573, H (type of R. fasciculare var. perrobustum)]. — Scale bars: a – 100 µm (9–14); b – 1 mm (1–8).$

short-rectangular to rounded-quadrate in 4–5 tiers at the mouth, forming a dark brown strip; *stomata* superficial, bicellular with rounded openings, 13–16 in 2 rows at the base of the urn; *peristome teeth* 16, narrowly lanceolate, (425-)525-550(-650) µm long, brown to reddish-brown, with a low basal membrane, 25–40 µm tall, deeply split nearly to the base into 2–3 filiform branches, sometimes only perforate below, densely covered throughout with fairly low papillae. *Spores* spherical, brownish, finely papillose, 12–18 µm in diameter. *Calyptra* conical-mitrate, (2.0-)2.3-2.8(-3.2) mm long, deeply lobed at the base, pale brown below, dark brown and papillose at the tip, smooth, non-plicate.

Etymology — The specific epithet derives from the generic name *Anomodon* and the Greek suffix *–ides* which designates affinity. The species was named by reference to its general habit which resembles *Anomodon viticulosus* (Hedw.) Hook. & Taylor.

Diagnostic characters and differentiation — Codriophorus anomodontoides is one of the largest and most robust and coarse species in the genus. Its typical expressions are very distinct and difficult to mistake but, because it is generally quite variable, smaller and atypical phenotypes have quite often been misunderstood and misinterpreted. Hence the taxonomic concept of C. anomodontoides was rather unclear and vague as evidenced by the long list of heterotypic synonymous names presented by various authors (Noguchi 1974, 1988; Cao 2000; Cao et al. 2003), some of which actually refer to other species of the C. fascicularis complex. In general, C. anomodontoides has been considered a species in its own right (e.g., Sakurai 1937a; Cao 2000; Cao et al. 1998, 2003) or as a variety, var. atroviride Cardot, within the broadly conceived Racomitrium fasciculare. Notwithstanding its taxonomic status, the existing concept of C. anomodontoides has been based upon gametophyte characters that are particularly subject to variation, such as leaf shape, branching pattern and the stature of the plants. For example, Noguchi (1974, 1988) defined this species as "a large plant with the leaves long attenuate from a widely ovate base and acuminate to obtuse and often cristate apex" and contrasted it to C. brevisetus which is "a medium-sized plant with the leaves shortly and narrowly attenuate from a widely ovate base and rounded, not cristate apex". Likewise, Cao et al. (2003) distinguished C. anomodontoides on the basis of "slightly keeled leaves, recurved throughout on both sides, with linear basal cells" and contrasted it to C. brevisetus which has "strongly keeled leaves, slightly recurved in the lower part, with elongate-linear basal cells". These characters cannot serve as a safe discrimination of either species as the length of their basal cells markedly overlap if the measurements from their descriptions are taken into consideration: 18–40 µm long in C. brevisetus and 20–60 µm long in C. anomodontoides.

As presently understood *Codriophorus anomodontoides* is circumscribed as follows: (1) plants mostly large and robust, rigid and coarse; (2) stem erect or ascending, sparsely or freely, irregularly branched, very rarely with short, tuft-like lateral branchlets; (3) leaves lanceolate to ovate-lanceolate, slenderly long-acuminate to shortly and broadly acuminate, broadly canaliculateconcave throughout; (4) leaf apex acute, subacute to narrowly rounded-obtuse, denticulate-crenate, dentate, cristate to papillose-crenate; (5) leaf margins unistratose over their entire length, broadly to narrowly recurved almost throughout; (6) costa situated at the bottom of a deep, wide-angled furrow, extending to three quarters or, seldom, five sixths of the leaf length, often spurred above, in transverse section distinctly convex on the ventral side, flattened or canaliculate on the dorsal side, bistratose throughout or, very seldom, with a 2-3-stratose dorsal stereid band at the extreme base; (7) laminal cells unistratose and elongate throughout; (8) alar cells differentiated, forming brown to yellow-brown, convex and somewhat decurrent auricles; (9) supra-alar cells rectangular, straight-walled, forming a 1(-2)-seriate pellucid marginal border of (7-)11-18(-24) cells; (10) innermost perichaetial leaves oblong to oblong-lanceolate, hyaline throughout; (11) setae single or geminate in the perichaetium, (4-)5-12(-20) mm long, twisted once to the left immediately below the urn, dextrorse below; (12) capsule obloid to cylindrical, (1.5-)1.8-2.2(-2.5) mm long, often sulcate when dry, lustrous; (13) exothecial cells rectangular, thick-walled, arranged in regular longitudinal rows; (14) peristome teeth lanceolate, (425-)525-550(-650) µm long, brown to reddish-brown, with a low basal membrane, split nearly to the base into 2-3 filiform prongs, densely papillose throughout.

Among the species of the Codriophorus fascicularis complex, C. anomodontoides is distinguished by the unique anatomical structure of its costa which is always convex on the ventral side, especially in the upper and median parts, as is clearly visible in transverse sections. Only at the extreme base, is the costa flat or only slightly convex ventrally but in this part it is 3(-4)-stratose, with a distinct dorsal stereid band of two or very occasionally three layers of small cells with markedly incrassate walls. Additionally, the costa is quite often canaliculate on the dorsal side, thus giving it the peculiar appearance of being bent inwards. The convexity of the costa on the ventral side is unknown in any other species of sect. Fascicularia and is occasionally observed in some plants of C. acicularis from North America. Moreover, the costa in C. anomodontoides ceases 3/4 of the way up the leaf and only occasionally does it extend higher up, to 5% of the leaf length, usually as a narrow branch of the forked apex, having a peculiar rounded shape in transverse section. Such plants may be confused with C. brevisetus, especially as both species share the dentate and cristate leaf apex. However, the uppermost laminal cells are consistently rectangular and unistratose in C. anomodontoides and this combination of characters, coupled with the anatomical structure of the costa should be sufficient for the safe determination of the plants, notwithstanding their stature and ramification.



FIGURE 87. Codriophorus anomodontoides. — 1–5. Transverse sections of leaves, sequentially from base to apex. 6. Outlines of transverse leaf sections, sequentially from base to apex. — [1, 6 from Sakurai 1641, MAK (type of *R. bandaiense*); 2 from Faurie 343, PC (lectotype of Racomitrium fasciculare var. brachyphyllum); 3 from Higuchi s.n., MAK-B33022; 4 from Ikegami 19334, PRC; 5 from Deguchi 8718, HIRO]. — Scale bars: $a - 100 \mu m$ (6); $b - 100 \mu m$ (1–5).

Codriophorus anomodontoides is unlikely to be mistaken for *C. corrugatus*, since its rigid and stiff leaves are not wavy, corrugate and attenuate, even those with longacuminate and subulate apices. Furthermore, the short costa, extending to mid-leaf and flattened on the ventral side, should dispel any doubts regarding the identity of *C. corrugatus*. Likewise, *C. anomodontoides* should not be confused with *C. fascicularis*, especially with the plants lacking a nodose appearance due to the presence of the short lateral tuft-like branchlets. Both species share the unistratose and elongate laminal cells, but the leaf apex in *C. fascicularis* is entire and the costa is subpercurrent and always distinctly flattened on the ventral side throughout its whole length.

Codriophorus anomodontoides was occasionally misnamed as C. varius, for example by Cardot (1904) who reported this North American species from Korea. Later, this author changed his mind regarding the identity of this specimen (*Faurie 23*, PC) and included it as one of the syntypes in the concept of *Racomitrium fasciculare* var. *orientale* (Cardot (1908a). This material actually represents *C. anomodontoides* and is indeed morphologically very similar to epilose ecads of *C. varius*. However, fertile plants of the latter species are distinct at a glance by their very long cylindrical capsules with very long peristome teeth. Microscopically, *C. varius* is distinct by its short distal laminal cells and the strong costa that is distinctly convex on the dorsal side in the proximal part and flat on the ventral side throughout its whole length.

Variability — Although *Codriophorus anomodontoides* is a distinct and well-defined species, it exhibits a remarkable interpopulational variability in the stature, size and colour of the plants, as well as branching of the shoots, which is doubtless conditioned by changing environmental factors. In addition, there is some variation in the shapes of leaves and leaf apices and this has prompted various authors to recognise some phenotypes as separate taxa. Accordingly, the list of synonyms of *C. anomodontoides* is quite impressive and consists of six specific and five varietal names.

There is large scale variation in plant size, with the largest specimens from the Kosugi-dani valley (Ikegami s.n., MAK-B20520) and Mizukami-mura, Kuma-gun (Mayebara s.n., MAK-B57613) in Japan, reaching, respectively, 17 and 20 cm in length. The majority of specimens have relatively long stems, 6-13 cm, although quite a number of specimens are only 3-4 cm long. The plants are generally coarse and large but occasionally some populations comprise gracile and more delicate individuals, for example from Mt Akagi (Deguchi s.n., HIRO-17126). The type of branching is also subject to remarkable variation, although in general sparsely and irregularly ramified plants predominate, with those freely and more regularly branched in a minority. Sometimes, the plants have relatively rich short lateral tuft-like branchlets, giving the shoots a nodose appearance, for instance the specimen from Kobe, Japan (Ford 290, BM). The colour of the tufts certainly depends on the exposure of the plants to light and combinations of various shades of yellow, green and brown predominate, although occasionally some specimens have a nice golden- or rufous-brown colour.

The foliage is rather uniform but there are some differences among various populations in leaf arrangement and orientation of the leaf apices. The latter are generally appressed to homomallous on drying and only occasionally are they somewhat crisped or contorted, for example in the plants from Yakushima Island (*Kuwahara 667*, NY). The leaf shape is quite variable, ranging from narrowly lanceolate and long-subulate to broadly ovate-lanceolate and shortly acuminate. The leaves are generally straight to slightly curved and only very rarely are they distinctly falcate as in the plants from Iida city in Nagano Prefecture on Honshu in Japan (*Nishimura s.n.*, HIRO-5355). The leaf apices vary from narrowly acute and sharply dentate-cristate to narrowly rounded-obtuse and crenulate-papillose.

In most populations the costa extends for three quarters of the leaf length but sometimes it ceases somewhat higher, reaching to 5% way up the leaf. It is often a single, narrow branch of the forked apex of the costa which does this, simultaneously exhibiting a peculiar spherical shape in transverse section. Robustness of the costa is fairly stable and its width varies from 55 to 75 µm on average. The costa is bistratose throughout and distinctly convex on the ventral side, especially in the upper and median parts and this convexity of the costa is the most important diagnostic character of Codriophorus anomodontoides. The convexity is usually less prominent near the base and in this part the costa is usually flat on the ventral side. Here, the costa is also more prominently convex dorsally, often with a row of stereid cells, and in one case (Deguchi s.n., HIRO-7126) it projects strongly on the dorsal side, consisting of 2(-3) rows of small stereid cells.

Leaf areolation is remarkably stable throughout the lamina, consisting of unistratose and elongate cells, mostly $30-50 \mu m$ long on average. Sometimes in short-leaved plants, for example those represented by the lectotype of *Racomitrium fasciculare* var. *brachyphyllum*, the apical leaf cells are short-rectangular to isodiametric (Fig. 86.14) and this probably has been the main reason for discrepancies in the interpretation of this taxon, especially because the leaf apex is almost entire, only papillose-crenulate on some leaves. However, the costa in these plants is distinctly convex on the ventral side (Fig. 87.2) and this character is decisive for the association of such phenotypes with *Codriophorus anomodontoides*.

The sporophytes of *Codriophorus anomodontoides* exhibit remarkable uniformity and only minor variations in the length of the setae and capsule size and shape are observed in the various populations.

Reproduction — Most populations of *Codriophorus anomodontoides* are fertile, but in general sporophytes are not produced in great abundance.

Taxonomic and nomenclatural notes — *Codriophorus anomodontoides* was described by Cardot (1908*a*) on the

FIGURE 88. Codriophorus anomodontoides. — 1. Portion of branch with mature sporophyte. 2. Perigonium. 3–4. Outer perigonial bracts. 5. Inner perigonial bract. 6. Inner perigonial bract with antheridia. 7–8. Outer perichaetial leaves. 9–10. Inner perichaetial leaves. 11. Apex of innermost perichaetial leaf. 12. Transverse section of seta. 13. Epidermal cells of vaginula. 14–15. Operculate capsule, dry. 16. Operculate capsules, wet. 17. Calyptra. 18. Transverse section of mid-calyptra. 19. Exothecial cells in mid-urn. 20. Exothecial cells and stomata at base of urn. 21. Peristome teeth, exothecial cells at orifice, annulus and spores. — [1, 14–17 from *Kuwahara* 637, NY; 2, 7–13, 19–21 from *Deguchi s.n.*, HIRO-8718; 3–6 from *Schofield* 53139, CANM; 18 from *Chuang* 1412, ALTA]. — Scale bars: a – 0.5 cm (1) and 1 mm (3–6); b – 100 µm (11–13, 18–20); c – 1 mm (2) and 100 µm (21); d – 1 mm (7–10, 14–17).



basis of five specimens collected in Korea and Japan. No comment on the affinities of this new species was presented, except for comparison of its habit to *Anomodon viticulosus*. The species was approved by Sakurai (1937*a*) who reported one more plant from Mt Myoko on Honshu (*Sakurai 1006*) and illustrated two leaves of it. Unfortunately, this specimen has not been located in the Sakurai herbarium at MAK and the shape of the leaves in the drawings is very strange for *C. anomodontoides* because they are oblong-ligulate, broadly rounded at the apex and have percurrent or subpercurrent costae. They far more closely resemble leaves of an *Anomodon* species, not *C. anomo-dontoides*.

Noguchi (1974) considered *Racomitrium anomodontoides* to be a variety of *R. fasciculare* for which he used the name var. *atroviride*. This variety was described by Cardot (1908*a*) from five specimens from Japan, three of which have been located and examined. They represent *Codriophorus fascicularis* since they have a narrowly acute and entire leaf apex, elongate laminal cells in the distal half and a costa ending at ³/₄ of the way up the leaf with a flat ventral side in transverse section. On the other hand, another variety described by Cardot (1908*a*) from Korea, *Racomitrium fasciculare* var. *brachyphyllum* is evidently identical to *C. anomodontoides* on account of its costa that is distinctly convex ventrally.

Noguchi (1974) placed in synonymy with *Racomitrium* fasciculare var. atroviride, thus inferentially with *Codrio*phorus anomodontoides, six additional species names, namely *Racomitrium sawadae*, *R. bandaiense*, *R. hedwigio*ides, *R. canaliculatum*, *R. formosicum* and *R. yakushimense* and two varietal names, *R. bandaiense* var. ramosum and *R. hedwigioides* var. *chrysophyllum* proposed by Cardot (1905) and Sakurai (1937*a*, *b*, 1942). All these taxa except *R. sawadae* are actually identical to *C. anomodontoides*, whereas *R. sawadae* is conspecific with *C. brevisetus*. In addition, to the list of synonyms of *C. anomodontoides* is added *Racomitrium nipponicum*, as well as *R. fasciculare* var. *erosum* and *R. fasciculare* var. *perrobustum*. The first species was described from Japan by Sakurai (1937*a*), whereas the latter two varieties were described by Brotherus (1904, 1927) from the Hawaiian Islands.

Chromosome number --- Not available.

Habitat — Codriophorus anomodontoides is an acidophilous saxicole growing commonly on granite or siliceous stones, boulders, rock outcrops and cliffs and steep slopes, on stony ground and on thin soil and humus over rocks. It is associated with moist or wet and shaded or dry and exposed habitats, occurring frequently on stones along streams, on river or road banks, often in mixed broadleaved and coniferous forests. It usually grows in pure tufts but sometimes in loose patches in which various bryophyte species have occurred as associates. Of other *Codriophorus* species only *C. carinatus* has occasionally been found in a mixed stand.

Geographical distribution — Codriophorus anomodontoides is a Far East Asian temperate species weakly penentrating into the tropics in the Hawaiian Islands in the Pacific area from where it was recorded as *Racomitrium* fasciculare var. erosum (Bartram 1933), in the Philippines and in Taiwan and Hainan (Fig. 89). It has its maximum



FIGURE 89. Global distribution of Codriophorus anomodontoides.

occurrence in Japan but, interestingly, it does not occur on Hokkaido. In mainland Asia it is widely distributed in south-east, south central and north central China, becoming rare and localised on the Korean Peninsula and in north-east China where it reaches its northernmost locality in the Lesser Khingan Range in Manchuria at lat. *ca* $46^{\circ}30'$ N (Fig. 90). The altitudinal range of the species is very broad and extends from near sea level to 3100 m on Mt Fuji in Japan, although most localities in this country are concentrated at elevations from 300 to 1700 m. In mainland Asia *C. anomodontoides* grows from 700 to 2700 m on Mt Erlang in Shaanxi Province, whereas on Taiwan it grows at higher elevations, from 500 to 3090 m. In the Philippines it occurs only in altimontane localities at 1160–2800 m, whereas in the Hawaiian Islands it has been recorded at lower altitudes, 245–1065 m.



FIGURE 90. Distribution of Codriophorus anomodontoides in Asia.

EXSICCATI

CHEN - Musci Sinici Exsiccati No. 42 (MO, TENN).

- HATTORI *Musci Japonici* No. **60** (BM, CANM, COLO, E, F, FH, G, HIRO, JE, M, MICH, MO, O, POZG, PR, S, TENN, US, W); No. **62** (as *Racomitrium carinatum*) (BM, CANM, COLO, F, FH, G, H, HIRO, JE, KRAM, MICH, MO, O, POZG, PR, S, TENN, US, W).
- INOUE *Bryophyta Selecta Exsiccata* No. **795** (Alta, Br, Canm, Colo, F, G, H, JE, KRAM, MICH, MO, S, TENN).
- LIN *Bryophytes of Taiwan* No. **242** (ALTA, MICH, MO); No. **243** (ALTA, H, MICH, MO).
- Noguchi *Musci Japonici* No. **892** (BM, CANM, COLO, F, G, JE, KRAM, M, MICH, PR, S, TENN, US, W); No. **995** (BM, CANM, COLO, F, G, JE, M, MICH, S, TENN, US, W); No. **1138** (BM, BR, CANM, COLO, F, G, JE, M, MICH, MO, POZG, S, TENN, US, W).
- Noguchi & Hattori *Musci Japonici* No. 164 (Alta, BM, BR, Canm, Cas, Colo, F, G, Gzu, Je, Kram, M, Mich, Mo, Pr, S, Tenn, US, W); No. 539 (Alta, BM, Canm, Colo, F, G, Gzu, Je, Kram, M, Pozg, Pr, S, Tenn, US, W).
- Noguchi & Iwatsuki *Musci Japonici* No. **1245** (Br, CANM, F, G, GZU, KRAM, MICH, MO, POZG, S, TENN, US).

SPECIMENS EXAMINED

ASIA. CHINA. ANHUI PROV. Jinzhai Co.: Jin Zhai Xian, The White Horse Forestry Centre, 1500 m, Zeng Z.-M. T0196 (MO). She Xian Co.: Mt Huang, Gao Chien 30500 (IFSBH, KRAM), Chen P.-Ch. 7139 (MO) and Chen P.-Ch. et al. 6581 (MO); Huangshan, under Li Si Tai, Chen P.-Ch. et al. 6909 (MO, TENN). GUANGXI PROV. Longsheng Co.: San-men village, Wu P.-C. 345 (DUKE, MO, NY) and 1480 m, Wu P.-C. 1195-2 (MO). Shang-si Co.: Hong-qi forest station, Gao Chien & Chang 2171, 2177 & 2220 (ALTA). Xing-an Co.: Mt Miao-er, Gao Chien & Chang K.-Ch. 1744 (ALTA). GUIZHOU PROV. Jiangkou Co.: Fanjing Mountain Reserve, trail from Tongkuang (Copper Mine) site to Jin-ding (Gold Top Peak) through Hui-xiang-ping, ca 900-2000 m, Tan 91-861 (FH). Leishan Co.: vicinity of Xiangshui Rock reservoir, at the foot of Mt Leigong, ca 800 m, Tan 91-824 (FH). Suyyang Co.: Mt Kangkeshen, 1500 m, Gao Chien 32782 (IFSBH, KRAM). Yin-jiang Co.: Mt Fanjing, 1200 m, Guo Zi-ye 107105 & 10708 (ALTA), 1900 m, Peng Yi-qin 30193 (ALTA) and 2200 m, Chen You-ming 10017 (ALTA), Tu Yu-lin F-21 (ALTA), Gao Chien & Chang Kuang-chu 411 (ALTA), Chen Jia-xiu 50303 (ALTA) and Su Yu-hua 40086 (ALTA). HAINAN PROV. Lingshui Co.: ca 9 km NW of Forest Station, 850-1070 m, Redfearn et al. 36201 (FH, MO); ca 9 km NW of the Diao Lu Shan Forestry Station, slopes to summit of Mt Da Diao Lu Shan, 850-1070 m, Reese et al. 17893 (MO, NY). HEILONGJIANG PROV. Wu-yiling Co.: Yi-chun City, Dongshan Mt, Gao Chien 602 (ALTA). HUNAN PROV. Liu-yang Co., Mt Da-wei, Gao Chien & Chang Kuang-chu 311 (ALTA, IFSBH, KRAM) & 466, 545, 547 & 410 (ALTA). JIANGXI PROV. Xiu-shui Co.: Long Gang Distr., 950 m, Tan Ce-ming 951213 (MO). JILIN PROV. Changbai Co.: Mt Changbai, Liu 9272 (IFSBH, KRAM); Mt Changbai, S slope, 2400 m, Gao Chien 7406 & 7453 (ALTA). GUANGDONG PROV. Heyuan Co.: Loh Fau Mountain (=Luofushan Mountain), Merrill 11156 (BM, H, H, NY, UC). HONG Kong. Lan Tau Island, Lan Tau Peak, 1000 m, Herklots 25A-B & 35 (BM). LIAONING PROV. Feng-cheng Co.: Mt Feng-huang, Gao Chien 6989 (ALTA) and Kobayasi 3908 (BM); Mt Funhang, Gao Chien 5917 (IFSBH, KRAM). Kuandian Co.: Baishilazhi Nature Reserve, Cao Tong 38387 (IFSBH, KRAM); Bai-shi-la-ji Mts, Bai-shi-la-ji National Natural Reserve, Xiang-shui-gou at Hu-li Mt, ca 900 m, Buck 23786 & 23791 (NY). SHAANXI PROV. Taibei Co.: Mt Taibai, Wei 6647 (IFSBH, KRAM). SI-CHUAN PROV. Nanchuan Co.: Mt Jinfu, 1050 m, Wu 21190 (ALTA, F, MO) and 1150 m, Hu 267 (DUKE, NY); Chongqing City, Wang-Mei-zhi 860433 (CAS). Tianquan Co.: Mt Erlang, 1800-2700 m, Cao Tong & Gao Chien 18351 (IFSBH, KRAM). ZHEJIANG PROV. Hangzhou Co.: West Tian-mu Mountain slope, trail to Lao-tian temple, 350-1200 m, Tan 93-573 (FH). Lin-an Co.: Mt Xi-tian-mu, Wu Pan-Cheng 1089, 1106 & 1107 (MO). Lin-Hai Co.: Mt Kuocang Shan, 760 m, Gao Chien 616 (MO). Lishui Co.: Mt Jiulong, Hong Ru-lin & Liu Zhong-ling 171 & 179 I (ALTA).

JAPAN. HONSHU. *Aomori Pref.*: Hakkoda, 1100 m, *Faurie 2917* (PC – syntype of *R. fasciculare* var. *orientale*). *Aichi Pref.*: Mt Dantosan,

Shidara-cho, Kitashidara-gun, Toyama s.n. (MAK-B7045); Mt Dando, prov. Mikawa, Toyama 772 (s). Akita Pref.: Iwamisannai, Kawabe-cho, Kawabe-gun, Furuja s.n. (MAK-B51816); Mt Jimba, N of Odate, Faurie 3388 (PC - lectotype of Racomitrium anomodontoides). Fukui Pref.: Mt Sanri, Saito s.n. (MAK-B57847). Fukushima Pref.: Nishi-shirakawa-gun, Nishigo-mura, Kanko Spa, 720-900 m, Suzuki s.n. (HIRO-20621); Onisawa, Takine-machi, Tomura-gun, Takahashi s.n. (MAK-B7915); Moniwa, Fukushima City, Higuchi s.n. (MAK-B33022); Mt Bandai, Mt Akahani, Inawashiro-machi, Yama-gun, Sakurai s.n. (MAK - isotype of Racomitrium bandaiense); Iwashiro, Mt Bandai, 2000 m, 3 Sept 1929, sine collector (s). Gifu Pref .: Ono-gun, Nyukawa-mura, Chosi-dani, 1000-1200 m, Mizutani 14604 (ALTA, BR, CANM, COLO, KRAM, S); Hagiwara-chyō, Mashita-gun, Mt Gozen, 920 m, Magofuku 10713 (s), 930 m, Magofuku 10651 (s) and 950 m, Magofuku 10603 (BR, s) & 10702 (s). Gunma Pref.: Mt Akagi (Mt Kurobi), Fujimi-mura, Seta-gun, 1000 m, Deguchi s.n. (HIRO-17126) and ca 1400 m, 1955, Hiroi s.n. (WTU) and Takahashi s.n. (MAK - isotype of Racomitrium nipponicum); Nanmoku-mura, Kanra-gun, Takei 90 (TNS); Mt Akagi (Mt Kurobi), Mt Haruna, Okamura 1047 (NICH); Mt Tanigawa-dake, Tone-gun, Sakurai (MAK-B6987). Hiroshima Pref.: Ko-nukui, Kake-cho, Yamagata-gun, 490 m, Nakashima s. n. (HIRO-2872); Shimoyama, Togouchi-cho, Yamagata-gun, ca 460 m, Nakashima s.n. (HIRO-3150); Mt Gorinzan, Kake-cho, Yamagata-gun, ca 600 m, Nakashima s.n. (HIRO-3584); Otsukego, Togouchi-cho, Yamagatagun, ca 680 m, Nakashima s.n. (HIRO-3231); Anabukuro, Kake-cho, Yamagata-gun, ca 520 m, Nakashima s.n. (HIRO-3485); Kuroutsu-kyo, 30 Jul 1962, Ando s.n. (PR); Ryuzu-kyo Gorge, Gardiner s.n. (BM); Nabara-kvo, 23 Sep 1972, Ando s.n. (G. s); Yuki-cho, 140 m, 20 May 1973, Ando s.n. (G, S); Sandankyo, Noguchi s.n. (NICH-8904), 300 m, 5 May 1956, Ando s.n. (MO) and 630 m, 20 Nov 1976, Ando s.n. (KRAM); Oono, Saiki-gun, 400 m, 22 Nov 1959, Ando s.n. (DUKE); Nukui, Kake-cho, 350 m, 1 Jul 1962, Ando s.n. (мо); Miyajima I., 10 m, 20 Mar 1967, Ando s.n. (ALTA, G). Hyogo Pref .: Nishinomiya City, Namase, Ui s.n. (MAK-B7785); Yabu-gun, Sekinomiya-cho, Mt Hyônosen, 700 m, Miyata 4496 (NICH) and 1400 m, Miyata 4626 (BISH); Kobe, Ford 290 (BM); Mt Rokko, Kobe City, Uno s.n. (MAK - isotype of Racomitrium bandaiense var. ramosum) and Ui s.n. (MAK-B13821); Kinosaki, Tajima (old name for N region of Hyogo Pref.), Kono 266 (H). Mt Rokkô, Tagawa 278 & 339 (KYO); Inohana-dani, SW of Sumoto, Isl. Awazi, Tagawa 1238 (KYO); Onzui Government Forest, Okutani-mura, Sisô-gun, Tagawa 726 (KYO): Sisô-gun. Mt Hunakosi, Tagawa 2038 (KYO) Ibaraki Pref.: Mt Tsukuba, Shibasaki s.n. (MAK-B100485); Prov. Hitachi, Mt Tsukuba, Sasaoka 4559 (BM). Iwate Pref.: Rikuzen, Arne, Oct 1907, Jishiba s.n. (s); Uraiwate, Iwate-gun, Koyama s.n. (MAK-B57619); Iwate-gun, Matsuo-mura, Hachimantai, ca 1400 m, Watanabe 5008 (NICH). Kanagawa Pref .: Hakone Mts, Kamifutago, 27 Oct 1926, sine collector (s, W); Mt Hutago, 25 Jul 1915, Jishiba s.n. (H); Mt Atago, Takahashi 1285 (BM, O) & 1611 (BM, NY) and Sasaoka 1285 (O); Hakone-pass, 28 Apr 1923, sine collector (s); Hakone Pass, Bisset s.n. (NY); Mt Hakone, 29 Aug 1929, Noguchi s.n. (WTU) and ca 1500 m, Sakurai 207 (H) and Jul 1910, Sakurai s.n. (O) and Tamura 41 (FH, H); Prov. Sagami (=Kanagawa Pref.), Hakone, Yumoto, Sasaoka 4936 (BM); Mt Hutago, Hakone-machi, Ashigarashimo-gun, sine collector (MAK-B100773); Hakone-machi, Ashigarashimo-gun, sine collector (MAK-B207); Mt Oyama, Naka-gun, sine collector (MAK-B7050); Prov. Sagami, Gora, Sasaoka 5251 (BM); Yokosuka, Savatier 278 (BM); Hakone Mts., National Park, ca 300 m, 16 May 1954, Redfearn s.n. (COLO, MICH, NY, US, WTU), 756-J-54 & 792-J-54 (DUKE, MO, TENN), 767-J-549 (DUKE, MO) & 767-J-54 & 753-J-54 (MO, TENN); Miyama sunagode, 25 Apr 1907, sine collector (US). Kyoto Pref.: Okukaya Pass, Kaya-cho, 150-250 m, 9 Oct 1967, Mizutani s.n. (BR, CANM, COLO, G, JE, KRAM, M, MICH, MO, S, TENN, US, W) [Musci Japonici No. 1138]; Mt Kurama, Sakyo-ku, Kyoto City, Sakurai s.n. (MAK-B71); Kyoto, 20 Oct 1917, Sasaoka (BM). Asiu Experimental Forest of Kyoto University, Tii-mura, Kitakuwada-gun, Tagawa 996, 1102 & 1013 (KYO) Mie Pref.: Oodaigahara, en route from Dogura mountain lodge to Momonoki mountain cottage, Miyagawa-mura, Taki-gun, 720 m, Deguchi s.n. (HIRO-7994); Mt Oodaigahara, Takaki 309 (F); Mt Oodaigahara, Takaki 5892 (s); Kimoto, Asadani valley, Kumano city, 230 m, Deguchi s.n. (HIRO-7560); Komono-cho, Yunoyama, ca 400 m, 11 May 1958, Nakajima s.n. (CANM, COLO, DUKE, MICH, MO, PR, TENN); Mt Asakuma, near Ise, 16 Aug 1959, Tsuchiga s.n. (PR); Ise city, Numaki-cho, Isunoki, 100 m, Magofuku 12912 (s); Ohuchiyama-mura, Watarai-gun Ohiradani, 180 m, Magofuku 13347 (s); Kuki, Owase-shi, ca 300 m, Sakuma 3623 (TNS); Nunobiki no Taki, Mihune Mura, Minamimurô-gun,
Tagawa 2349 (KYO, W); Mt Hirakura-yama, Misugi-mura, Ichishi-gun, Toyama 2456 & 2704 (куо); Uotobi-kei, Aiga, Miyama-cho, Kitamurogun, Magofuku 1241 (MAK-B51819); Osugi-Ugui-dani, Miyagawa-mura, Takaki-gun, Magofuku s.n. (MAK-B51821); Osugi-dani valley, Miyagawa-mura, Taki-gun, Takaki s.n. (MAK-B51813); Kawakamihachiman, Mizugi-mura, Isshi-gun, Magofuku s.n. (MAK-B51817); Prov. Ise, Mt Komono, Sasaoka 5688 (BM) and 29 Apr 1932, Murata s.n. (WTU); Prov. Ise, Suzuka, 25 Oct 1913, Sasaoka s.n. (BM); Prov. Ise, Shonai, Sasaoka 407 (WTU). Miyagi Pref.: Is. Kinkasan, Ojika-gun, Higuchi 1145 (MAK); Mt Katta-dake, Katta-gun, Higuchi s.n. (MAK-B57787); Mt Katta, Oct 1910, Uematsu s.n. (s); Sendai, 3 Mar 1912, sine collector (BM), 31 May 1908, Iishiba s.n. (DUKE), 21 Dec 1906, Iishiba s.n. (G), 3 May 1908, Iishiba s.n. (WTU), Feb 1907, Uematsu s.n. (JE) and Iishiba 343 (H); Mt Omaetake (= Mt Gozendake), Uematsu 589 (H). Nagano Pref.: Nishimata-gawa, Iida-city, 1200-1300 m, Nishimura s.n. (HIRO-5355); Mt Surikogiyama, Iida city, 1830 m, Higuchi s.n. (HIRO-8410) and 2000 m, Nishimura s.n. (HIRO-7367); Kamiina-gun, Ôshika-mura, 1400 m, Takaki 12078 (NY, TENN); Mt Kuruma-yama, Suwa City, Takaki 6461 (MAK); Mt Akadake, Mt Yatsugatake, Suwa-gun, sine collector (MAK-B57751); Kami-ina-gun, Hase-mura, Todai, 1220 m, Watanabe 18721 (NICH); Mt Yatsugatake, Inoue s.n. (NICH-10810); Shinano (=Nagano Pref.), Mt Yatsugatake, Uematsu 742 (M); Mt Yatsugatake, Jul 1927, Inoue s.n. (WTU); Mt Ontake, ca 2500 m, 25 Aug 1953, Nagano s.n. (WTU); Mt Ontake, near Nigorigo Spa, Iwatsuki & Smith J-459 (NY); Mt Kurohime, Iwasaki s.n. (MAK-B57639); Mt Yatu, 7 Aug 1922, Iishiba s.n. (WTU); Prov. Sinano, Mt Yatu, 9 Aug 1922, Iishiba s.n. (G); Mt Shirouma, Takaki s.n. (MAK-B16375). Nara Pref.: Kotako Valley, Kawakami-mura, Yoshino-gun, 600 m, 3 Apr 1977, Nakajima s.n. (ALTA, BR, CANM, COLO, F, G, H, JE, KRAM, MICH, MO, S, TENN) [Bryophyta Selecta Exsiccata No. 795]; Sanjogatake, en route from Seijo-Ochashi to summit of Mt Sanjo, Tenkawa-mura, Yoshino-gun, 1000 m, Deguchi s.n. (HIRO-6389) and 1050 m, Deguchi s.n. (HIRO-6411); Sanjogatake, en route from Mt Shichiyodake to Mt Gyojagaeti, Yoshino-gun, 1380 m, Deguchi s.n. (HIRO-6690); Sanjogatake, en route from Dorogawa to Seijo-oohashi via Janokura, Tenkawa-mura, Yoshino-gun, 900 m, Deguchi s.n. (HIRO-6257); en route from Dorogawa to Kawai, Tenkawa-mura, Yoshino-gun, ca 800 m, Deguchi s.n. (HIRO-3620 & 3639); en route from Tamaigawa to Mt Tamakisan, Totsukawa-mura, Yoshino-gun, 300 m, Deguchi s.n. (HIRO-7351); Mt Wasamata, Kamikitayama-mura, Yoshino-gun, 1260 m, Deguchis.n. (HIRO-10442) and 1300 m, Deguchis.n. (HIRO-10450 & 10455); Oodaigahara, en route from Oodaigahara parking area to Kaitaku, Kamikitayama-mura, Yoshino-gun, 1350 m, Deguchi s.n. (HIRO-7691) and 1490 m, Deguchi s.n. (HIRO-7637); Oodaigahara, en route from Shiokaradani valley to Sengokugura via Nakanotaki fall, Kamikitayama-mura, Yoshino-gun, 1500 m, Deguchi s.n. (HIRO-7945); Mt Oodaigahara, Takaki 5892 (MICH, S, WTU); Mt Oodaigahara, Yoshino-gun, Toyama 762 (MAK); Takamisan, way from Oomata to Myojindaira ski ground, Higashi Yoshino-mura, Yoshino-gun, 460 m, Deguchi s.n. (HIRO-8098); Shakagatake, en route from Zenki to Zenkiguchi, Yoshino-gun, 700 m, Deguchi s.n. (HIRO-6860); en route from Ozasano-Yado to Shofugen, Yoshino-gun, 1580 m, Deguchi s.n. (HIRO-6611); Mt Kirigamine, 27 Jun 1949, Takaki s.n. (s); Yamato, 15 Apr 1909, Sakurai s.n. (M). Niigata Pref.: Higashi-kambara, Mikawa, May 1948, Ikegami s.n. (ALTA, BM, BR, CANM, CAS, COLO, F, G, JE, KRAM, M, MICH, MO, S, US, W) [Musci Japonici No. 164]; Higashi-kambara, Mikawa, Kawaguchi, Ikegami 9715 (MICH); Iwafune-gun, Sekikawa-mura, Sawa, 100 m, 24 Nov 1957, Ikegami (ALTA, CANM, DUKE, MO, NY, TENN, US) & Ikegami s.n. (BM, CANM, COLO, F, G, JE, KRAM, M, MICH, PR, S, TENN, US, W) [Musci Japonici No. 892] and Ikegami 49971 (PR, TENN); Iwafune, Kuwakawa, 150 m, Ikegami 22084 (PR); Nishi-kubiki, Ichuburi, 20 m, Ikegami 19504 (PR, TENN); Nishikubiki-gun, Mt Amakazari, ca 1500 m, Yano 189 (NICH); Kamo, Kooto, 150 m, Ikegami 26330 (PR); Higashi-kambara, Tsugawa, 60 m, Ikegami 19334 (PR, TENN); Ginzandaira, Kitauonuma-gun, Iwasaki 343 (MAK); Aka-dani (Yunhira-dani) valley, Shibata City, Ikegami s.n. (MAK-B57749); Mt Myoko, Nakakubiki-gun, Iwasaki s.n. (MAK-B57615) and Faurie 206 (PC); Kita-kambara, Mt Gozu, 600 m, Ikegami 45536 (TENN); Yashiro, Arai City, Iwasaki s.n. (MAK-B57675a); Sado I., Hatano, Saruhachi, Ikegami 879 (MICH, WTU); Saruhachi, Hatano-cho, Sado-gun, 30 Apr 1939, Ikegami s.n. (MAK - isotype of Racomitrium hedwigioides var. chrysophyllum). Okayama Pref .: Mt Naginosen near Tsu-yama, ca 600 m, Kodama 2133 (KYO); Bittyu-cho, 150 m, 15 May 1961, Ando s. n. (PR); Otani-gawa river side, Sanyo-cho, Akaiwa-gun, Toda s.n. (MAK-B52404). Osaka Pref .: Yokodani, Takihata, Kawachi, Nagano city, ca 200 m, Deguchi s.n. (HIRO-3186 & 3184, KYO); Mt Iwawakisan, Kawachinagano City, Ui s.n. (MAK-B7784); Toyno-gun, Nishinose-mura, ca 800 m, 5 May 1956, Nakajima s.n. (WTU). Saitama Pref.: Taiyoji temple, Oochigawa, Otaki-mura, Chichibu-gun, Nagano s.n. (MAK-B57618), Nagano s.n. (MAK-B51812 & B57746); Oochigawa, Otaki-mura, Chichibugun, Nagano s.n. (MAK-B51810 & B51811); Mt Mitsumine, Otaki-mura, Chichibu-gun, Nagano s.n. (MAK-B57788 & B57617); Prov. Musashi, Chora - Mt Shiraishi, Chichibu-gun, Maeda 3632 (CANM); Mt Maeshiroiwa, ca 1200 m, 25 Jul 1954, Noguchi s.n. (WTU); Mt Azusashiraiwa, Chichibu, Nagano 100067 (BR). Shiga Pref .: Mt Hiei, Shiga-gun, sine collector (MAK-B3224). Shimane Pref.: Dangyo-kei, 5 Nov 1956, Ando s.n. (PR); Muikaichi-cho, 600 m, 5 May 1966, Ando s.n. (G). Shizouka Pref.: Prov. Izu, Mt Amagi, Sasaoka 4732 & 7211 (BM); Prov. Izu, Mt Higane, Sakurai 334 (PC). Tochigi Pref.: Nikko near Yokohama, 1875, Shaul s.n. (BM - chirotype of Racomitrium brevipes), Faurie 424 (H) & 525 (PC), Gono 104 (M), Bisset (BM, PC – type of Racomitrium canaliculatum), Kamiji 94 (F, FH), Sakurai s.n. (MAK - type of Racomitrium hedwigioides) and Nov 1913, Emery s.n. (TENN); Mt Nikko, Shimozuke, Okamura 693 (H). Tokyo Pref .: Izu Islands, Isl. Miyake, Watanabe 27 (TNS); Isl. Hachijo, ca 850 m, 26 Aug 1955, Hiroi s.n. (WTU). Tottori Pref .: en route from Kawadoko to Amidanotaki fall, Daisen-cho, Seihaku-gun, 700 m, Deguchi s.n. (HIRO-6121). Toyama Pref.: Mt Tateyama, ca 1200 m, 21 May 1961, Honda s.n. (WTU). Wakayama Pref.: Nishimuro-gun, Otô-mura, area of Yasukawa River, 450 m, 27 Mar 1971, Nakajima s.n. (BR, CANM, F, G, GZU, KRAM, M, MICH, MO, S, TENN, US) [Musci Japonici No. 1245]; Yasukawa riverside, Shimokawakami, Ootô-mura, Nishimuro-gun, 530 m, 26 Dec 1971, Deguchi s.n. (HIRO-8593) and 600 m, Deguchi s.n. (HIRO-8718); Mt Koya Okunoin, ca 800 m, Mizutani 4475 (M); Kōyasan, en route from Gokurakubashi to Kōyasan, Kōya-cho, Ito-gun, 630 m, Deguchi s.n. (HIRO-8476); Mt Koya, Aug 1941, Iwasaki s.n. (WTU); Shingu, en route from Ichinotaki fall to Ninotaki fall, Nachikatsuura-cho, Higashi muro-gun, 380 m, Deguchi s.n. (HIRO-7023); Shingu, en route from Funata to Nunobinotaki fall, Shingu city, 25 m, Deguchi s.n. (HIRO-7126); Shingu, Kawayu, Hongu-cho, Higashimuro-gun, 930 m, Deguchi s.n. (HIRO-7193); at back between Kurozō and Oosugi valleys, Hongū -cho, Higashi-muro-gun, 300 m, Deguchi s.n. (HIRO-9809), 350 m, Deguchi s.n. (HIRO-9875) and ca 400 m, Deguchi s.n. (HIRO-9921); Oosugidani valley, Hongū-cho, Higashimuro-gun, 300 m, Deguchi s.n. (HIRO-9804); Yomura, Hongu-cho, Higashimuro-gun, Ui s.n. (MAK-B7926); Kurusugawa, en route from Kurozōdani valley to Shizukawa, Hongū-cho, Higashimuro-gun, 320 m, Deguchi s.n. (HIRO-7289); Kurusugawa, Kurozōdani valley, branch of Ootōgawa river, Hongū-cho, Higashi muro-gun, 280 m, Deguchi s.n. (HIRO-7213) and 320 m, Deguchi s.n. (HIRO-7235); E side of Mt Toragamine, Nakaheji-cho, Nishimuro-gun, ca 300 m, Deguchi s.n. (HIRO-9378); Narumigawa river, Kozagawa-cho, Higashimuro-gun, ca 150-200 m, Deguchi s.n. (HIRO-10258); Ito-gun, Mt Kohya, Iwasaki s. n. (NICH-16172); Nanagawa, Sasaoka 5536 (BM); Yotsumura, Ui 1109 (H); Kinomoto, 13 Nov 1928, Sasaoka s.n. (BM); Shingu City, near Shingu, Ui s.n. (MAK-B7786). Yamagata Pref.: Ubayu, Faurie 2810 (s syntype of Racomitrium anomodontoides; Yonezawa City, near Namegawaonsen, ca 850 m, Igarashi 7578 (TNS). Yamaguchi Pref.: Nagatokyo, 16 Jul 1966, Miake s.n. (TNS). Yamanashi Pref.: Mt Kentoku-zan, Mitomi-mura, Higashiyamanashi-gun, Morita s.n. (MAK-B37638); Fujiyoshida-shi, Mt Fuji, ca 3100 m, Watanabe 4371 (NICH). KYUSHU. Fukuoka Pref.: Mt Shaku-dake, Nogata City, ca 610 m, Kuwahara 2639 (NY); Nogata City, Mt Fukuchi, ca 850 m, Kuwahara 2673 (NY); Mt Seburi, Siibaratoge - Onigahara, ca 800 m, Kuwahara 2848 (NY); Yamegun, ca 300 m, Kuwahara 2499 (NY). Kagoshima Pref.: Yakushima Island, Anbo, Schofield 53139 (CANM, DUKE) & 53124 (CANM, DUKE, MO, s); Anbo, ca 180 m, Yaku-machi, Kumage-gun, Watanabe 24150 (TNS); area of Anbo-gawa and Hanano-ego, 1280-1600 m, Iwatsuki, Smith & Suzuki 11156 (F); Kosugidani, 15 Jul 1957, Noguchi s.n. (NY); near and above Anbo-gawa, dam below Kosugidani, 660-700 m. Iwatsuki & Sharp 14136 (US); between Anbō-gawa dam and Kosugidani, 600-750 m, Iwatsuki & Sharp 14136 (TENN); Yakushima to Hananoega from Osugidani Kanko, ca 1200 m, Kuwahara 667 (NY); Hana-no-ego bogs, Iwatsuki et al. J-1224 (NY); Hana-age-gawa, 50 m, Iwatsuki et al. J-1032 (NY); Yakushima Is., 420 m, Iwatsuki & Smith J-921 (NY); above Tainokawa, 150-450 m, Iwatsuki et al. J-1063 & 1096 (NY); slopes of the Tainokawa valley above the sugar mill, 250-450 m, Iwatsuki & Sharp 14481 (TENN); Kosugi-dani valley - Arakawa-guchi, Ikegami s.n. (MAK-B20520); Mt Miyanouradake, sine collector (MAK-B2813); Hananoego,

Anbo river, 4 Aug 1936, Takaki s.n. (MAK - type of Racomitrium yakushimense); Iles Liou-Kiou, Yaku-Sima, Oct/Nov 1899, Faurie s.n. (PC); slopes of the Tainokawa valley above the sugar mill, 250-450 m, Iwatsuki & Sharp 14481 (US, WTU); from Kosugidani to Hananoego, 1400-1700 m, 5 Dec 1964, Iwatsuki & Sharp 14244 (WTU) & 14244a, 15352 & 15340 (TENN); near "Wilson's Tree" above Kosugidani, 1000-1200 m, Iwatsuki & Sharp 15101 & 15216 (TENN) and 1175 m, Iwatsuki & Sharp 14033 (TENN); valley of the Suzukawa between Onoaida and the falls, 150-500 m, Iwatsuki & Sharp 14374 (TENN, WTU) and Iwatsuki & Sharp 15570 (TENN); Yakushima Isl., Hasimoto s.n. (NICH-8698) and Faurie 1063 (H); Is. Sakura-jima, Shin s.n. (MAK-B16325) and Doi s.n. (MAK-B2909 & B2911); Mt Sakurajima, Narahara s.n. (NICH-3995). Kumamoto Pref.: Gokanosho, ca. 600 m, May 1958, Muraoka s.n. (CANM, TENN); near Hitoyoshi, ca. 600 m, 2 March 1952, Mayebara s.n. (ALTA, BM, BR, CANM, COLO, F, G, GZU, JE, KRAM, M, MO, POZG, PR, S, TENN, US, W) [Musci Japonici No. 539] & Mayebara s.n. (DUKE, MICH, PR); Hitoyoshi, Mayebara s.n. (MAK-B57744) and Mayebara s.n. (MAK-B57748); Mt Yahazu, Minamata city, 19 July 1936, Kaneda 657 (MAK-B7925, s); Onigatake, Minamata city, 26 May 1935, Kaneda 50 (s); Mt Ichibusa, Kuma-gun, 12 Jan 1936, Mayebara s.n. (MAK-B7475 & B9115); Mt Kinimi-dake, Kuma-mura, Kuma-gun, 21 Aug 1935, Takahashi s.n. (MAK-B6862): Ishochi, Kuma-mura, Kumagun, 15 March 1955, Mayebara s.n. (MAK-B57614 & B57862); Mizukami-mura, Kuma-gun, Mayebara s.n. (MAK-B57613); Mt Onigatake, Minamata City, 26 May 1935, Kaneda s.n. (MAK-B5007); Nishikino, Otsu-machi, Kikuchi-gun, Takaki s.n. (MAK-B4409); Mt Naidaijin-yama, Yabe-cho, Kamimashiki-gun, Kaneda s.n. (MAK-B6154 & B6128); Mt Fukaba, 23 July 1934, Takaki s.n. (NICH-13855); Midukami-mura, ca 700 m, 5 July 1959, Mayebara s.n. (0); Higo, Mt Shakanoora, Aug 1915, Tashiro 1365 (H, WTU); Mt Ichifusa, 6 Dec 1936, Mayebara s.n. (TENN); Mt Aso, Nishikino, 4 Nov 1934 Takaki 314 (F); Mt Ohira (Oohira), Kuma-gun, Mayebara s.n. (MAK-B57637). Miyazaki Pref.: Hachinosu, N of Nichinan, 50-100 m, Schofield & Iwatsuki 51772 (ALTA, CANM, DUKE); Kitago, Inohae valley, Iwatsuki M35774 (M); Inohae valley, N of Obi, Kitago-cho, Minaminaka-gun, ca 100-200 m, Iwatsuki et al. 14978 (TENN); around Obi, Nichinan, Hattori 70029 (TNS); Hyūga, Mt Osuzu for the Hachinosu, ca 650 m, Kuwahara 241 (NY); Hyūga, Mt Osuzu, ca 550 m, Kuwahara 250 (NY), ca 1200-1400 m, Kuwahara 413 (NY), ca 1400 m, Kuwahara 637 (NY), and 1200-1600 m, Kuwahara 272 (NY); Hyūga, Mt Osuzu, Yatogi fall, ca 550 m, Kuwahara 292 (NY); Kaeda valley near Miyazaki City, 3 Jun 1983, Steere s.n. (NY); Kaeda River Valley, Glime 4503 (NY); Mt Kirishima, Iwasaki s.n. (MAK-B57616) & 30 Mar 1933, Noguchi s.n. (WTU); Kirishima, circumference of the Onami (pond), Kuwahara 42 (NY); Kobayashi, 650 m, Iwatsuki & Smith 77 (NY). Ôita Pref.: Mt Sobo, Samandani valley, ca 650 m, 17 Oct 1952, Noguchi s.n. (BM, CANM, COLO, DUKE, F, FLAS, G, JE, KRAM, M, MICH, MO, PR, S, TENN, US, W) [Musci Japonici No. 995]; Mt Sobo, ca 650 m, 17 Oct 1952, Noguchi s.n. (CANM, MICH, TENN), ca 1700 m, 23 Aug 1954, Noguchi s.n. (WTU) and ca 1750 m, Kuwahara 2039 (NY); Shimoke, Fukayabakei, ca 400 m, Nov 1946, Noguchi s.n. (BM, CANM, COLO, E, F, FH, G, HIRO, JE, KRAM, M, MICH, O, POZG, PR, S, TENN, US, W) [Musci Japonici No. 60]; Mt Yufu, Yufuin-cho, Ooita-gun, 1500 m, Deguchi s.n. (HIRO-11163 & 11175); Prov. Bungo, Kasagi-dani, Mt Kuju, Arao s.n. (MAK-B9129). Saga Pref.: Mt Kurogami, Prov. Hizen, Sasaoka 5129 (BM); Mt Tara-dake, Fujitsu-gun, sine collector (MAK-B100769). SHIKOKU. Ehime Pref.: Nii, Sumino, Mar 1947, Oti s.n. (BM, CANM, COLO, F, FH, G, H, HIRO, KRAM, MICH, MO, O, PR, S, TENN, US, w) [Musci Japonici No. 62]; Dôzangoe Hütte - Mt Nishiakaishi, Besshiyama-mura, Uma-gun, 1150 m, Deguchi s.n. (HIRO-11349, 11350 & 11351) and 1600 m, Deguchi s.n. (HIRO-11395 & 11394); Mt Nishiakaishi, Niihama City, Kochi s.n. (MAK-B57786); Mt Mae-Akaishi - Mt Higashi-Akaishi, Besshiyama-mura, Uma-gun, 1680 m, Deguchi s.n. (HIRO-11436, 11439, 11460 & 11521); Karei, Awa, 30 Dec 1905, Okamura s.n. (FH, H) & 316 (NICH); Kamiukena-gun, Mt Ishizuchi, 1420 m, Une s.n. (HIRO-1766); Kamiukena-gun, Omogokei, Une s.n. (HIRO-1792); Yuya, Matsuyama City, Kochi s.n. (MAK-B57789); Yokominedera, Komatsu-cho, Shuso-gun, Kochi s.n. (MAK-B57740); Chogi, Saijo City, Ochi s.n. (MAK-B51818); Mt Iyofuji, Saijo City, sine collector (MAK-B57610); Doi, Komatsu-machi, Shuso-gun, Kochi s.n. (MAK-B57625); Gongengoe pass - Kômata, Doi-cho, Uma-gun, 1350 m, Deguchi s.n. (HIRO-11481); Saijyo-shi, Mt Ishizuchi, ca 1800 m, Watanabe 20165 (NICH); Prov. Iyo, Izumi, Sasaoka 6227 (BM); Prov. Iyo, Asahi 12 Nov 1930, Sasaoka s.n. (BM). Kochi Pref.: Mt Irazu, Tosa, *Okamura 643* (н). *Tokushima Pref.*: Mt Tsurugi, 1700–1900 m, *Koponen 36464* (н); between Koboke and Ooboke, Miyoshi-gun, ca 100 m, *Deguchi 4413* (куо).

NORTH KOREA. Kumkang-san (= Diamond Mts), *Faurie 366* (H, NY – syntype of *Racomitrium anomodontoides*), 14 Jul 1979, *Hojoon Hwang s.n.* (PRC) and 900 m, Jul 1981, *Frank s.n.* (PR).

SOUTH KOREA. CHEJU-DO PROV. Pukcheju-gun Co.: Hallasan National Park, along Songp'anak Trail toward Mt Hanna at Chiaallaehatdaep'iso Camp W of hwy 11 from Songp'anak Rest Area, 1500 m, *Shevock 16377A* (CAS, KRAM); Kanrasan Saisyuto Zenranando Chosen Nippon (= Mt Hanra, Chedzu I.), Uno s.n. (MAK-B57611) and Uno s.n. (MAK-B57745); Ile Quelpaert (= Cheju I.), 1200 m, Faurie 92 (s – syntype of Racomitrium fasciculare var. brachyphyllum). GANGWAN PROV. Tjyang-Tjyen (= Gangwan Province near Seoul), Faurie 343 (H, NY, PC – isolectotype of Racomitrium fasciculare var. brachyphyllum). NORTH GYEONGSANG PROV. Uleung Co.: Quen San Island (= Dokdo I.), Faurie 23 (PC – syntype of Racomitrium fasciculare var. orientale).

TAIWAN. Chia-vi Co.: between Tong-pu and Pai-mu-lin, near Mt Morrison, 2500-2900 m, Iwatsuki & Sharp 2410 (TENN). Ilan Co.: Mt Tai-ping-shan, 2000-2200 m, Ching-chang Chuang 2219 (ALTA, CANM, MO); Central Mountain Range, Chi-Lan Forest Recreation Area, between 1-2 km before Yuan-Yang (Mandarin Duck) Lake Nature Preserve, Shevock, Lin Shu-Hong & Lai Kwo-Shang 18224 (CAS, KRAM). Pingtung Co.: Kwai-ku, 2190 m, Ching-chang Chuang 1402 (ALTA, CANM, MO) & 1412 (ALTA, CANM, MO); Kwai-ku to Mt Pei-ta-wu-shan, 2190-3090 m, Ching-chang Chuang 1498 (ALTA, CANM) & 1520 (CANM, NY); Ako, Mt Daibu, Matsumura 1311 (H). Taichung Co.: Mt Notaka, Taichu (= name of uncertain locality in Taichung Co.). Nakamura s.n. (MAK-B57790); Mt Noko (= Mt Nengao), 5 Aug 1926, Suzuki s.n. (MAK isotype of Racomitrium formosicum); Hsueh Shan Mo, 17 km above Anma-shan at edge of logging area near Chunghsueh-shan, ca 2500 m, Iwatsuki & Sharp 2769 (TENN). Taipei Co.: Tatun Shan, 500-1090 m, Ching-chang Chuang 5463 (ALTA, CANM, KRAM, MO) and ca 1090 m, 24 Nov 1974, Lin s.n. (ALTA, H, MICH, MO) [Bryophytes of Taiwan No 243]; Taitum (= Mt Datun), Yangmingshan National Park, Faurie 51 (PC) & 163 (BM, PC). Taitung Co.: Haituan Hsiang, Hsiangyang Shan, ca 3080 m, 25 Dec 1977, Lin s.n. (ALTA, MICH, MO) [Brvophytes of Taiwan No 242]; Yakou, hillside near South Cross Hwy, 2750 m, Lai 9501 (FH, G, MO, US).

OCEANIA. U.S.A. HAWAHAN ISLANDS. *Maui Island*: W Maui, *Baldwin 573* (H, NY – type of *Racomitrium perrobustum*), ca 1065 m, *Baldwin 102* (FH, NY), *Baldwin 1192* (H – type of *Racomitrium erosum*) and 1876, *Baldwin s.n.* (NY); West Maui Mts., Honokohau Valley, in *Metrosideros* forest, 335–610 m, *Bishop 2068* (BISH); Honokohau Valley, ca 245–335 m, *Bishop 2056 & 2057* (BISH).

PHILIPPINES. LUZON. Between Durongawan III and Ilalim, Mt Banahao, 2300–2800 m, *Iwatsuki & Sharp 14352 & 16321* (TENN). **MINDORO**. Dulagang river bank, Mt Halcon System Baco, 1160 m, *Tan* 87-215 (H).

13. *Codriophorus corrugatus* Bednarek-Ochyra (Figs 91–94)

Codriophorus corrugatus Bednarek-Ochyra, Bryologist 107: 377, *f.* 1–77. 2004. — TYPE CITATION: China, Prov. Sichuan, Song Fan County: near Huang Long Temple, lat. 32°20' N, long. 103°30' E; on soil in primeval *Abies–Picea* forest, alt. 3,040–3,460 m; 8 June 1983, coll. Si He 30455 [Holotype: "China Encoded in TROPICOS Grimmiaceae Racomitrium fasciculare var atroviride Card. Det. Si He, 1994 Sichuan Song Fan County. Near Huang Long Temple. In primeval Abies–Picea forest. <30404–30595> On soils. 32°20' N, 103°30' E 3040–3460 m Si He 30455 8 June 1983 Missouri Botanical garden Herbarium (MO)" – Mo!; isotype: KRAM!).

Grimmia fascicularis (Hedw.) Müll.Hal. fo. *subsimplex* Arnell, Ark. Bot. 13(2): 62. 1913. — TYPE CITATION: [Russia, Siberia, in the valley of the Lena River] Auf einem Kalkberg am östlichen Flussufer Kumachsur gegenüber, forma subsimplex, reichlich gesammelt und mit *Hylocomium proliferum*, *H. rugosum*, *Thuidium abietinum*, *Tortula ruralis*, *Dorcadion Killiasii* usw. vergesellschaftet [Lectotype (vide Bednarek-Ochyra 2004c: p. 377): "Naturhistoriska



FIGURE 91. Codriophorus corrugatus. — 1. Habit. 2. Portion of branch, wet. 3–15. Leaves. 16–28. Leaf apices. — [1–2, 9–13, 18, 20–25 from *He* 30455, M0 (holotype); 3–6 from *Tan & Yu 95-1730*, FH; 7–8, 17 from *Nilsson-Ehle s.n.*, 30 Jul 1898, H; 14–15, 19, 26–28 from *Frahm s.n.*, 14 Aug 1988, KRAM; 16 from *Deguchi 12483*, HIRO]. — Scale bars: a – 1 mm (3–15); b – 1 mm (20–28); c – 0.5 mm (16–19); d – 0.5 cm (2) and 2 cm (1). (Reproduced from *The Bryologist*, 107: 378, 2004, with permission).



FIGURE 92. Codriophorus corrugatus. — 1–3. Branch leaves. 4–9. Cauline leaves. 10–15. Leaf apices. — $[1-5, 10-11 \text{ from Annenkhanov s.n., 16 Jul 2002, KRAM; 6–7, 13 from Deguchi s.n., HIRO-12326; 8–9, 14–15 from Musci japonici 596, KRAM; 12 from Jinno s.n., HIRO-14730]. — Scale bars: a – 1 mm (1–9); b – 100 µm (10–15).$

Riksmuseum, Stockholm. Grimmia fascicularis (Schrad.) f. simplex Sibiria, in valle flum. Lena, Kumachsur, 70°30' lat. bor. 31/7 1898 Leg. H. Nilsson-Ehle. Det. H. Wilh. Arnell." – s!; isotypes: H!, LE!, s!]. First synonymised with *Codriophorus corrugatus* by Bednarek-Ochyra (2004*c*: p. 377).

Plants small, medium-sized to large, slender to relatively robust, usually coarse, rather stiff and rigid, dull, dark or light yellow-green to yellow-brown, sometimes olive-green or olive golden above, brown to dark brown below, forming wide loose patches or growing in dense turves. Stems ascending to erect, less often prostrate, (1-)3-10 cm long, sparsely fasciculate-branched, often with many short tuft-like horizontal lateral branchlets, rarely unbranched, in transverse section circular, lacking central strand, comprising 4-5 layers of small sclerenchymatous cells with brown strongly thickened walls and small lumina surrounding the 5-7-stratose medulla composed of large hyaline to yellowish-hyaline cells with moderately to strongly thickened walls; rhizoids usually very sparse at base of stem or scattered along the stems, very rarely abundant in clusters on prostrate stems, long, poorly branched, thick, dark brown to blackish-brown with varnish-like lustre; axillary hairs numerous at stem and branch tips, filiform, hyaline throughout, composed of 14-15 cells, with 2-4 short basal cells and elongate, cylindrical upper cells. Stem and branch leaves similar in size and shape, the latter often being narrower and usually more slenderly long-acuminate, erect, appressed and somewhat curved, rarely closely imbricate when dry, loosely erect to spreading or sometimes squarrose-recurved when moist, 2.5-4.5 mm long, 0.6-1.0 mm wide, ovate-lanceolate to narrowly lanceolate, from a widely ovate base shortly acuminate to slenderly long acuminate, usually with a fine serpentine, corrugated and strongly wavy acumen, acute to filiform at the narrow, concolorous or sometimes subhyaline or blunt and wider, muticous tip, slightly decurrent, plicate at base, deeply concave and broadly canaliculate throughout; margins unistratose throughout, entire below, cristate, dentate to papillose-crenulate at the apex, revolute in the proximal part, broadly recurved above, mostly variously infolded in the snake-like acumen; costa single but often laterally spurred above or forked at the apex,



FIGURE 93. Codriophorus corrugatus. — 1. Portion of stem section. 2–4. Axillary hairs. 5–6. Leaf apices. 7. Mid-leaf cells. 8. Supra-basal leaf cells. 9. Basal juxtacostal cells. 10. Alar cells. 11. Outlines of transverse leaf sections, sequence from base to apex. 12–25. Transverse sections of costae and leaves. — [1-11, 17-21 from from *He 30455*, MO (holotype); 12–16 from *Frahm s.n.*, 14 Aug 1988, KRAM; 21–23 from *Nilsson-Ehle s.n.*, 30 Jul 1898, H; 24–25 from *Deguchi 12483*, HIRO]. — Scale bars a – 100 µm (2–4); b – 100 µm (1, 5–10, 12–25); c – 0.5 mm (11). (Reproduced from *The Bryologist*, 107: 379, 2004, with permission).

disappearing in mid-leaf or somewhat above, concolorous and usually imperceptibly merging into the laminal cells above or sharply demarcated from the laminal cells, bright to dark yellow, weak but very variable on the same plant, (30-)40-60(-70) µm wide near the base, usually gradually tapering upwards, lying in the proximal part in a deep, narrow-angled groove partly enclosed by the strongly infolded leaf lamina, in transverse section flat on both ventral and dorsal surfaces or somewhat curved on the dorsal side in the lower part, bistratose throughout, sometimes with tristratose spots at the extreme base, with 6-9 large ventral cells and 6-12 small, substereid dorsal cells; laminal cells unistratose throughout, densely covered on both surfaces with large, flat papillae, with strongly sinuose to nodulose and porose thick walls, rectangular to long rectangular, (25-)30-70(-90) µm long, 6-8 µm wide, in the subulate acumen and upper part, becoming longer and linear in the median and lower parts, up to 150 µm long; basal cells rectangular, shorter and wider than the upper cells, 30-50 µm long, 8–10 µm wide, strongly nodulose and porose, not sinuose-walled, intensely bright yellow and forming a distinct 1-2-seriate colourful strip at the insertion; alar cells subquadrate to short-rectangular, 20-30 µm long, 15-25 µm wide, with moderately to strongly thickened porose walls, yellow to dark brown, forming distinct, decurrent, somewhat convex auricles; supra-alar cells subquadrate to rectangular, 10-40(-50) µm long, 8-15 µm wide, thin- to thick-walled, usually pellucid, with straight to moderately sinuose walls, forming a distinct uniseriate border composed of 5-10 cells. Dioicous. Perigonia bud-like, to 2.5 mm long; outer perigonial bracts ovate to ovate-lanceolate, to 2 mm long, short- to long acuminate, subacute or broadly obtuse, cristate at the apex, with a costa disappearing in mid-leaf; inner perigonial bracts ovate, broadly acute, to 0.8 mm long, strongly concave, brownish-green; antheridia club-shaped, brownish, up to 21 per perigonium, with a few hyaline or hyalinebrownish paraphyses nearly as long as the antheridia. Outer perichaetial leaves ovate-lanceolate, to 3 mm long, 0.7–0.9 mm wide, gradually tapering to the broadly acute or obtuse, cristate, somewhat ruffled apex, with a costa extending to mid-leaf or somewhat higher; inner perichaetial leaves oblong-lanceolate to oblong-ovate, short-acuminate, broadly acute, with a short costa ceasing usually below mid-leaf and an areolation of hyaline, thin-walled cells throughout the bracts. Setae exserted, straight, 4-8(-12) mm long, mostly one per perichaetium, occasionally geminate or triple, yellowish-brown when young, becoming dark to blackish-brown with age, lustrous, smooth, dextrorse almost throughout but with a single torsion to the left immediately below the capsule, epidermal cells elongate with thick walls, in transverse section composed of a single row of sclerenchymatous cells with strongly thickened outer walls and 5–6 rows of large, thick-walled yellowish-hyaline medullary cells, becoming resorbed in the central part in older setae; vaginula dark brown, to 1 mm long, with elongate, thick- and sinuosewalled epidermal cells. Capsules straight, erect, obloid to cylindrical, distinctly tapering towards the seta and orifice, 1.5-2.0 mm long, 0.7-0.9 mm wide, light to dark brown, smooth, lustrous, pachydermous; operculum erect, long rostrate with a straight or somewhat obliquely inclined rostrum nearly as long as the urn; annulus revoluble, consisting of 2 rows of cells, the outer enlarged, thick-walled and vesiculose; exothecial cells variable, mostly oblong to rectangular but mixed with isodiametric, irregular to subquadrate, 20-50(-60) µm long, 8-15(-20) µm wide, thick-walled, becoming rounded towards the mouth and forming a distinct, 4-6-seriate orange-brown rim; stomata numerous, 15-20 per urn, disposed in 2-3 layers at the base of the urn, bicellular, round-pored; peristome single, composed of 16 teeth, with or without a low basal membrane, to 20 µm tall, 640-760(-950) µm long, yellow- or orange-brown to dark brown, split to the base into 2 filiform, terete, weakly articulated prongs, densely papillose with tall, conical papillae. Spores globose, pale brownish, finely papillose, 14-20 µm in diameter. Calyptra conicalmitrate, somewhat roughened at the apex, naked, non-plicate, brown.

Etymology — The specific epithet, signifying wavy, refers to the leaf apices which are often snake-like and strongly wavy or ruffled at the margins and this characteristic feature makes *Codriophorus corrugatus* easily distinguishable from all other species of the genus.

Diagnostic characters and differentiation — Codriophorus corrugatus is characterised by the following set of characters in combination: (1) plants small, medium-sized or large, slender to robust, usually coarse and rather stiff and rigid; (2) stem ascending to erect, sparsely fasciculate-branched, often with many short, horizontal, tuft-like branchlets; (3) leaves ovate-lanceolate to narrowly lanceolate, slenderly long acuminate; (4) leaf acumen serpentine, corrugated and usually extremely wavy; (5) leaf apex acute to filiform, concolorous or subhyaline, cristate or papillose-crenulate; (6) leaf margins unistratose, entire except for the apex, revolute in the proximal portion, broadly recurved distally, variously infolded in the snakelike acumen; (7) costa single, often laterally spurred or forked at the apex, extending to mid-leaf or only somewhat above, (30-)40-60(-70) µm wide near the base,

FIGURE 94. Codriophorus corrugatus. — 1. Portion of branch with mature sporophyte. 2. Perigonium. 3–4. Outer perigonial bracts. 5. Inner perigonial bracts. 6. Inner perigonial bract with antheridia. 7. Epidermal cells of vaginula. 8. Transverse section of seta. 9–10. Outer perichaetial leaves. 11–12. Inner perichaetial leaves. 13. Apex of innermost perichaetial leaf. 14. Mature capsule with calyptra. 15–17. Operculate capsules, wet. 18–19. Deoperculate capsules, wet. 20. Calyptra. 21. Transverse section of mid-calyptra. 22. Exothecial cells in mid-urn. 23. Exothecial cells and stomata at base of urn. 24. Peristome teeth, exothecial cells at orifice and spores. — [1, 13, 24 from *Deguchi 12483*, HIRO; 2–12, 14–23 from *Frahm s.n.*, 14 Aug 1988, KRAM]. — Scale bars: a – 1 mm (9–12) and 100 µm (24); b – 1 mm (2); c – 0.25 cm (1), 2 mm (14–20) and 100 µm (7–8, 13, 21–23); d – 1 mm (3–6). (Reproduced from *The Bryologist*, 107: 380, 2004, with permission).



situated in a deep, narrow-angled groove, partly enclosed by the strongly infolded leaf lamina, in cross- section bistratose throughout, with 6-9 large ventral cells and 6-12 small, substereid dorsal cells, flat dorsally and ventrally; (8) laminal cells unistratose throughout, linear in the proximal part, elongate-rectangular distally; (9) basal marginal cells subquadrate to rectangular, forming a distinct, pellucid, uniseriate border consisting of 5-10 cells; (10) innermost perichaetial leaves hyaline throughout; (11) setae exserted, 4-8 or, occasionally, to 12 mm long, dark to blackish-brown, twisted to the right with a single torsion to the left immediately below the capsule on drying; (12) capsules obloid to cylindrical, 1.5-2.0 mm long; (13) peristome teeth divided to the base into 2 filiform branches, vellow- or orange-brown to dark brown, densely papillose, arising from a low basal membrane which is sometimes lacking.

Codriophorus corrugatus is distinct and readily distinguished from all other species of *Codriophorus* section *Fascicularia* and subsection *Fasciformes* by its peculiar serpentine leaf acumen which is corrugated or ruffled in the upper part and this unique form of the leaf subula is unknown in any species of the genus *Codriophorus*, except for some populations of *C. laevigatus*. This leaf apex shape is coupled with a short costa which typically extends to mid-leaf or only a little higher in some leaves. Despite the obvious distinctness of this combination of characters, the species has been commonly mistaken, especially in Japan, with every other species of subsect. *Fasciformes*, especially with *C. fascicularis* resulting from the lack of lectotypification and precise circumscription of the latter species.

Codriophorus corrugatus appears to be most closely related to C. anomodontoides with which it shares the dentate-cristate or papillose-crenulate leaf apex and the placement of the costa in a deep channel in the proximal part. However, the costa in C. anomodontoides is generally longer and extends to ²/₃ of the way up the leaf, the basic difference between these species lying in its anatomy. In C. corrugatus the costa is flat on the ventral surface, while in C. anomodontoides it is distinctly convex ventrally as is clearly seen in transverse sections of the leaves (see Fig. 87). In addition, C. corrugatus has very long peristome teeth, 640-760 µm and in one case even 910-950 µm long, which are split nearly to the base into two terete filiform segments which are more than twice as long as those in C. anomodontoides where they do not exceed 300 µm.

Codriophorus corrugatus may also be mistaken for C. fascicularis in which, however, the costa extends to $\frac{3}{4}$ or higher up the leaf and is entire throughout or rarely spurred or forked at the tip. Also it is not grooved or, if so, the groove is shallow and wide-angled. In contrast, in C. corrugatus, the costa vanishes in mid-leaf, only exceptionally extending higher up on some leaves and, moreover, it is frequently spurred and forked at the apex. It lies at the bottom of a deep, narrow-angled groove which is partially enclosed in the upper part by the strongly infolded leaf lamina. The leaf apex in C. fascicularis is

entire, whereas that in *C. corrugatus* is cristate or papillose-crenulate. The peristome teeth in *C. fascicularis* are generally shorter, up to 600 μ m in length.

The third species of *Codriophorus* subsect. *Fasciformes*, *C. brevisetus*, shares with *C. corrugatus* the shape of the costa in transverse section, but is at once distinct in its variously bistratose leaf margins in the distal portion and the long costa that extends to at least ³/₄ of the way up the leaf and usually ceases a short distance from the apex (see Fig. 81).

The corrugated and wavy leaf apices are known in some populations of the austral *Codriophorus laevigatus* but this species is unlikely to be mistaken for *C. corrugatus* and not just for phytogeographical reasons. It is at a glance distinct by having hyaline to yellowish-hyaline leaf hair-points, distinctly multiplicate leaves and welldifferentiated auricles composed of large, isodiametric to shortly rectangular, yellowish-brown to orange-brown cells with moderately thick to strongly incrassate walls, usually forming distinct decurrencies.

Confusion of *Codriophorus corrugatus* with species of the type section of the genus is improbable because their costa, 3–5-layered in the median and basal parts, as well as isodiametric to shortly rectangular laminal cells in the distal portion immediately preclude it.

Variability — Codriophorus corrugatus exhibits some morphological variation with regard to the size of the plants, branching pattern, leaf size and shape as well as shape of the leaf apex, but all taxonomically important characters show only slight variation and are easily observed in all populations of the species. The Japanese and Alaskan plants are rather smaller and more slender in comparison with those from mainland Asia where some populations are represented by luxuriant handsome plants, to 10 cm tall, for example the type material from Sichuan. In general, the majority of plants are sparsely fasciculate-branched, with many regular short tuft-like lateral branches which are observed throughout the species' whole range. Very rarely, the stems of one plant from Kamchatka (Czernyadjeva 8, KRAM) lack any branches and lateral tuft-like branchlets and the plants are represented by unbranched, filiform shoots, to 2.5 cm tall, with a dense foliage of closely imbricate leaves.

The leaves are subject to considerable variation, especially in size and shape and in the length of the subulate point. The leaf length ranges from 2.5 to 4.5 mm, and the leaf shape varies from ovate-lanceolate to narrowly lanceolate, with the apex being shortly acuminate to slenderly long-acuminate, sometimes very long, filiform and subhyaline at the extreme apex. The latter shape of the leaves is typical for the plants from the southernmost part of the range in China and Southern Siberia and these plants have usually short, tuft-like lateral branchlets, whereas the plants from Japan and more northerly latitudes have mostly smaller, ovate-lanceolate and shortly acuminate leaves and fairly often the stems are sparsely fasciculate-branched, without short tuft-like horizontal lateral branchlets. Despite the varying length of the leaf subula, the characteristic corrugated and wavy shape of the acumen is perfectly preserved in all plants, making *C. corrugatus* a practically unmistakable species.

Sporophytically, *Codriophorus corrugatus* shows little variation. Sporophytes commonly occur singly in the perichaetium, but occasionally 2 or 3 capsules are assembled in a single perichaetium (e.g., *Yasuda s.n.*, 1 May 1900, H). The setae are usually short, 4–8 mm, but sometimes they are longer, 9–12 mm (e.g., *Uematsu 233*, H). Likewise, the peristome teeth are usually 640–760 µm long, but occasionally they may be much longer, 910–950 µm (*Yasuda s.n.*, 1 May 1900, H).

Reproduction — Codriophorus corrugatus frequently produces sporophytes, sometimes in great profusion, but only in Japan. Also, the only North American specimen is fertile with quite abundant sporophytes. In contrast, all plants from mainland Asia are consistently sterile.

Taxonomic and nomenclatural notes — Codriophorus corrugatus has only recently been described as a separate species on the basis of specimens from East Asia (China, Russia, Japan) which had previously been variously named as *Racomitrium fasciculare*, *R. fasciculare* var. atroviride, *R. fasciculare* var. brachyphyllum, *R. brevisetum*, *R. canaliculatum* and *R. anomodontoides*, while a single specimen from North America (Alaska) had been determined as *R. varium* (Bednarek-Ochyra 2004c). When carefully searching through the bryological literature, the author became aware that there had been earlier recognition of this taxon. Arnell (1913) distinguished one of two specimens of *R. fasciculare* from the valley of the

lower Lena River in Arctic Siberia as a separate form, *Grimmia fascicularis* fo. *subsimplex*. He did not observe the essential diagnostic characters of *Codriophorus corrugatus* but distinguished his new form on account of the branching pattern, pointing out that the main difference of this taxon from the type form of *R. fasciculare* was the lack of short tuft-like lateral branches, a feature frequently observed in arctic and northern boreal plants of *R. fasciculare* from, for example, Spitsbergen, Bear Island and Iceland. This form had totally fallen into oblivion and examination of the type material revealed that it perfectly fitted the concept of what had been described as *Codriophorus corrugatus*. Accordingly, the name of this form has been reduced to synonymy with this species name (Bednarek-Ochyra 2004*c*).

Chromosome number — Not available.

Habitat — The habitat data for *Codriophorus corrugatus* taken from the labels are rather scanty and incomplete, thus making detailed ecological characterisation of the species difficult. They are relatively most complete for Chinese plants which were collected on rocks, boulders, shaded slopes and soil in alpine meadows, in shaded and dry gorges, as well as on the ground in primeval *Abies–Picea* forest. It appears to be associated in China with calcareous areas as indicated on the label of the species growing in association with *C. corrugatus* such as *Tortella tortuosa* (Hedw.) Limpr., *Ditrichum flexicaule* (Schwägr.) Hampe, and *Didymodon ferrugineus* (Besch.) M.O.Hill, which are indicators of calcareous substrates. Likewise,



FIGURE 95. Global distribution of Codriophorus corrugatus.



FIGURE 96. Distribution of Codriophorus corrugatus in East Asia.

Arnell (1913) described the specimens from the valley of the Lena River as collected on calcareous ground together with *Abietinella abietina* (Hedw.) M.Fleisch., *Rhytidium rugosum* (Hedw.) Kindb., *Orthotrichum killiasii* Müll.Hal., *Hylocomium splendens* (Hedw.) Schimp. and *Syntrichia ruralis* (Hedw.) F.Weber & D.Mohr. Habitat data for the Japanese and Kamchatkan populations are very scanty and general. On the labels of some specimens it is indicated that they were collected from rock (but with no indication of its type), boulders and cliffs, sometimes in partial shade. The Alaskan plant came from birch-spruce forest without any more detailed data. The association of *C. corrugatus* with base-rich habitats is in remarkable contrast to its close relative *C. fascicularis* which is an acidophilous species.

Geographical distribution — *Codriophorus corrugatus* is an east-Asian north-western North American disjunct boreal-temperate-montane species (Fig. 95). Only occasionally it penetrates into the Arctic where it has so far been recorded only twice by the lower Lena River in Eastern Siberia (for details of collecting sites in Arctic Siberia see Konstantinova & Filin 1998). In the northern part of its Asian temperate range (Fig. 96), the species is known from a fell-field in the subalpine belt at an elevation of 300 m in southern Kamchatka and from high altitudes in the Jablonovy Khrebet (= Yablonovy Range) and in the Western Sayan Mountains in Southern Siberia, where it was collected at an altitude of ca 2300 m. By contrast, in the southern temperate part of its range, C. corrugatus occurs only in the mountains in the Chinese provinces of Qinghai, Shaanxi and Sichuan at altitudes from 3040 to 4200 m and Japan, which is the main centre of its occurrence. In Japan, it is widespread and locally abundant on Hokkaido and northern Honshu where it has maximum occurrence at elevations from 1000 to 2300 m, occasionally ascending to 3000 m and descending to 350 m. The only North American locality of C. corrugatus is situated in the boreal zone in south-eastern Alaska.

EXSICCATI

- NOGUCHI & HATTORI *Musci Japonici* No. **596** (as *Racomitrium fasciculare*) (BISH, BM, COLO, JE, KRAM, MICH, S, TENN, US, W).
- NOGUCHI & IWATSUKI *Musci Japonici Exsiccati* No. **1291** (as *Racomitrium fasciculare*) (ALTA, BISH, BR, COLO, hb. Frahm, KRAM, MO, POZG, S, TENN, US).

SPECIMENS EXAMINED

ASIA. CHINA. QUINGHAI PROV. *Nangqen Co.*: vicinity of Small Dragon Canyon (Xiao-lung-gou), about 30 km from Nangqen town, road to the site of *Sinodoxa*, 4000–4200 m, *Tan 95–1730* (FH, KRAM, MO). SHAANXI PROV. *Qinling Co.*: without closer locality data, *Huang Quan 1411* (MO). SICHUAN PROV. *Heishui Co.*: near km 20, highway to Heishui, 4100 m, *Redfearn et al. 35496A* (KRAM, MO). *Songpan Co.*: near Huang Long Temple, 3040–3460 m, *He 30455* (KRAM, MO – type); Zhangla to Huanglong Highway, 3700 m, *Allen 7109 & 7124* (KRAM, MO); Huanglong, *ca* 3000 m, *Redfearn et al. 35267B* (MO); Hwy Zhangla to Huanglong, 3700 m, *Redfearn et al. 35230* (MO).

JAPAN. HOKKAIDO. Abashiri Pref.: Mt Shari, Kamishari-mura, Shari-gun, 1000 m, Deguchi s.n. (HIRO-12518). Kamikawa Pref.: Mt Furano, Kamifurano-cho, Sorachi-gun, 1015 m, Deguchi s.n. (HIRO-12326); Mt Ponkaun – Ten ninkyo gorge, Biei-cho, Kamikawa-gun, Deguchi s.n. (HIRO-12315); Mt Daisetsu, ca 1900 m, 10 July 1956, Kuwahara s.n. (BISH, BM, COLO, JE, KRAM, MICH, S, TENN, US, W) [Musci Japonici No. 596]. Shiribeshi Pref.: Mt Yotei, Kutchan, Abuta-gun, 1500 m, Deguchi s.n. (HIRO-12597). Soya Pref .: Mt Rishiri, Higashi-Rishiri-cho, Rishiri-gun, Deguchi s.n. (HIRO-12093) and 350 m, Deguchi s.n. (HIRO-12075). Tokachi Pref.: Mt Nipesotsu, Kami'shihoro-cho, Kato-gun, 2000 m, Deguchi s.n. (HIRO-12465 & 12483, KRAM) and 1620 m, Deguchi s.n. (HIRO-12445); Tokachiyama (= Mt Tokachidake), 1905, Faurie 3386 (NY). HONSHU. Akita Pref.: Mt Yakeyama, Tazawako-machi, Senpoku-gun, Higuchi s.n. (MAK-57750). Aomori Pref.: Mt Hakkoda, Sato s.n. (MAK-6995) and Uematsu 233 & 311 (H), July 1907, Uematsu s.n. (H) and 1 May 1900, Yasuda s.n. (H). Fukushima Pref.: Oza, Yataro-goya-Chozo-goya, Higuchi 3718 (NICH); Mt Azuma, Higuchi s.n. (MAK-57683); Yashiro-goya - Chozo-goya, Ozegahara, Hinoemata-mura, Minamiaizu-gun, Higuchi s.n. (MAK-57685). Gifu Pref.: Mt Ontake, Yunotani Valley near Nigorigo Spa, 1800 m, 29 Aug 1975, Iwatsuki et al. s.n. (ALTA, BISH, BR, COLO, hb. Frahm, KRAM, MO, POZG, S, TENN, US) [Musci Japonici Exsiccati No. 1291]; Mt Ontake, ca 2200 m, Noguchi 32213 (NICH); Mt Ontake, below Hinotaki Falls, ca 1800 m, Iwatsuki & Smith J-368 (NY); Mt Ontake, via Hidasan-cho, Sannoike Pond, Marishiten Peak, Sainokawara, Ninoike Pond, Iwatsuki & Smith J-493 (NY); Kamidakara-mura, Yoshiki-gun, Sasaoka 1287 (0). Gunma Pref.: Azuma-gun, Mt Asama, 2200 m, Jinno s.n. (HIRO-14708) and 2000 m, Jinno s.n. (HIRO-14706); Mt Konsei, Sasaoka 6586 (TENN) & 6597 (BM). Nagano Pref .: Mt Yatsu, 2600 m, Yano 345 (NICH); Shimotakai-gun, Mt Yokote, 2250 m, Jinno s.n. (HIRO-14730); Mt Yatsugatake, Takahashi s.n. (MAK-57764) and Takaki s.n. (MAK-57741); Kumanoyu, Shiga-hogen, Yamanouchi-machi, Shimotakai-gun, Tezuka s.n. (MAK-57682); Mt Natsuzawa (near Natsuzawa Spa), Shinano, Jishiba 879 (H); Mt Komagatake, Tezuka s.n. (MAK-57743); Shigakogen, Shimotakai gun, Botanical Garden of Shinshu University, ca 1600-1700 m, 20 July 1972, Kashiwadani s.n. (HIRO); Mt Komagatake, ca 3000 m, Sakurai 190 (H). Niigata Pref.: Mt Myoko, Nakakubiki-gun, Sakurai s.n. (MAK-1005) and Iwasaki s.n. (MAK-57622); Naka-uonuma-gun, Mt Naeba, Jinno s.n. (HIRO-14729). Tochigi Pref .: N slope of Mt Nantai-san, Nikko City, no collector (MAK-101761); Nikko, Iishiba 27 (NICH); Mt Nantai, Osada 6473 (FH). Toyama Pref.: Mt Tateyama, near Midagahara Hotel, 2000-2100 m, Iwatsuki & Sharp 42 (TENN). Yamanashi Pref.: N slope of Mt Fuji, Smith J-289 (NY).

RUSSIA. FAR EAST. *Kamchatka*: by the road from Nachikanskoy Pereval [=Nachika Pass] to the village of Nachika, *Ramenskiy 445 & 448* (KRAM, LE); pereval [=pass] from Shchapinska dolina [=valley] to Kronoki, *Savicz 6232* (KRAM, LE); middle course of Bannaya River, 270 m, 7 Aug 2002, *Czernyadjeva s.n.* (KRAM, MW); South Kamtchatkan Nature Reserve, Koschelevsky volcano, *Czernyadjeva N8 & N9* (KRAM, LE) and *Czernyadjeva N 16* (PRC). SIBERIA. *Buryatia*: Kurumkanskij District, Dzherginskij State Reserve, 9 km NNW of Dzhirga River sources, 16 Jul 2002, *Anenkhonov s.n.* (KRAM, MW). *Krasnoyarsk Territory*: Western Sayan Mountains, Borus Range, *ca* 2300 m, Aug 1888, *Argunoff s.n.* (H). *Republic Sakha/Yakutia*: Bulun District, in valle fluminis Lena, Kumachsur (probably Kumakh-Suurt), 31 Jul 1898, *Nilsson-Ehle s.n.* (H, LE, S); Bulkur, 4 Sep 1898, *Nilsson-Ehle s.n.* (s).

NORTH AMERICA. USA. ALASKA. Anchorage Co.: George Parks Highway between Anchorage and Fairbanks mi. 147, E side of Dyer's Lake, 14 Aug 1988, Frahm s.n. (hb. Frahm, KRAM, MA, MO, NY).

B2. Subsection Chrysei (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra

Codriophorus subsect. *Chrysei* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. ≡ *Racomitrium* sect. *Chrysea* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 64. 1995. — Type: *Codriophorus laevigatus* (A.Jaeger) Bednarek-Ochyra & Ochyra (*Racomitrium laevigatum* A.Jaeger).

Plants robust, yellowish-green to brown, rarely blackish below, forming deep tufts, usually with many short tuft-like lateral branchlets. *Leaves* appressed on the main stem, flexuous on branchlets when dry, erect-spreading when moist, linear-lanceolate, from an ovate

base gradually narrowing to a much elongated, sometimes flexuous, filiform acumen, terminated with a hyaline to yellowish-hyaline, denticulate to serrate hair-point, with some longitudinal plicae, yellowish-brown at the insertion; *margins* unistratose throughout, recurved on both sides, incurved and channelled in the upper part, appearing somewhat crenulate due to large, low papillae in the upper part; costa wide, vanishing in the upper part of the leaf, plano-convex, in cross-section bistratose throughout, with a convex ventral side; laminal cells unistratose throughout, with large and low papillae densely covering the whole leaf, linear, with thick and nodulous to sinuose longitudinal walls, becoming longer and wider towards the base; basal marginal cells differentiated into a row of hyaline, translucent cells with straight walls; angular cells quadrate to short-rectangular, becoming much wider than the adjacent basal cells, with smooth to sinuose, incrassate walls, forming distinct, often somewhat inflated and decurrent auricles. Dioicous. Innermost perichaetial leaves oblong-lanceolate to elliptical, concave and convolute, distinctly longitudinally plicate, abruptly contracted into a short acumen or truncate, with an areolation of chlorophyllous cells in the distal part. Setae 1-3 per perichaetium, erect, flexuose, brown to reddish-brown, smooth, twisted to the right. Capsules exserted. Mature sporophytes unknown.

Subsection Chrysei is a monotypic taxon, comprising only Codriophorus laevigatus from southern South America and some coterminous islands in the South Atlantic. It is diagnosed by the following set of characters: (1) yellowish-hyaline to hyaline, denticulate leaf hair-point; (2) plicate leaves; (3) distinct, yellowish- to orange-brown auricles composed of short cells with incrassate walls; (4) convolute and strongly longitudinally plicate innermost perichaetial leaves with a short acumen or truncate and notched at the apex; (5) chlorophyllous cells with thick and sinuose walls in the innermost perichaetial leaves. It is unknown in subsect. Fasciformes with which it shares the external appearance of the plants, leaf areolation and a mostly bistratose costa in transverse section but differs in particular in the sporophyte characters, including the unique shape and structure of the perichaetial bracts. Possibly, additional differentiae are to be found in the structure of the peristome but so far no mature capsules have been detected in C. laevigatus.

Codriophorus laevigatus (A.Jaeger) Bednarek-Ochyra & Ochyra (Figs 97–100)

Codriophorus laevigatus (A.Jaeger) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 141. 2003. \equiv *Racomitrium laevigatum* A.Jaeger, Ber. Thät. S. Gall. Naturw. Ges. 1872–1873: 90. 1874. \equiv *Grimmia laevigata* Mitt., J. Linn. Soc. Bot. 12: 104. 1869, hom. illeg. [non Grimmia laevigata (Brid.) Brid. 1819]. — TYPE CITATION: Magellan, Hermite Island, inter caespites G. lanuginosae, J. D. Hooker [Holotype: "E Rhacomitrio lanuginoso var Hermite Island Cape Horn Dr Hooker" – NY-Mitten!]. Grimmia willii Müll.Hal. in Neumayer, Deutsch. Exp. Int. Polarforsch. 2: 316. 1890. = Racomitrium willii (Müll.Hal.) Kindb., Enum. Bryin. Exot. 108. 1891. — TYPE CITATION: Austro-Georgia, ad rupes im Hintergrunde des Thales rechts am Südwest-Gletscher cespites magnos sistens, 10. Majo 1883 [Lectotype (selected here): "N° 45 Grimmia (Rhacomitrium) Willii C. Müll. nsp. Fundort: Am Felsen im Hintergrund des Thales rechts am SW-Gletscher in grossen Polstern. Süd-Georgien, 10/V 83 Will Südpolarexpedition" – HBG!; isotypes: M!, PC!]. First synonymised with Racomitrium laevigatum by Robinson (1975: p. 17).

Racomitrium loriforme Dusén, Ark. Bot. 6(10): 26. 1907. — TYPE CITATION: Patagonia occidentalis in valle fluminis. Rio Aysen in terra saxosa [Lectotype (*selected here*): "479. Rhacomitrium loriforme Dus. Patag. occ. in valle fluminis Rio Aysen in terra. Jan 1897. P. Dusén" – s-Dusén!; isotypes: BM!, H-Brotherus!, JE-Herzog!, M!, s! (2 specimens), s-Dusén!, s-Roth!, w!]. First synonymised with *Racomitrium laevigatum* by Robinson (1975: p. 17).

R. plicatum Herzog *in* Donat, Rev. Sudamer. Bot. 3: 65. 1936. — TYPE CITATION: Chile: Territorio del Aisen. Glaciares del Lago San Martín (L1), c. 900 m, leg. A. Donat, II.1933 (no. 16/II)) [Holotype: "Herbarium Haussknecht, Jena. Rhacomitrium plicatum Herz. n. sp. Moose d. Patagon. Inlandeis Expedition 1932/33. L.1, 90 m. Empetrum -Assoziation leg. A. Donat, 23.II.33 n. 16/II" – JE-Herzog!; isotypes: JE-Herzog!, s!]. First synonymised with *Racomitrium laevigatum* by Bednarek-Ochyra (1993: p. 87).

R. scabrifolium E.B.Bartram, Farlowia 2: 311. 1946. — TYPE CITA-TION: Chile: Prov. de Magellanes, Fuegia occid., Fjordo de Agostini, No. 2068 [Holotype: "Rhacomitrium scabrifolium sp. nov. Chile: Prov. de Magellanes: Fuegia occid., Fjordo de Agostini. H. Roivainen no. 2068" – FH-Bartram!; isotypes: FH!, H!]. First synonymised with *Racomitrium laevigatum* by Robinson (1975: p. 17).

R. breutelioides Dixon *in* Christiansen, Res. Norw. Sci. Exp. Tristan da Cunha 1937–38, 48: 26. 1960. — TYPE CITATION: Tristan da Cunha, on ground in fern country, 600 m, above Settlement, No. 74 [Holotype: "Herb. H. N. Dixon. Ref. No. 74. Rhacomitrium breutelioides Dix. sp. n. On ground in fern country, above settlement, 600 m; Tristan da Cunha. Coll. Christophersen & Mejland, 21 Dec. 1937. Comm. Bot. Mus. Oslo" – BM-Dixon!; isotypes: FH-Bartram!, o!]. First synonymised with *Racomitrium laevigatum* by Bednarek-Ochyra & Ochyra (1992: p. 8).

Plants medium-sized to large, mostly coarse and robust, stiff and rigid, in deep, luxuriant, loose tufts or compact wefts, pale yellowish-green, bright yellow tinged with brown to golden-yellow or golden-yellow throughout or only above, brown to blackish-brown or rarely blackish below. Stems erect or ascending, 2-15 or, occasionally, to 20 cm long, sparsely or abundantly irregularly branched, commonly with numerous, closely arranged, short, tuftlike horizontal, lateral branchlets, giving the shoots a pinnulate, nodose appearance, in transverse section circular, without central strand, composed of 4-5 layers of small cortical cells with brown and strongly incrassate walls surrounding 6-7 layers of large medullary cells with moderately thickened, yellow walls; axillary hairs filiform, hyaline throughout, composed of 6-14 short cells, sometimes elongate in the apical part. Stem and branch

FIGURE 97. Codriophorus laevigatus. — 1. Habit, dry. 2. Portion of shoot, dry. 3. Portion of shoot, wet. 4–6. Stem leaves. 7–9. Branchlet leaves. 10. Portion of transverse section of stem. 11–15. Axillary hairs. 16. Leaf apex. 17. Upper laminal cells at margin. 18. Upper laminal cells. 19. Mid-leaf cells. 20–22. Alar and supra-alar cells. 23. Basal juxtacostal cells. 24–28. Transverse sections of leaves, sequentially from apex to base. — [All from *Christophersen & Mejland 74*, BM (holotype of *R. breutelioides*)]. — Scale bars: 1 mm (4–9); b – 1 cm (1); c – 100 μ m (10–28); d – 0.5 cm (2–3). (Reproduced from *Fragmenta Floristica et Geobotanica*, 37: 9, 1992, with permission).





FIGURE 98. Codriophorus laevigatus. — 1. Habit, wet. 2. Portion of stem, dry. 3. Portion of stem when wet. 4–8. Stem leaves. — [1, 3, 6 from Dusén 479 bis, BM (isotype of Racomitrium loriforme); 2, 7 from Christophersen & Mejland 74, BM (holotype of R. breutelioides); 4 from Will 45, HBG (lectotype of Grimmia willi); 5 from Ochyra 616/95, KRAM; 8 from Donat 16/11, JE (lectotype of Racomitrium plicatum)]. — Scale bars: a – 1 mm (2); b – 1 mm (4–8); c – 1 cm (1); d – 1 cm (3).

leaves similar in shape, crowded, erect and appressed at the base, with a flexuose-spreading or reflexed, sometimes somewhat curved, often wavy acumen when dry, erectspreading to patent when moist, (1.5-)3.0-4.0(-4.5) mm long, (0.7-)0.9-1.3(-1.5) mm wide, from a broadly ovatelanceolate, subcordate, somewhat clasping, not or shortly decurrent, more or less distinctly longitudinally multiplicate base gradually narrowed to a narrow, long, channelled acumen, terminating with a short, 0.1-0.3 mm, yellowishhyaline to hyaline, smooth-celled, denticulate hair-point; *branchlet leaves* generally similar to stem leaves, but usually narrower and longer, (3.2-)4.0-7.0(-8.0) mm long, 0.4-0.6(-0.9) mm wide, mostly penicillate when dry, often subsecund when wet, gradually tapering to a slender, filiform, linear-canaliculate to strap-shaped, flexuose or ruffled to wavy acumen; *margins* narrowly recurved to broadly revolute on both sides in the lower 4/5-5/6, erect below the apex, entire throughout, distinctly crenulate,



FIGURE 99. *Codriophorus laevigatus.* — 1. Portion of stem cross-section. 2–5. Axillary hairs. 6–7. Leaf apices. 8. Laminal cells below apex. 9. Mid-leaf cells. 10. Upper laminal cells (in 8–10 papillosity of the laminal cells is partly indicated). 11. Basal juxtacostal cells. 12–13. Alar cells. 14–22. Cross-sections of leaves, a sequence from base to apex. — [1, 12, 17–18, 20–22 from *Christophersen & Mejland 74*, BM (holotype of *Racomitrium breutelioides*); 2–5, 9, 11, 13, 15–16 from *Ochyra 616/95*, KRAM; 6, 10 from *Dusén 479 bis*, BM (isotype of *R. loriforme*); 7–8 from 4 from *Will 45*, HBG (lectotype of *Grimmia willii*); 14, 19 from *Donat 16/II*, JE (lectotype of *R. plicatum*)]. — Scale bars: a – 100 µm (1); b – 100 µm (2–22).

especially in the upper part, owing to low and large papillae; costa narrow, indistinct and faint, concolorous with the laminal cells with the exception of the extreme base, (35-)50-60(-75) µm wide, mostly vanishing at $\frac{1}{2}-\frac{3}{4}$ of the leaf length, in transverse section biconvex or planoconvex, with convex ventral side, lying at the bottom of a deep, wide-angled and open channel, in transverse section bistratose throughout, except for a tristratose portion at the extreme base, flat or convex, consisting of 4-9 cells on the ventral side, flat to slightly convex on the dorsal side, composed of 4-8, equal-sized or much smaller, substereid or stereid cells near the base; lamina cells unistratose throughout, densely covered on both surfaces with large, low papillae, in upper and median parts short- to long rectangular, with distinctly sinuose lateral walls, (8-)15-45(-60) μm long, 5-8(-11) μm wide, becoming long rectangular to linear above the base, to 75 µm long, with the lumina $3-5 \mu m$ wide and with longitudinal walls nodulose and equal to or thicker than the width of the lumina; *cells at the insertion* shortly rectangular in 2–3 rows, with strongly incrassate and porose walls, 8-10 µm wide, 20-25 µm long, intensively bright yellow- or golden-brown; alar cells well-differentiated, large, isodiametric to shortly elongate, usually 25-45 µm long, 15-25 µm wide, yellowish- to orange-brown, with porose, moderately thick to strongly incrassate walls, forming distinct, flat somewhat swollen, usually shortly decurrent auricles; supra-alar cells similar to those of the lamina cells or differentiated in a single row of 5-10(-15) hyaline, pellucid cells with straight or weakly sinuose walls. Dioicous. Perigonia bud-like, to 2.0-2.2 mm long; outer perigonial leaves ovate-lanceolate, gradually narrowed to a filiform acumen, 2.0-2.2 mm long, 0.9-1.0 mm wide, with a distinct costa vanishing below the apex; inner perigonial bracts broadly ovate, acute, deeply concave, 0.9-1.0 mm long, 0.8–0.9 mm wide, consisting of 13–18 pale brown antheridia, intermixed with short, bright brown to goldenbrown paraphyses, reaching about half the length of the antheridia. Perichaetia large, appearing lateral due to innovations; outer perichaetial leaves oblong-lanceolate, rather abruptly narrowed to a long, filiform, mostly recurved acumen, hyaline at the extreme tip, 3.5-5.0 mm long, 0.9-1.1 mm wide, with a faint costa, concolorous with the laminal cells, extending to the acumen and areolation similar to that on the vegetative leaves; innermost perichaetial leaves oblong, 4.0-4.2 mm long, 0.9–1.0 mm wide, convolute, strongly plicate, abruptly contracted into a short acumen or truncate and notched at the apex; *costa* faint, concolorous with the laminal cells, ending a few cells below the apex; laminal cells chlorophyllous throughout, rectangular, with thick, sinuose walls, 25-50 µm long, 5-8 µm wide, becoming short-rectangular to isodiametric, $12-18 \mu m \log 7 - 12 \mu m$ wide, at the margin in the distal portion. *Setae* 1–3 per perichaetium, erect, flexuose, brown to reddish-brown, smooth, $12-18 \text{ mm} \log (young)$, twisted to the right; *vaginula ca* $1.5 \text{ mm} \log g$, brown, with long-rectangular, with strongly sinuose and incrassate wall. *Capsule* exserted. *Young calyptra* long cylindrical, $2.8-3.0 \text{ mm} \log g$, multistratose in cross-section, non-plicate, brown, distinctly papillose above. *Mature sporophytes* unknown.

Etymology — The specific name is derived from the Latin word *laevigatus* which means smooth and polished and alludes to the non-papillose leaf hair-points which markedly contrast with the roughly papillose hyaline apical part of the leaves in *Racomitrium lanuginosum* with which *Codriophorus laevigatus* was discovered for the first time by J. D. Hooker in a mixed stand on Hermite Island near Cape Horn.

Diagnostic characters and differentiation — Codriophorus laevigatus is a large and handsome moss that is unlikely to be mistaken for any other species of this genus, the following combination of characters being instantly diagnostic: (1) plants large and robust, with an attractive, characteristic bright or pale yellow, goldenyellow to yellow-green or yellowish-brown colour; (2) stems erect, with many, regularly arranged short, lateral, tuft-like branchlets; (3) leaves ovate-lanceolate, from an ovate, ovate- or oblong-lanceolate, subcordate and plicate base gradually tapering to a long, filiform, canaliculate, linear to strap-shaped, flexuose and often wavy acumen; (4) leaf apex terminated with a short, hyaline or yellowish-hyaline, denticulate hair-point; (5) costa faint, concolorous with the laminal cells, vanishing in mid-leaf or reaching three quarters of the way up the leaf, situated at the bottom of a deep groove, wide but very unpronounced and scarcely raised on the dorsal surface and nearly of the same thickness as the lamina, in transverse section flat dorsally, convex on the ventral side and bistratose throughout, except for the extreme base; (6) laminal cells unistratose throughout, short- to long rectangular throughout, becoming linear above the base; (7) alar cells subquadrate to short-rectangular, with thick to strongly incrassate walls, forming distinct, fairly swollen to flat, yellowish- to orange-brown, usually decurrent auricles; (8) supra-alar cells not differentiated or pellucid, with straight to weakly sinuose walls, forming a single row of 5-10 cells; (9) perichaetia large and seemingly lateral owing to innovations; (10) innermost perichaetial leaves convolute, tightly sheathing the seta, strongly plicate, rapidly constricted into a short acumen or truncate and notched at the apex, with an areola-

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FIGURE 100. *Codriophorus laevigatus.* — 1. Plant with immature sporophytes, wet. 2. Perigonium. 3. Outermost perigonial leaf. 4–5. Median perigonial bract. 6–7. Inner perigonial bracts. 8. Innermost perigonial bract with antheridia and paraphyses. 9. Perichaetium and two immature sporophytes. 10. Young calyptra. 11. Transverse section of calyptra. 12. Transverse section of seta. 13. Epidermal cells of vaginula. 14. Outermost perichaetial leaf. 15. Median perichaetial leaf. 16–17. Innermost perichaetial leaves. 18. Apex of innermost perichaetial leaf. — [All from Chile, *K. Reiche s.n.*, H]. — Scale bars: a – 0.5 cm (14–17), 4 mm (10) and 200 μ m (11, 13); b – 1 cm (1) and 1 mm (8); c – 0.5 cm (9), 2 mm (2) and 200 μ m (12); d – 1 mm (3–7); e – 100 μ m (18).



tion of chlorophyllous cells throughout and subpercurrent costa.

Codriophorus laevigatus is a very remarkable species which at first glance has a resemblance to some species of *Breutelia*, for example *B. integrifolia* (Taylor) A.Jaeger which has a similar geographical range to that of *C. laevigatus* (Matteri 1984; Newton 1974). Similarities include the nodose lateral branchlets that are remarkably regular, of equal size and distance apart, plant colour, the form and plication of the leaves, and the rigidly deflexed leaves of the tuft-like branchlets. However, microscopic examination of the leaf areolation of elongate cells with sinuose walls and large flat papillae disposed over the cell walls immediately indicate the affiliation of this moss with *Codriophorus*.

Within this genus *Codriophorus laevigatus* could be readily fitted into sect. *Fascicularia* on account of its nodose branching, elongate laminal cells throughout the leaf and, primarily, the anatomical structure of the costa that is bistratose almost throughout and situated at the bottom of a deep groove. The robust stature of the plants, regular pinnate branching of tuft-like branchlets, as well as the costa convex on the ventral side make *C. laevigatus* somewhat similar to *C. anomodontoides*, but it occupies a very isolated position and is only distantly related to other species of this section. Apart from the very isolated geographical range, there are several structural gametophyte and sporophyte characters which support segregation of this species into a subsection of its own, subsect. *Chrysei* (Bednarek-Ochyra 1995).

Although sporophyte characters of Codriophorus laevigatus are incompletely known owing to the lack of fully mature capsules, the form of its perichaetial leaves is unique and unknown in any other species of the genus and they are very indicative of the relationships of the species. The innermost perichaetial bracts are strongly convolute and distinctly longitudinally plicate and have an areolation of chlorophyllous cells with sinuose and thick walls throughout the lamina. Additionally, they are truncate at the apex or abruptly short-acuminate. The mature capsules are unknown in C. laevigatus but judging from the length of the immature calyptrae, which are 2.8-3.0 mm long, they may be remarkably long and cylindrical. The young setae are dextrorse when dry but possibly in mature sporophytes they would exhibit similar seta torsion to that in C. fascicularis, i.e. twisted once to the left immediately below the urn and then twisted to the right below. Of gametophyte characters, the presence of the yellowishhyaline to hyaline leaf hair-point, the strongly plicate leaf bases and well-developed angular cells, composed of thick-and often sinuose-walled, isodiametric to shortly rectangular cells and forming usually swollen, distinct and yellowish- to orange-brown decurrencies would also be unique in sect. Fascicularia and additionally indicate the remote alliance of this austral species with the northern taxa of Codriophorus.

Bartram (1946) compared his new species *Racomitrium* scabrifolium with *Bucklandiella*. *ptychophylla* (Mitt.) Bednarek-Ochyra & Ochyra (then placed in the genus

Racomitrium), a New Zealand species (Sainsbury 1955) which is known from Chile (Bartram 1952) and South Georgia (Bell 1974). The two species share plicate leaves, but *B. ptychophylla* leaves possess an acute and chlorophyllous apex lacking a hyaline hair-point, and their costa is percurrent, multistratose and much thicker than the leaf lamina, as is clearly seen in transverse section. Moreover, the costa is distinctively convex on the dorsal side and the plants lack short, tuft-like lateral branchlets.

Variability — Codriophorus laevigatus is an exceptionally stenotypic species and shows little variation. Usually plants growing in exposed sites are darker in colour, shorter and much more densely ramulose, though occasionally some plants from South Georgia have filiform branches that are almost entirely devoid of nodose lateral branchlets (e.g., Greene 657, AAS, KRAM). This species has been described several times in various parts of its geographical range under a variety of names. All of these, now considered to be synonymous with C. laevigatus, are typical geographical taxa which were uncritically described without reference to the earlier literature, principally because the specimens were obtained from previously uninvestigated areas. Interestingly, as had already been noted in part by Roivainen (1955), the descriptions of Grimmia laevigata from Hermite Island near Cape Horn (Mitten 1869), G. willii from South Georgia (Müller 1890), Racomitrium loriforme and R. plicatum from western Patagonia (Dusén 1907; Donat 1936), R. scabrifolium from Tierra del Fuego (Bartram 1946) and R. breutelioides from Tristan da Cunha (Dixon 1960) are very similar in relation to their important diagnostic features. Admittedly Müller (1890) described an excurrent costa in Grimmia willii but this was evidently the result of careless observation, as already noted by Cardot (1908b), because the costa in all South Georgian specimens, including the type material, ends well below the apex.

Reproduction — The species is consistently sterile and no plants with fully mature sporophytes have so far been discovered. Only a single specimen from Chile, bearing no detailed locality, collector or collecting date, which was communicated to V. F. Brotherus by K. Reiche, has several immature sporophytes and fully developed perichaetia as well as some male shoots with perigonia. In addition, numerous perigonia were found in another specimen from Chile in western Patagonia (*Engel 5445*, H).

Taxonomic and nomenclatural notes — Codriophorus laevigatus was first described as Grimmia laevigata from material collected on Hermite Island near Cape Horn by J. D. Hooker during his memorable Antarctic expedition of 1839–1843 on the ships *Terror* and *Erebus* under the command of Captain James Clark Ross (Mitten 1869). Because Mitten's G. laevigata is illegitimate as a younger homonym of G. laevigata (Brid.) Brid. of 1826, the specific epithet laevigatus was legitimised by Jaeger (1874), when he transferred this species to Racomitrium Brid. as R. laevigatum A.Jaeger. This species has long remained



FIGURE 101. Distribution map of *Codriophorus laevigatus* on South Georgia. Inset: Global range of the species. The arrowed dot indicates where the species occurs on the Juan Fernandez Islands.

totally neglected and was resurrected from obsolescence by Robinson (1975) and since then this species name has gained wide acceptance (e.g., Seki 1974; Deguchi 1984, 1991; Matteri 1985).

Codriophorus laevigatus was collected for a second time over 40 years later on Subantarctic South Georgia during the German International Polar-Year Expedition of 1882-1883. It was described by Müller (1890) as a separate species, Grimmia willii, who showed the close resemblance of this species to Racomitrium fasciculare, from which it differed in its more robust stature. The species was soon transferred to Racomitrium by Kindberg (1891) as R. willii. This name has long been in use for this species (Cardot 1908b; Cardot & Brotherus 1923; Roivainen 1955; Bell 1974; Greene 1986). Interestingly, Roivainen (1955) placed Grimmia laevigata in synonymy with Racomitrium willii, despite evident priority of this name, along with the other two species names, Racomitrium loriforme and R. scabrifolium. The former species was described by Dusén (1907) from material collected ten years earlier in western Patagonia in the Aisén Region of Chile, but without any comment on its affinity. The latter was described by Bartram (1946) on the basis of several specimens collected from the Tierra del Fuego archipelago. He pointed out the similarity of its plicate leaves to those in R. ptychophyllum of New Zealand, indicating the smooth laminal cells and absence of short lateral branchlets as distinctive. Both species were correctly reduced to synonymy with R. laevigatum by Robinson (1975).

In the meantime Codriophorus laevigatus was next described as a separate species, Racomitrium plicatum, by Th. Herzog (in Donat 1936) from specimens collected by the "Gea" Expedition of 1933 to Cordillera Central Patagónica in the vicinity of Lago San Martin in the Aisén Region of Chile. No taxonomic comment on the affinity of this new species was given in the protologue but the specific name clearly indicates that it referred to the plicate leaves of this species. R. plicatum was considered to be identical to R. laevigatum by Bednarek-Ochyra (1993). Finally, Dixon (1960) in his posthumously published paper on the mosses of Tristan da Cunha collected by the Norwegian Scientific Expedition of 1937-1938 described R. breutelioides as a new species but without any indication of its relationships. This species name was reduced to synonymy with R. laevigatum by Bednarek-Ochyra & Ochyra (1992).

Chromosome number — Not available.

Habitat — Codriophorus laevigatus is associated with a wide range of habitats, predominantly with moist sites, although quite often it grows in dry and open situations. On mainland South America and in Tierra del Fuego it is mainly associated with open pluvial moorland and other wet habitats, forming beautiful, large, often semiglobose colonies in which it may reach a height of 15–20 cm (Roivainen 1954, 1955). It usually grows on wet or dry peat in bogs, swamps and fens, on hummocks along riversides, on soil and humus in grassland, forest and woodland composed of *Nothofagus antarctica* (T.F.Forst.) Oerst., *N. pumilio* (Poepp. & Endl.) Krasser, *N. betuloides* (Mirb.) Blume and *Drimys winteri* T.F.Forst., on stony ground in alpine *Empetrum rubrum* heath and on fell-fields. On South Georgia *C. laevigatus* grows in generally moist or dry, open or sheltered sites, usually associated with *Chorisodontium aciphyllum* peat banks, on scree, on rock ledges and in rock crevices, on gravelly soil and in seepage areas, at the edge of melt-water pools, in *Festuca erecta* grassland and *Rostkovia magellanica* marshes. On Tristan da Cunha the species was found in alpine *Empetrum rubrum* heath.

Geographical distribution — *Codriophorus laevigatus* is an amphi-atlantic south-temperate species (Fig. 101,

inset). It is widely distributed but scattered along the western fringes of southern South America in the Nothofagus zone, ranging from lat. ca 40° S in the Valdivian region to Tierra del Fuego, with an isolated occurrence on the Juan Fernandez Islands (Brotherus 1924b; Robinson 1975) (Fig. 102). In addition, it is quite frequent on South Georgia in the Subantarctic (Fig. 101) and it was also recorded at highly disjunct stations on Tristan da Cunha (Bednarek-Ochyra & Ochyra 1992) and Gough Island in the South Atlantic (Fig. 101). The occurrence of the species on these highly isolated islands is one more piece of evidence confirming the stronger affiliation of the moss flora of this group of islands to southern South America rather than Africa, although these islands are closer to southern Africa. It is very probable that the Tristan da Cunha and Gough Island occurrences of C. laevigatus



FIGURE 102. Distribution map of Codriophorus laevigatus in South America.

The altitudinal range of *Codriophorus laevigatus* extends from sea level to the alpine zone, up to 1200 m in the Fuegian region and 900 m in western Patagonia. On South Georgia the species grows commonly from sea level to 150 m, with some occasional records at 215 m. On the other hand, on oceanic islands it occurs exclusively at high elevations: 1100–1350 m on the Juan Fernandez Islands and 600–2000 m on Tristan da Cunha.

EXSICCATI

MATTERI – *Musci Fuegiani Exsiccati* No **48** (Alta, Ba, Brnm, Kram, Mo), **20, 50 & 62** (BA, KRAM).

MATTERI - Musci Patagonici Exsiccati No 12 (BA, KRAM, hb. Frahm).

SPECIMENS EXAMINED

AFRICA. TRISTAN DA CUNHA. Upper Crater, lake at Cove Gulch, *ca* 2000 m, *Christophersen* 1800B & 1800F (BM, FH, O); on ground in fen country, above settlement, 600 m, *Christophersen & Mejland* 72 (BM); *Empetrum* heath, above Burntwood, 1200 m, *Christophersen & Mejland* 784 (BM, FH, O – type of *Racomitrium breutelioides*); above Settlement, 600 m, *Christophersen* 74 (BM, FH). GOUGH IS-LAND. Gonydale, South End, *ca* 500 m, *Wace* 608 (BM).

SOUTH AMERICA. ARGENTINA. SANTA CRUZ. Lago Argentino, Seno Mayo, pequeña bahía al NE del Seno, Matteri & Schiavone 4890 (KRAM); Lago Argentino, Bahía Onelli, trail to Glaciar Onelli, Matteri & Schiavone 5053 (KRAM, hb. Frahm). TIERRA DEL FUEGO. Depto. Río Grande: Estancia María Cristina Pastizal, Schiavone, Matteri & Piñeiro 4420 (ALTA, BRNM, KRAM, MO, S); Estancia La Pampa 1.5 km SE of Tolhuin, Schiavone & Ochyra 616/95 (KRAM); Estancia Buenos Aires, Antonijevic 384A (KRAM); Rancho Hambre, 140 m, Roivainen 1989 (KRAM, MO). Depto. Ushuaia: Lago Escondido, Cerro Gabriela, 580 m, Roivainen 635 (AAS, ALTA, CANM, H, KRAM, MICH, MO, NY, S, TENN); Estancia Escondido, ca 80 m, Hyvönen 2201 (KRAM, NY) and ca 100 m, Hyvönen 2238 (KRAM); Paso Garibaldi, 420 m, Roivainen 677 (FH, G, KRAM, NY); trail to Glaciar Martial, ca 600-1000 m, Schiavone & Ochyra 484/95 (KRAM), ca 900-1200 m, Schiavone & Ochyra CM6946 & CM6897 (KRAM) and 1100 m, Schiavone & Ochyra 517/95 (KRAM); Valle de Tierra Mayor, Schiavone & Ochyra CM7107 (KRAM); Lapataia, between Laguna Verde and Laguna Negra, Matteri 783 (AAS, KRAM, S); Río Pipo, Drehwald P244 (KRAM); Río Caleta, 595 m, Hyvönen 2342 (KRAM); Peninsula Mitre, N part, ca 110 m, Hyvönen 3114 & 3115 (KRAM). ISLA DE LOS ESTADOS. Between Puerto Cook and Puerto Vancouver, Hässel de Menendez 17400 (AAS, KRAM, S, TENN).

CHILE. ACONCAGUA. Juan Fernandez: Masafuera, in tummo pigo "Fases de los Cabro" dicto, 1100-1200 m, Skottsberg 148 (BM, FH, H, NY, S); Correspondencia, 1100-1200 m, Skottsberg 174 (S) and ca 1350 m, Skottsberg 147 (s). Los LAGOS. Prov. Valdivia: W slope of Cordillera Pelada, 3.1 km by road W of El Mirador on road between La Union and Punta Hueicolla, 840 m, Crosby 12855 (MO, hb. Frahm). Prov. Osorno: Parque Nacional Puyehue, upper part of Refugio Antillanca, ca 1000 m, Deguchi 31289 & 31311 (HIRO); Llanquihue, around Lago Chapo, ca 40 km SE of Puerto Montt, ca 250 m, Deguchi 25541, 25548 & 25577 (HIRO). AISÉN. Valley of Río Aisén, Dusén 479 bis (BM, JE, NY, O, PC, S, W - type of Racomitrium loriforme); glaciers of Lago San Martín, ca 900 m, Donat 16/II (JE, S -type of Racomitrium plicatum) and Donat 44 (JE); between Coihaique and Puerto Aisén, Velo de Novia, Drehwald P515 (KRAM); Parque Nacional de Rio Simpson, along route 245, ca 150-220 m, Deguchi 25694 (HIRO); Estancia Río Romero, Ventisquero Nef, 300 m, Seki 1067, 1074, 1001-1100, 1065, 1060 & 1068 (H); Río Exploradores, Estancia Río Circo, ca 50 m, Seki 453 (H); Prov. Aisén, Río Exploradores, Bahía Exploradores, Río Teresa - Río Verde - Estancia Río Circo, Seki 722 (H); Río Norte, W coast of Lago General Carrera, Yoshida & Milo 2426 (H). MAGALLANES. Ultima

Ensperanza: Puerto Bellavista, Lago Azul, Matteri B2053 (AAS, KRAM); Puerto Toro, Orillas del Seno, Matteri B2353 (AAS, KRAM, NY); Margen Occidental de Puerto Toro, glacier of Cerro Balmaceda, Matteri B2661 (AAS, KRAM); Canal Smyth, Munos Garnero, Pt. Ramirez, Skottsberg 412 (H, S, PC); Moon Corrie, Abra Kelly, ca 790 m, Hoppe 64 (AAS, KRAM); near glacier at head of Fjordo Peel, Engel 5445 (H); Brunswick Península, about 12 km S of Lago Parrillar, ca 310 m, Deguchi 26364, 26365, 26366 (HIRO). Tierra del Fuego: Bahía Sarmiento, Roivainen 2465 (FH, H) & 131A (S); Monte Buckland, 500-700 m, Roivainen 241 (FH); Fjordo Finlandia, Roivainen 1904 (AAS, FH, H, KRAM); Fjordo Finlandia, Brazo Aino, Roivainen 1970 (FH, H), 130A & 1543 (s); Fjordo Finlandia, Monte Nylandia, 28 Feb 1929, Roivainen s.n. (AAS, H); Fjordo de Agostini, Bahia Groth-Hansen, Roivainen 2068 (AAS, FH, H - type of Racomitrium scabrifolium) & 135A (s); Fjordo de Agostini, Brazo Izguierdo, Roivainen 160A (H, S); Puerto Yartou, Pico Nariz, Roivainen 820 (FH, H); Río Azopardo, Dusén 209 (H, S) and 600 m, Halle & Skottsberg 410 (PC) & 409 (s). Isla Hoste: SW of Seno Ponsonby, 100 m, Adams 33 (AAS, KRAM). Isla Navarino: S and central part, 400-650 m, Hyvönen 2756 (KRAM). Chile, without closer locality data, plants with young sporophytes, without date, Reiche s.n. (H). Isla Hermite: without locality data, Hooker s.n. (NY - type of Racomitrium laevigatum).

SUBANTARCTICA. SOUTH GEORGIA. Bird Island: Bird Island, near head of large corrie below Roché Peak, ca 185-215 m, Greene 407 (BM, H, S). Right Whale Bay: cove S of Nameless Point, 15 m, Bell 456 &, 457 (AAS, KRAM); Nameless Point, 150 m, Bell 464 & 468 (AAS, KRAM); SW side of Reef Point, ca 6 m, Greene 657 (AAS, H, KRAM); Binder Beach, N-facing tussock/scree, ca 6 m, Bell 361, 363, 364 365 366, 367 & 372 (AAS, KRAM) & 362 (BM, NY); N-facing scree slopes on S side of valley behind Right Whale Bay, 150 m, Bell 411 (H, O), 414 & 419 (AAS, KRAM); N-facing rock outcrop W of Craigie Point, ca 150 m, Bell 443 (AAS, KRAM) & 447 (BM, S). Bay of Isles: below N peak of Murphy Wall, ca 150 m, Greene 1218 (AAS, H, KRAM). Prince Olav Harbour: N shore of North Bay, ca 75 m, Greene 1654 (AAS, KRAM, NY) & 1681 (BM, H, S). Stromness Bay: N-facing scree slope SW of Husvik, ca 30 m, Bell 301, 302, 303, 304 & 305 (AAS, KRAM); near stream running N down slopes S of Husvik, 10 m, Bell 327 & 328 (AAS, KRAM) & 326 (BM); near stream W of Husvik, ca 30 m, Bell 340, 341, 342 & 348 (AAS, KRAM); S shore of Husvik, near Kelp Point, Edwards CG 106 (AAS, KRAM); valley running SW from Husvik, ca 3 m, Greene 3133 (BM, NY, S); near E end of valley, running NE of Husvik, ca 30 m, Greene 1403 (BM, H, S); ca 750 m inland from Husvik whaling station, ca 150 m, Greene 1471 (AAS, KRAM, NY); W side of Olsen Valley, opposite to Ruby Peak, ca 30 m, Greene 3007 (AAS, KRAM); N end of Olsen Valley, ca 60 m, Longton 181 (BM, S); valley behind Stromness whaling station, ca 30 m, Greene 3240 (AAS, KRAM); near head of valley running NE from Stromness whaling station, ca 50 m, Greene 3308a (BM); valley running NW from Husvik, 30 m, Longton 61 (AAS, KRAM, NY, s); stream from Hodges Glacier to Gull Lake, ca 105 m, Greene 1845 (AAS, KRAM, S); NW side Gull Lake, 150 m, Bell 135, 136, 137 & 138 (AAS, KRAM) & 135 (S); slope down to E bank of stream from Gull Lake, 15 m, Clarke CG 200 (BM, NY); S side Gull Lake, 150 m, Bell 133 (BM, NY). Cumberland West Bay: Jason Harbour, Skottsberg 269 (H, PC, S); near head of Sphagnum Valley, ca 150 m, Greene 1587 (BM); valley behind Papua Beach, ca 30 m, Greene 2913 (BM); in centre of valley overlooking Maiviken, 150 m, Bell 1287 (AAS, KRAM). Moraine Fjord: Dartmouth Point, W-facing slopes overlooking Moraine Fjord, ca 75 m, Bell 177 (H, O), 180, 181, 182, 183, 184, 186 & 191 (AAS, KRAM); Hestesletten, W shore of Moraine Fjord, ca 3 m, Greene 3510 (AAS, KRAM) & 3511 (BM, S); Moraine Fjord, Skottsberg 34 (BM, PC, S) and 70 m, Smith M15C (AAS, KRAM) & M6 (BM, S). Cumberland East Bay: Bore Valley, 100 m, Bell 85 (BM) and ca 215 m, Bonner 268 (BM); S shore of large lake in N part of Bore Valley, ca 105 m, Greene 1933 (BM); S side of King Edward Cove, 75 m, Smith 1156 (BM); above Hope Point, 50 m, Bell 127, 128, 129, 130, 131 & 132 (AAS, KRAM); Horse Head, 6 m, Clarke CG 345 (AAS, KRAM); NW of Horse Head, Smith M142B (AAS, KRAM); behind snout of Harker Glacier, 1.5 m, Bell 220 (BM); W of Brown Mountain, ca 215 m, Bell 150, 159 & 162 (AAS, KRAM) & 152 (BM, H, O). Barff Peninsula: on S side Sörling Valley overlooking Cumberland East Bay, 100 m, Bell 1371, 1372 & 1373 (AAS, KRAM); valley running SW from Ocean Harbour, 150 m, Longton 298 (AAS, KRAM, NY); N corner of cirque behind Ocean Harbour, 30-60 m, Longton 307 (BM). Royal Bay: N-facing cliff overlooking Royal Bay, 25 m, Bell 238 (BM)

& 240, 241, 248, 252, 253 & 254 (AAS, KRAM); head of Whale Valley, 200 m, *Bell 493* (AAS, KRAM); W side of Whale Valley, 150 m, *Bell 1306, 1310, 1312 & 1313* (AAS, KRAM); & *1308* (BM); E side of S end of N part Whale Valley, *ca* 200 m, *Bell 1325, 1326, 1327, 1328, 1329* (AAS, KRAM); at head of S part of Whale Valley, 10 m, *Bell 1342* (AAS, KRAM); cliff overlooking Moltke Harbour, N side, *ca* 120 m, *Bell 1357* (AAS, H, KRAM); N side of Moltke Harbour, 50 m, *Bell 958* (BM, S); NW shore of Moltke Harbour, *ca* 6 m, *Greene 2317* (AAS, KRAM, NY); S facing slopes of Mt Krokisius, *ca* 150 m, *Greene 2317* (AAS, KRAM, NY); scree slopes to E of Mt Krokisius overlooking Cape Harcourt, 140 m, *Bell 1346* (BM, H, NY, O); below Coffin Top, 150 m, *Bell 494* (AAS, KRAM); inadequately localised, "am Felsen im Hintergrund des Thales rechts zum SW-Gletscher

in grossen Polstern", Will 45 (HBG, M, PC – type of Grimmia willii). Gold Harbour: on slopes to N of Gold Harbour, 200 m, Bell 265 & 269 (AAS, KRAM) & 270 (BM, S); E-facing slope N of Gold Harbour, 200 m, Bell 273, 274, 275, 276, 277, 278, 279, 280, 281, 282, 283, 284, 285 & 286 (AAS, KRAM); Gold Head, 25 m, Lawson 52 (AAS, ALTA, DUKE, KRAM). Undine Harbour: Hope Valley, between Survey Isthnus and lower glacial plain, Greene 703 (AAS, KRAM). Wilson Harbour: sea level, Greene 1141 (BM). King Haakon Bay: without closer locality data, Longton 811d (AAS, KRAM). Nuñez Peninsula: between Esmark Glacier and Holmestrand Peninsula, ca 25 m, Smith M114 (BM), & M115 (AAS, KRAM) & M120 (BM); between Esmark Glacier and Holmestrand Peninsula, ca 50 m, Greene 2742 (BM, H, NY, S).

B3. Subsection Piliferi (Bednarek-Ochyra) Bednarek-Ochyra, stat. et comb. nov.

Codriophorus subsect. *Piliferi* (Bednarek-Ochyra) Bednarek-Ochyra, *stat. et comb. nov.* ≡ *Racomitrium* sect. *Pilifera* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 64. 1995. ≡ *Codriophorus* sect. *Piliferi* (Bednarek-Ochyra) Bednarek-Ochyra, & Ochyra *in* Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. — Type: *Codriophorus varius* (Mitt.) Bednarek-Ochyra & Ochyra (*Grimmia varia* Mitt.).

Plants large and robust, fairly coarse, green, yellow or yellow- to greyish-green, forming rather loose, deep tufts or fairly dense, intricate patches, erect, ascending to prostrate, sparingly dichotomously branched or sometimes with numerous short lateral branchlets. Leaves appressed, often falcato-secund when dry, spreading to squarrose-recurved when wet, ovate-lanceolate to lanceolate, gradually tapering to a slender or broader acumen, terminated with a hyaline, flat, denticulate, straight or flexuose, erect or recurved hair-point or muticous, subacute to narrowly rounded-obtuse at the apex, plicate and concave at the base, broadly carinate to narrowly canaliculate-concave distally, shortly decurrent; margins entire, unistratose throughout, recurved and revolute on both sides from the base almost to the apex; costa percurrent or subpercurrent, clearly demarcated from the laminal cells, situated at the bottom of a deep, narrow-angled and partly enclosed channel, strongly convex dorsally, flat on the ventral side, in cross-section bistratose, elliptical to curved in the distal portion, rectangular to crescent-shaped, strongly flattened, 3-4-layered in the proximal portion, with 1-2 layers of dorsal stereid cells; laminal cells unistratose throughout, distinctly papillose with large, flat papillae covering the longitudinal walls and major parts of the lumina, shortly rectangular to isodiametric at the apex, long rectangular below; alar cells short-rectangular, thick- and sinuosewalled, forming flat, short decurrencies; supra-alar cells differentiated in 1-2 rows, hyaline, straight-walled, forming a distinct, pellucid marginal border, extending to 15-19 cells up the leaf margin. Dioicous. Innermost perichaetial leaves oblong-lanceolate, plicate, broadly acute to rounded-obtuse at the apex, with bluntly serrate margins, hyaline throughout. Setae 1-2 per perichaetium, smooth, straight, twisted to the right. Capsules exserted, erect, smooth, long cylindrical; operculum long rostrate, with a straight rostrum; exothecial cells oblong to long rectangular, thick-walled; peristome teeth very long, arising from a low basal membrane, dark reddish-brown, finely papillose to nearly smooth, divided nearly to the

base into 2 filiform branches. *Spores* globose, finely papillose. *Calyptra* long, conical-mitrate, verrucose at the tip.

Subsection *Piliferi* is a monotypic taxon that consists of only *Codriophorus varius*, a western North American endemic. It is characterised by the following set of characters: (1) hyaline, flat, denticulate leaf hair-point; (2) plicate leaf base; (3) rectangular to lunate and strongly flattened costa on the dorsal side, bistratose in the upper half, 3–4-layered in the lower half with 1–2 layers of dorsal stereids; (4) shortly to long rectangular laminal cells; (5) convolute, plicate and entirely hyaline innermost perichaetial bracts, subacute to rounded-obtuse and bluntly serrate at the apex; (5) long cylindrical capsule with a long rostrate operculum; (6) very long, peristome teeth, deeply split nearly to the base into two thread-like branches.

Codriophorus varius, the only species of subsect. Piliferi, shares the nodose habit and leaf areolation of elongate cells with the taxa of the two remaining subsections of sect. Fascicularia, but differs primarily in the anatomy of the costa which is 3-4-stratose in the lower half with 1-2 dorsal rows of stereid cells, the long cylindrical capsule and the very long peristome teeth (1.0-1.8 mm) that are probably the longest in the genus (peristome teeth are still unknown in C. laevigatus). Another peculiar feature of this subsection is the presence of a hyaline hair-point on the leaves, a character making it similar to subsect. *Chrysei*, but in this latter taxon the costa is entirely bistratose throughout and the innermost perichaetial leaves are entirely chlorophyllous. In contrast, species of subsect. Fasciformes always lack hyaline leaf hair-points and the costa is bistratose throughout most of its length, except for the extreme base where it has tristratose patches and only occasionally is it entirely tristratose in the lower part.

Codriophorus sect. Piliferi was originally recognised as a section, Racomitrium sect. Pilifera, to accommodate three species, R. varium, R. carinatum and R. lepervanchei Besch. (Bednarek-Ochyra 1995). Later, this section was given a name in *Codriophorus* (Ochyra *et al.* 2003). Here, the section is reduced to a subsection within *Codriophorus* sect. *Fascicularia* and considered to be a monotypic taxon comprising only *C. varius*. The other two species are excluded from the subsection, *C. carinatus* being placed in subsect. *Hydrophilus*, while *R. lepervanchei* is correctly a member of *Bucklandiella*, *B. lepervanchei* (Besch.) Bednarek-Ochyra & Ochyra, which is closely related to or possibly conspecific with *B. emersa* (Müll.Hal.) Bednarek-Ochyra & Ochyra.

15. Codriophorus varius (Mitt.) Bednarek-Ochyra & Ochyra (Figs 103–105)

Codriophorus varius (Mitt.) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, Cens. Cat. Polish Mosses: 140. 2003. = Grimmia varia Mitt., J. Linn. Soc. Bot. 8: 21. 1864. = Racomitrium varium (Mitt.) A.Jaeger, Ber. Thät. S. Gall. Naturw. Ges. 1872-1873: 97. 1874. — TYPE CITATION: British Columbia, Lyall and Douglas; and also in Observatory Inlet [British Columbia, 55°15' N, 129°49' W]. [Lectotype (vide Cao et al. 1998: p. 16): "Brit. Columbia near 49th parallel Dr Lyall" - NY-Mitten!; isolectotypes: "Oregon Boundary Commision. 1858-//9/ Grimmia (Rhacomitrium) varia Mitten Near the 49th parallel of Lat. Dr. Lyall" - BM-Hooker! (2 specimens), NY!; syntypes: (1) "N.W.C. Am. Douglas. W. 419 Trichost. aciculare fol. angust. setis longioribus Douglas" - NY-Mitten!; (2) "W. 416. N.W.C. Am. Douglas Trichost. n. sp. ad fasciculare?" - NY-Mitten! (2 specimens); (3) "Columbia Douglas" - NY-Mitten! (2 specimens); (4) "Observatory Inlet" - NY-Mitten!].

Racomitrium canescens (Hedw.) Brid. var. *lutescens* Lesq. & James, Man. Moss N. Am.: 151. 1884. — TYPE CITATION: USA: on shaded rocks, California (*Bolander*). [Lectotype (*selected here*): "Racomitrium (b) canescens var. lutescens L. & J. Manual p. 151 rocks 9/4 63 Marin Co Cal^a" – NY!; isotypes: "222. Racomitrium canescens, var. lutescens Foliis pellucide acuminatis angustius areolatis vix papillosis. Hab. in rupibus umbrosis ripariis Californiae (Bolander)" – FH!, G-Boissier! (2 specimens), G-Duby!]. First synonymised with *Racomitrium varium* by Renauld & Cardot (1892: p. 87).

Racomitrium oreganum Renauld & Cardot, Bot. Gaz. 13: 198, *f. 15.* 1888 (viii). — TYPE CITATION: Oregon: on rocky hill-sides. (Th. Howell) [Holotype: "Rhacomitrium oreganum Ren. et Card. Oregon: on rocky hillsides leg. Th. Howell" – PC-Cardot!; isotypes: "No. 7. Howell's Pacific Coast Mosses – Oregon North American Mosses. From the Herbarium of Columbia College. Racomitrium Oreganum, Ren. & Card. Coll. Thomas Howell March 1885. Oregon City. Oregon. Distributed by E. G. Britton. – BM!, CANM!, FH! (2 specimens), MO!, NY! (4 specimens), US!]. First synonymised with *Racomitrium varium* by Renauld & Cardot (1890: p. 61).

Grimmia speciosa Müll.Hal. in Röll, Bot. Centralbl. 44: 388. 1890. ≡ Racomitrium speciosum (Müll.Hal.) Kindb., Enum. Bryin. Exot.: 108. 1891. — TYPE CITATION: Vancouver Island, Victoria, 22. Majo 1888 [Lectotype (selected here): "Racomitrium speciosum C.M. N. Amer., Vancouver Island 18 22/5 88 Röll com. C. Müller 1890 Herbarium N. C. Kindberg" – BM!; isotype: G, JE, NY, S-Kindberg!]. First synonymised with Racomitrium varium by Frye (1918: p. 7).

Plants large and robust, coarse, occasionally mediumsized or small, loosely caespitose or forming fairly dense, intricate patches, stiff and rigid, yellow, green, yellow-, olive or dirty green above, brown to rarely blackish-brown below, sometimes brown throughout or greyish-green above due to leaf pilosity. Stems erect, ascending or procumbent, 5-12 cm, sometimes to 20 or, rarely, only 1.5 cm long, sometimes denuded at the base, sparingly dichotomously long-branching or sparsely fasciculatebranched, sometimes pinnate-branched due to many short, lateral, horizontal branches or nodose owing to lateral tuft-like branchlets, occasionally nearly unbranched, in transverse section circular, lacking a central strand, consisting of 10-13 layers of large, hyaline, moderately thickwalled medullary cells and a 3-5-stratose cortex of stereid cells with small lumina and strongly incrassate, brown or blackish-brown walls; rhizoids sparse at the base of erect stems, reddish-brown, glistening, branched or scattered in small clusters along creeping stems; axillary hairs filiform, hyaline throughout, composed of 9-15 rather short, barrel-shaped cells. Leaves crowded, erect, closely imbricate to loosely appressed, often falcato-secund when dry, spreading to squarrose-recurved when moist, straight to somewhat falcate, decurrent, concave below, broadly keeled to narrowly canaliculate-concave above, ovatelanceolate to lanceolate, (2.5-)3.0-3.7(-4.0) mm long, 1.0-1.2(-1.5) mm wide, from an ovate, plicate base slenderly or broadly acuminate, ending in a hair-point or muticous, subacute to rounded-obtuse, sometimes cucullate at the apex; hair-point hyaline, 0.1-0.75 or, occasionally, 1.2 mm long, becoming progressively longer up the stem or branches, rather stiff, straight or flexuose, erect to recurved, flattened, narrow throughout or narrow above and becoming widened towards the insertion and embracing a small part of the upper lamina, not or fairly long decurrent down the margins, finely and irregularly spinulosedenticulate with short narrow spicules or finely denticulate; margins entire and unistratose throughout, recurved to revolute from the base almost to the apex or somewhat below it; costa single, unbranched and unspurred, percurrent or subpercurrent, ending several cells below the leaf tip, well-defined and clearly delimited from the laminal cells, olive-green to yellow-brown, strong, 75-100(-110) µm wide at the base, gradually tapering upwards, lying at the bottom of a deep, fairly narrow-angled and partly enclosed furrow, in transverse section prominently convex dorsally, flat ventrally, bistratose, reniform to elliptical, with 3(-4)ventral cells not differentiated from the dorsal ones in the distal portion, 3-4-stratose, rectangular to lunate and strongly flattened in the proximal part, with 4-7 ventral cells approximately of the same size and shape as those in the central row and small stereid cells in 1 or sometimes 2 dorsal rows; laminal cells unistratose throughout, pellucid, with thickened and strongly sinuouse longitudinal walls, short-rectangular to quadrate at the extreme tip and at the margins, (8-)13-20(-30) µm long, 7-8 µm wide, becoming elongate, (20-)30-45(-50) µm long, 7-8 µm wide in mid-leaf and long rectangular towards the base, (20-)35-60(-75) µm long, 5-8 µm wide; basal cells rectangular, 25-50 µm long, 5-10 µm wide, with strongly incrassate, nodulose and porose walls, forming a distinct vellow- or orange-brown belt along the leaf insertion; alar cells similar to the basal cells, differing only in being somewhat broader, 25–50 µm long, 13–20 µm wide, forming a yellow-brown or yellow, pellucid, flat, somewhat decurrent group; supra-alar cells rectangular, 20-50 µm long, 7–8 μ m wide, with moderately thickened and straight or somewhat sinuose walls, forming a pellucid hyaline marginal border of 15-19 cells, often with the second, shorter row consisting of up to 9 similar cells. Dioicous. Perigonia gemmiform, to 2.2 mm long; outer perigonial bracts lanceolate, to 2.2 mm long, 0.8 mm wide, ovate-lanceolate, similar to the vegetative leaves; inner perigonial bracts ovate, shortly acuminate, muticous, rounded-obtuse at the apex, 0.9-1.5 mm long, 0.9-1.0 mm wide, concave; innermost perigonial bract ovate, broadly acute, 1.0-1.1 mm long, 0.9-1.0 mm wide, concave, faintly costate, comprising about 20 club-shaped, antheridia intermixed with a few pale brownish-yellow paraphyses much shorter than the antheridia. Outer perichaetial leaves similar the vegetative leaves, ovate-lanceolate, 3–4 mm long, 1.1-1.2 mm wide, muticous or piliferous; inner perichaetial leaves convolute, concave, longitudinally plicate, oblong-lanceolate, 2.2-2.5 mm long, 0.9-1.0 mm wide, broadly acute to rounded-obtuse and apiculate, bluntly serrate due to projecting cell ends at the apex, hyaline throughout, with a thin-walled areolation and a faint costa ending far below the apex. Setae 1, or rarely 2, in the perichaetium, straight, erect, (0.6-)1.2-2.0(-2.2) cm long, dark brown throughout, sometimes yellow-brown above or reddish-brown below, smooth, glossy, twisted clockwise; vaginula dark brown to reddish-brown, 1.0-1.5 mm long, with rectangular to linear, thick- and sinuose-walled epidermal cells. Capsules exserted, erect, straight, cylindrical, (2.5-)3.0-4.2 mm long, 0.8-1.0 mm wide, smooth or somewhat sulcate when old and empty, lustrous, brown or yellowish-brown, pachydermous; operculum subulate, with a straight rostrum, (1.5-)2.0-2.3 mm long, reddishbrown, lustrous; annulus separating, consisting of 2-3 rows of large, vesiculose cells with strongly thickened walls; exothecial cells mostly elongate, oblong to long rectangular, (25-)50-70(-100) µm long, 10-15 µm wide, thick-walled, arranged in regular longitudinal rows, becoming rounded, quadrate to shortly rectangular, intensely dark or orange-brown in 4-7 tiers at the orifice, and shortrectangular to rounded with strongly incrassate walls at the base of the urn; stomata numerous at the urn base, 18-20 per capsule, arranged in 2-3 rows, rounded, 25-35 µm wide, bicellular, superficial, with rounded pori; peristome teeth 16, dark reddish-brown, sharply contrasting with the yellow-brown or light brown urn, 1.0-1.8 mm long, fragile and often broken, faintly papillose to nearly smooth, regularly split nearly to the base into 2, threadlike, terete, equal or unequal branches, nodose on account of distinct articulations, with a short basal membrane to 65 µm, and a low, hyaline preperistome to 50 µm. Spores spherical, pale brown, 12–15 µm in diameter, faintly papillose. *Calyptra* long, 2.3–3.0 mm, conic-mitrate, brown, darker and verrucose at the apex, naked, 4–5-lobed at the base.

Etymology — The specific epithet derives from the Latin *varius* meaning various, different or distinct, in reference to the clear distinctness of *Codriophorus varius* from *C. fascicularis* and *Niphotrichum canescens* with which Mitten (1864) compared his new species in the original description.

Diagnostic characters and differentiation — Codriophorus varius is one of the most distinctive and characteristic species of the genus which may be diagnosed as follows: (1) plants large, robust and coarse, stiff and rigid; (2) stems erect, ascending or creeping, often with only a few long branches, sometimes fasciculate- or pinnate-branched or with short, lateral horizontal branches, giving the plants a nodose appearance, sparsely radiculose below; (3) leaves appressed on drying, patent to recurvedsquarrose on wetting, ovate-lanceolate to lanceolate, mostly 3-4 mm long, plicate and concave at the base, narrowly canaliculate-concave to broadly carinate distally, *piliferous or muticous*, subacute to rounded-obtuse, sometimes cucullate at the apex; (4) hair-point hyaline, to 1.2 mm long, erect to recurved, straight or flexuose, flattened, narrow throughout or becoming widened towards the base, finely spinulose-denticulate to weakly denticulate; (5) costa entire, percurrent to subpercurrent, 75-100(-110) µm wide at the base, situated at the bottom of a deep, narrow-angled and partially enclosed groove, flat on the ventral side and distinctly convex on the dorsal side, elliptical to reniform, bistratose in the distal half, rectangular to crescent-shaped and markedly flattened, 3-4-layered in the proximal portion, with 4-7 ventral cells and a 1(-2)-layered dorsal stereid group; (6) margins entire and unistratose throughout, recurved to revolute from the base nearly to the apex; (7) laminal cells unistratose throughout, short-rectangular to quadrate at the apex, long rectangular below; (8) alar cells short-rectangular, thick-walled, forming yellow-brown or yellow, pellucid, flat, somewhat decurrent auricles; (9) supra-alar cells rectangular, straight-walled, forming a pellucid, 1-2-seriate basal marginal border extending 15–19 cells up the leaf; (10) innermost perichaetial leaves hyaline throughout, serrate at the apex; (10) setae straight, smooth, dextrorse; (11) capsules exserted, straight, long cylindrical, mostly 3-4 mm long, smooth, brown, lustrous; (12) exothecial cells rectangular, thick-walled, arranged in regular longitudinal rows; (13) peristome teeth very long, 1.0-1.8 mm, dark reddish-brown, finely papillose to subglabrous, deeply divided nearly to the base into two filiform prongs, with a short basal membrane and preperistome.

FIGURE 103. *Codriophorus varius.* — 1. Portion of branch with mature sporophyte, dry. 2. Plant with mature sporophytes, dry. 3–12. Leaves. 13–21. Transverse sections of three leaves, sequentially from base to apex. — [1 from *Mackenzie 296*, CANM; 2, 9–10 from *Schofield & Taylor 78966*, CANM; 3–4, 16–18 from *Lyall s.n.*, syntype of *Grimmia varia*, NY; 5–6 from *Howell 7*, isotype of *Racomitrium oreganum*, BM; 7–8 from *Bolander s.n.*, 9 Apr 1863, lectotype of *R. canescens* var. *lutescens*, NY; 11–15 from *Röll s.n.*, 22 May 1888, lectotype of *Grimmia speciosa*, BM; 19–21 from *Hermann 22807*; BM]. — Scale bars: a – 1 mm (3–12); b – 1 cm (2); c – 100 μ m (13–21); d – 0.5 cm (1).



Codriophorus varius is an isolated species which shows only distant affinity to other species of sect. Fascicularia within which it is positioned in a separate subsection. It, together with C. carinatus and C. laevigatus, are the only three species of the genus which have leaves typically terminated with a hyaline hair-point. However, the possibility of its confusion with these other species is non-existent. They are remotely separated geographically, occurring on different continents, but additionally they differ in essential structural characters. The hair-point in C. carinatus is very short, less than 125 µm, the upper laminal cells are short and isodiametric and opaque, the leaf margins are often bistratose distally and the costa is narrow, semi-terete, rectangular or reniform, and only rarely is it distinctly flattened at the base, with 3-5 enlarged ventral cells. In addition, it is not grooved or is situated in a shallow, wide-angled furrow in the basal part. The hair-point in C. laevigatus is longer, to 300 µm, but the costa is bistratose throughout and dictinctly convex on the ventral side, the alar cells forming prominent, somewhat convex auricles. Moreover, the plants have a handsome nodose habit owing to the presence of numerous lateral tuft-like branchlets.

The hyaline awn is markedly reduced or entirely wanting in a substantial number of *Codriophorus varius* populations so, unless carefully studied, such plants are likely to be confused with other species in western North America. Externally, they may resemble *C. ryszardii* which also produces fairly robust plants and has leaves of comparable size, a subpercurrent costa and cylindrical capsules with long rostrate lids. However, the leaves in *C. ryszardii* are narrowly lanceolate and distinctly erosodentate or cristate at the apex. Additionally, its costa is generally stouter and only shallowly grooved, the supraalar cells are similar to the adjacent laminal cells and do not form a pellucid border, and the peristome teeth are one third to half as long as those of *C. varius* as well as being densely spiculate-papillose.

The plants of *Codriophorus varius* with muticous leaf apices are likely to be mistaken for robust and coarse phenotypes of *C. fascicularis*, especially when sterile, and Mitten (1864) actually compared these species in his original description of the former. *C. fascicularis* is, however, distinct at once in having leaves distinctly plicate at the base, long rectangular upper laminal cells and a costa bistratose in cross-section almost throughout its whole length, except for the extreme base where it may be partially tristratose.

Epilose ecads of *Codriophorus varius* are externally similar to *Bucklandiella pacifica* (Ireland & J.R.Spence) Bednarek-Ochyra & Ochyra, a western North American endemic which partly shares its geographical range (Ireland & Spence 1987; Frisvoll 1988). Actually, T. C. Frye distributed this latter species in his *Moss Exsiccata* as No. 20 under the name *Racomitrium varium* and his specimen was used as one of the paratypes for the description of *R. pacificum*. Both species have similar rigid, ovate-lanceolate, erect-appressed to slightly secund leaves which are obtuse or subacute at the apex, with a strong, sub-

percurrent costa that is deeply grooved and 3–4-stratose in the proximal part. Careful microscopic examination should immediately exclude confusion since *Bucklandiella pacifica* has entirely smooth laminal cells that are mostly rounded-quadrate in the upper part, and its leaves are narrowly canaliculate in the distal half, and generally smaller, less than 3 mm, with the margins broadly recurved to $\frac{2}{3}-\frac{3}{4}$ of the leaf length on one side and more narrowly recurved to $\frac{1}{2}$ the leaf length or plane on the other side. Moreover, *B. pacifica* grows on frequently moistened rocks close to streams and creeks. The differences between the epilose phenotypes of *C. varius* and *C. depressus* are discussed under the latter.

Finally, *Codriophorus varius* has occasionally been mistaken for the Asiatic *C. anomodontoides* with which it shares similar robustness of the plants. However, the latter is very distinct in its peculiar anatomy of the costa which is strongly convex on the ventral side and is bistratose almost throughout.

Variability - Codriophorus varius has usually been a well understood and correctly circumscribed species (Lesquereux & James 1884; Frye 1918; Jones 1933; Lawton 1971) because it exhibits relatively little variation of taxonomically important characters, especially in leaf areolation and costa structure. The lack of excessive morphological variability of C. varius has resulted in relatively few synonyms of this species name. However, it has actually been described as a separate species on two occasions. Renauld & Cardot (1888a, b) recognised the plants from Oregon as Racomitrium oreganum, evidently without reference to a previously described taxon from this region. Soon afterwards these authors examined authentic material of C. varius and sank their own species, considering its name to be synonymous with Racomitrium varium (Renauld & Cardot 1890). On the other hand, Müller (in Röll 1890) described Grimmia speciosa from Vancouver Island and emphasised its difference from Racomitrium varium in the leaf stance on wetting, a character which has no taxonomic importance in this case. Finally, Lesquereux & James (1884) described this species as a variety, Racomitrium canescens (Hedw.) Brid. var. lutescens, on the basis of its denticulate hyaline hairpoint which is definitely different from the papillose awn in typical expressions of this species. At the same time, these authors described Racomitrium varium but they misinterpreted it and attributed to it an entire hair-point and round-quadrate upper laminal cells.

The most outstanding feature of this species is its hyaline hair-point. Its presence and length vary considerably within the same population and even the same shoot and its variation follows the general trends observed throughout the whole Grimmiaceae family. The hair-point is usually much longer on the uppermost leaves and becomes progressively shorter downwards, becoming markedly reduced or wanting on the lower leaves. It is mostly 0.5–0.7 mm long but sometimes it may be impressively long, to 1.2 mm, or distinctly shorter and reduced to



FIGURE 104. *Codriophorus varius.* — 1. Cross-section of stem. 2–3. Axillary hairs. 4–6. Leaf apices. 7. Upper laminal cells at margin. 8. Mid-leaf cells. 9. Basal juxtacostal cells. 10. Alar and supra-alar cells. — [1–3, 10 from *Schofield & Taylor 78966*, CANM; 4, 6 from *Röll s.n.*, 22 May 1888, lectotype of *Grimmia speciosa*, BM; 5 from *Norris 70697*, UC; 7–9 from *Howell 7*, isotype of *Racomitrium oreganum*, BM]. — Scale bar: 100 µm.

a hyaline tip. In extreme cases all leaves on the shoots are epilose, especially in plants growing in less exposed habitats. The hyaline awns are narrow throughout or distinctly widened towards the base, embracing a small part of the upper lamina and they differ also in the form of denticulation, from slightly denticulate to spiculose-denticulate. They are strict or flexuose, especially when longer, and straight or distinctly recurved, in particular on the stem or branch tips. The plants of *Codriophorus varius* vary in such usually modifiable characteristics as size, colour and branching pattern. They are generally large and robust, being on average 5–12 cm long, but sometimes they are excessively large, reaching 20 cm in length, for example on Sonora Island near Vancouver Island (*Schofield 64160*, ALTA, CANM, DUKE). The plants growing on exposed rocks usually form denser tufts and are fairly small, to 1.5 cm. As well, the colour of the plants varies markedly but is



strictly associated with exposure to the sun and typically plants growing in shady and moist situations are green to yellowish-green. The type of branching varies to a relatively large degree as in other species of the genus. Most often, the plants growing in shady and moist habitats are irregularly and sparsely branched with a few long branches, but sometimes they are regularly pinnately branched with short, lateral, horizontal branchlets, especially when occurring in open sites.

Reproduction — Most populations of *Codriophorus varius* are found in fine fruiting condition and sporophytes are usually produced in abundance.

Taxonomic and nomenclatural notes — Codriophorus varius was originally described by Mitten (1864) as Grimmia varia from specimens collected by Lyall and Douglas in British Columbia during the expedition for the Northwest Boundary Survey, along the 49th parallel and ten years later was transferred to Racomitrium as R. varium (Jaeger 1874). The species was compared to C. fascicularis from which it differed in being more robust and having short, nearly smooth and diaphanous leaf hair-points. In addition, its leaves were described as intermediate in outline between those of C. fascicularis and Niphotrichum canescens (Hedw.) Bednarek-Ochyra & Ochyra but wanting lax, hyaline decurrencies. Mitten's (1864) diagnosis is not entirely correct because he described the upper laminal cells as being 'roundquadrate', whereas they are in fact short-rectangular and quadrate at the extreme tip and margins, with sinuose walls, but never rounded. This error was later repeated by Lesquereux & James (1884) who, additionally, changed Mitten's designation of the hair-point as 'subentire' into 'entire'. This misleading description prompted Renauld & Cardot (1888a, b) to recognise a new species from Oregon, Racomitrium oreganum, which was soon considered by these authors to be conspecific with C. varius after examination of its type material (Renauld & Cardot 1890).

Another consequence of the incorrect description of *Codriophorus varius* by Lesquereux & James (1884) was the recognition of *Racomitrium canescens* var. *lutescens* from specimens collected by Bolander in California. In fact, this variety is a typical expression of *C. varius* as indicated by Renauld & Cardot (1892). Finally, Müller (in Röll 1890) described *Grimmia speciosa* from Vancouver Island, which a year later was given a name under *Racomitrium* (Kindberg 1891). Frye (1918) reduced *R. speciosum* to synonymy with *R. varium*.

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Chromosome number — Three populations of *Codriophorus varius* have so far been studied chromosomally and two different chromosome numbers have been discovered. In two populations from Washington the haploid chromosome number n = 12 was detected (Ireland 1965, 1967), whereas in the plants from British Columbia n = 13 was counted (Ramsay & Schofield 1981).

Habitat — Codriophorus varius is predominantly a saxicole associated with both basic (limestone) and acidic (granite, diorite, basalt, schistose, serpentine and sandstone) rocks, but less often it is also found on sandy or clayey soil and humus, as well as epiphytically on tree trunks, logs and at tree bases. It grows in a wide range of habitats, from protected, shaded and damp or wet to open, fully or diffusely lit and dry in coastal mixed and coniferous forests, woodlands, grasslands, forest glades, also on the banks of streamlets and outcrops in fens, in partially drained bogs, seepage, on roadcuts and earthy banks by roads and, occasionally, on the concrete walls of buildings. As a hydrophyte it thrives on stones, boulders, shale ledges, projecting outcrops, cliffs, cliff terraces and rock faces in or near rivers, streams, creeks and lakes and by waterfalls, usually in places above the flood line, but sometimes in occasionally submerged sites or on pockets of sand in stream beds. The species usually forms monospecific tufts, but occasionally some clumps of Codriophorus acicularis and Bucklandiella pacifica have been found as an admixture. Hübschmann (1978) recorded C. varius in two hydrophytic moss associations on Vancouver Island, namely in Scoulerietum aquaticae and Dichelymetum uncinati, in which it grows together with Scouleria aquatica Hook., Schistidium rivulare (Brid.) Podp., Fontinalis antipyretica Hedw., Dichelyma uncinatum Mitt. and Scleropodium obtusifolium (A.Jaeger) Kindb.

Geographical distribution — *Codriophorus varius* is a western North American endemic species (Fig. 106). It is widespread and locally common and abundant in coastal areas, from the Queen Charlotte Islands and Vancouver Island in British Columbia in the north, through to Washington and Oregon southwards to central California, west of the Cascade Mountains and only once recorded in the Rocky Mountains of northern Idaho. The species commonly occurs at low elevations, particularly in the coastal region, and only rarely is it found above 1000 m, with the highest locality situated at 1700 m in Siskiyou County in northern California.

Frye (1918) described the geographical range of *Codriophorus varius* as extending from Alaska to California

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FIGURE 105. *Codriophorus varius.* — 1. Portion of branch with seta and mature capsule, wet. 2. Perigonium. 3. Outer perigonial bract. 4. Inner perigonial bract. 5. Innermost perigonial bract and antheridia. 6–8. Perichaetial leaves, sequentially from outermost to innermost. 9. Apex of innermost perichaetial leaves. 10. Epidermal cells of vaginula. 11. Transverse section of seta. 12. Calyptra. 13. Transverse section of calyptra. 14. Operculum. 15. Operculate capsule with calyptra, wet. 16–17. Operculate capsules, wet. 18–20. Deoperculate capsules with peristomes, wet. 21. Exothecial cells in mid-urn. 22. Exothecial cells at base of urn and stomata. 23. Exothecial cells at capsule mouth, annulus, peristome and spores. — [1, 10–11, 13, 17–23 from *Schofield & Taylor 78966*, CANM; 2–9 from *Ireland 6401*, CANM; 12, 15 from *Mackenzie 296*, CANM; 14, 16 *Schofield 93147*, CANM]. — Scale bars: a – 1 mm (6–8, 12, 14) and 100 µm (23); b – 100 µm (11); c – 100 µm (9–10, 13, 21–22); d – 1 mm (2–5); e – 0.5 cm (1); f – 0.5 cm (15–20).



FIGURE 106. Global distribution of Codriophorus varius.

but so far no specimens of this species have been recorded from Alaska and its northernmost collections are from the Queen Charlotte Islands. Additionally, the species has been twice recorded from Asia. Cardot (1904) reported it from Korea but subsequently renamed the voucher specimen (*Faurie 23*, PC) as *Racomitrium fasciculare* var. *orientale*. It is actually identical to *C. anomodontoides*. Cao & Gao (1985) reported *C. varius* from Tibet but according to Cao *et al.* (1998) many specimens so named correctly belong to *Bucklandiella subsecunda*.

EXSICCATI

- Allen Mosses of the Cascade Mountains, Washington No. 31 (BM, CANM, COLO, DUKE, FH, H, MO, NY, TENN, UC, US).
- BAKER *Pacific Slope Bryophytes* No. **589** (DUKE, FH, M, MO, NY, S, UC, US, W).
- CRUM & ANDERSON *Mosses of North America* No. **560** (Alta, H, KRAM, O, S).
- Frye *Moss Exsiccati* No. **31** (alta, canm, cas, colo, f, g, h, kram, mo, o, pr, s, tenn, us, wtu).

- HOLZINGER *Musci Acrocarpi Boreali-Americani* No. 160 (BM, CANM, F, FH, H, MO, NY, O, PC, PR, UC, US, WTU); No. 419 (CANM, COLO, FH, MO, NY, S, UC, US); No. 238 (MO).
- MACOUN *Canadian Mosses* No. **101** (BM, FH, G, MO, NY, US); No. **460** (BM, CANM, E, FH, MO, NY).
- MACOUN Canadian Musci No. 100 (DUKE, FH, NY); No. 104 (BM, COLO, FH, MO, NY, PR, S, UC, US); No. 123 (DUKE); No. 290 (BM, DUKE, FH, US); No. 621 (CANM, FH, UC); No. 635 (BM, CANM, COLO, FH, MO, NY, UC).
- RENAULD & CARDOT *Musci Americae Septentrionalis Exsiccati* No. **29** (BM, NY).

SCHOFIELD - Bryophyta Canadensia No. 151 (NY).

SELECTED SPECIMENS EXAMINED

NORTH AMERICA. CANADA. BRITISH COLUMBIA. Lynn Canyon Park, Cook 4098 (CANM), Vitt 1915 (ALTA) and Schofield 13016 (ALTA , BCB, BM, BR, COLO, FLAS, H, MICH, MO, O, POZG, TENN, UC, US, W) [Bryoph. Canad. No. 61]; Lynn Canyon Park, Lynn Creek, Lyford & Schofield 200 (KRAM, OSC) and Schofield & Godfrey 67641 (ALTA, CANM, DUKE, NY); Cypress Creek, Schofield 35749 (CANM, COLO, DUKE, NY, S, TENN, US); Capilano Canyon, near Cleveland Dam, Schofield 13336 (CANM, DUKE, S); Caulfield, Whytecliff, 14 Apr 1951, Krajina s.n. (COLO); Rainy River, Port Mellon, Schofield & Boas 18025 (CANM); Sechelt Peninsula, Haslam Creek, Schofield & Boas 18077 & 18111 (DUKE); E side of Zephine Head, Gifford Penninsula, Schofield 63992 (ALTA, CANM, DUKE); Ocean Falls, Schofield 86295 (CANM, DUKE); Station Inlet, Desolation Sound, Schofield 63981 (CANM, DUKE); Deserted Bay, Princess Royal Beach, Jervis Inlet, Schofield 38172 (CANM, DUKE, NY, S, TENN); Lund, Malaspina Peninsula, Schofield & Boas 18170 (CANM, DUKE); Powell River, ca 80 m, Flowers 8006 (ALTA, COLO, NY); Boundary Bay, Crescent Beach, Schofield 28491 (DUKE); New Westminster, Apr 1902, Hill s.n. [Pac. Sl. Bryoph. No. 589] (DUKE, FH, M, MO, NY, S, UC, US, W); Delta area, near Burns Bog, Schofield 35777 (CANM, DUKE); Point Grey, Discovery Road, Schofield 36333 (DUKE); between Brittania Beach and Squamish, Schofield 13123 (NY) [Bryoph. Canad. No. 151]; Mt Noohalk, Norris 2279A (UC); head of Indian Arm, Schofield 40522 (CANM, DUKE); Bowyer Island, Howe Sound, Schofield 20748 (CANM); Gambier Island, West Bay, Howe Sound, Schofield 20719 (DUKE); Calvert Island, Keith Anchorage, Kwakshua Channel, Schofield 86072A (CANM, DUKE); Mt Buxton, Schofield & Williams 27877 (CANM, DUKE); Dease Island, in Fraser River delta, Schofield & Taylor 78966 (ALTA, CANM, DUKE, MO, S); Redonda Island, Pendrell Sound, Schofield 38515 (CANM, DUKE); at junction of Chilliwack River and Slesse Creek, Schofield 57619 (CANM, DUKE); near mouth of Slesse Creek, Schofield & Belland 84599 (ALTA, CANM, DUKE, MO): Borders Creek, 18 km E of Vedder Crossing on Chilliwack River, Schofield 22507 (DUKE); Harrison Lake, Schofield 105458 & 105462 (DUKE); Spuzzum, Fraser Canyon, Schofield & Harrison 81778 (CANM, DUKE); Yale, 17 May 1884, Macoun s.n. (CANM, S); ca 9 km N of Yale, bank of Fraser River, Schofield 81810 (CANM, DUKE); Bridal Falls, Popkum, Schofield 63559 (ALTA, CANM, DUKE); Harrison Hot Springs, E Fraser Valley, Schofield 105422 (DUKE); Capalino Canyon, Schofield & Mueller 6753 (DUKE, G, MO, S, UC). QUEEN CHARLOTTE ISLANDS. Gowing Island: Tasu, Tasu Sound, Schofield & Schofield 73673 (ALTA, CANM, DUKE); Tasu Mt, Schofield & Spence 83874 (CANM, DUKE). Graham Island: Foot Hill, 18 Jul 1957, Persson s.n. (DUKE, KRAM, MO, S); Dawson Inlet, Schofield & Vaarama 24643 (CANM, DUKE, s); Echo Inlet, 1957, Persson s.n. (ALTA, DUKE, H, hb. Frahm, KRAM, S); Tow Hill, NE of Massett, Schofield 14308 (CANM, DUKE, NY, S) & 29866 (NY, TENN); Trounce Inlet, Trounce Creek, Schofield 15639 (CANM, DUKE, s); Skidegate Mission, Schofield 29774 (TENN); Marie Lake, near source of Gold Creek, Yakoun River, Schofield 14209 (CANM, DUKE, S); Van Inlet, Schofield & Sjörs 32162 (CANM); Queen Charlotte City, 28 Jun 1957, Persson s.n. (s), Kunghit Island; Rose Harbour, Schofield 31866 (DUKE). Louise Island: South Low Island, Schofield & Vaarama 23943A (DUKE). Maude Island: Skidegate Inlet, Schofield 15696 (CANM, DUKE, S, WTU). Moresby Island: Botany Inlet, Tasu Sound, SW of Western Point of Botany Inlet, Schofield & Spence 83954 (ALTA, CANM, DUKE); Alliford Bay, Schofield 15771 (CANM, DUKE, S); N face Mt Moresby, Schofield 25267 (CANM, DUKE, S); Barge Point, Schofield 31942 (CANM, DUKE); E of Deena River Mouth, Schofield 30819 (DUKE); road from Copper Bay to Sheldens Bay, Schofield & Krajina 39648 (DUKE); Mosquito Lake, Schofield 100928 (ALTA, DUKE); Sewell Inlet, Schofield 57761 (FLAS); Copper River mouth, Schofield 15924 (CANM, DUKE, S); Gray Bay, Schofield 34740 (CANM, DUKE); Onward Point, Schofield 30192 (CANM, DUKE); Cumshewa Head, Schofield 32381 (DUKE). Tanu Island: Tanu, Schofield 32444 & 32450 (DUKE). STRAIT OF GEORGIA. Galiano Island: Bodega Hill, Schofield & Boas 17389 (CANM); Decanso Bay, Schofield 22750 (CANM, DUKE, S); Virago Point, Schofield & Boas 17314 (CANM, DUKE, S); ca 3.5 km N of Cock Road, Schofield 55461 (BR); Sturdies Bay, Schofield 55445 (BR). Mayne Island: Laura Point, facing Active Pass, Schofield & Boas 17556 (CANM, DUKE, NY, S, TENN, WTU); Village Bay, Parke Mountain, Ireland 69-171 (CANM); Gulf of Georgia, Vitt 1794 (ALTA, CANM). Pender Island: W of Hope Bay, Schofield & Boas 17239 (CANM, DUKE, S); Hope, Schofield & Williams 23443 (CANM, DUKE, S) & 16704 (CANM). Saturna Island: Lyall Cove, Schofield 107852 (MO). Read Island: NE coast, Schofield 38541 (DUKE) & 38544 (CANM, DUKE, NY, S, TENN). VANCOUVER ISLAND. Port Hardy, Winter Harbour, 10 Aug 1975, Hübschmann s.n. (GZU); Colwood near Victoria, Schofield 16421 (CANM, DUKE, s); Victoria, Mt Skirt, Apr 1929, Mackenzie s.n. (BM); Saanich Peninsula, Swartz Bay, Tryon Road, Schofield & Lyford 59791 (CANM, PR); Saanich Peninsula, Partridge Hills, Willis Bay Road, W of Durrance Lake, Halbert, Schofield & Price 1798 (DUKE, MO); Saanich Peninsula, Royal Oak area just off main road from Victoria to Swartz Bay, Halbert, Schofield & Price 1770 (DUKE); Goldstream Park, Schofield 16114 (CANM, DUKE) & 22633 (CANM, COLO, DUKE, KRAM, NY, S, TENN, US, W); Goldstream Park, along Arbutus Ridge, Horton 5265 (ALTA); Skutz Falls Fishway on Cowichan River between Cowichan Lake and Duncan, Halbert & Price 3050 (KRAM); Provincial Park, Englishman River, Hand 60 (CANM); Englishman River Falls, Hand 60-120 & 603A (CANM), 60-79 (MO, PR) & 6032 (DUKE, KRAM, UC); Little Qualicum Falls, Boas 1397 (DUKE); Horne Lake, W of Qualicum Beach, Schofield & Belland 84978 & 84986 (CANM, DUKE); junction of Cameron River and Little Qualicam River near Cathedral Grove, MacKenzie 388 (WTU); Cameron Lake, between Parksville and Port Alberni, ca 170 m, 23 Jul 1977, Düll s.n. (hb. Frahm, s); Shawnigan Lake, ca 200 m, Flowers 7621 (ALTA, COLO, NY, OSC, TENN); Shawnigan Lake, NW of Malahat, Hermann 25810 (ALTA); Victoria, at Esquimalt, 15 Mar 1929, MacKenzie s.n. (WTU); Cedar Hill near Victoria, Macoun 41 (CANM) [Canad. Musci No. 41]; Mt Finlayson, Cody 22964C (CANM) and Schofield & Djan-Chekar 104972 (DUKE); road from Mt Finlayson to Millstream, Halbert & Price 2214 (F); near Victoria, 22 May 1888, Röll s.n. (BM, G, JE, NY, S - type Grimmia speciosa); between Port Hardy and Coal Harbor, Merrifield 255 (osc); Amphitrite Point, 7 Jun 1909, Macoun s.n. (BM, CANM, E, FH, MO, NY) [Canad. Mosses No. 460]; Nanaimo River, 1887, Macoun s.n. (BM, CANM, FH, NY, S, UC, US) [Canad. Musci No. 100]; summit of Malahat Highway, Schofield 77347 (ALTA, CANM, DUKE); Nanoose Hill, Schofield 71737 (ALTA, CANM, DUKE, MO) & 82793 (DUKE); Nanoose Hill, Nanoose Bay, Schofield 60313 (ALTA, CANM, DUKE, MO); Cowichan River at Duncan, Halbert 4627 (CANM, DUKE, FH); Bear Creek, San Juan River, Boas 27 (CANM, DUKE); San Juan Point, Port Renfrew, Schofield 13765 (CANM, DUKE); Old Baldy Mt, Halbert 4514 (CANM, DUKE, FH); Mills Peninsula near Bamfield, Halbert 4136 (DUKE); Bamfield, 7 May 1974, Schofield 55555 (G, O, UC); Kangarcoroad, ca 7.5 km E of Sooke, Schofield 35940 (CANM, DUKE, S); Humpback Road, ca 12 km E of Sooke, Schofield 36006 (CANM, DUKE); Sooke Hills, Mackenzie 266 (CANM); Mt Matheson, Mackenzie 296 (CANM); Sidney, Macoun 105 (CANM); Colquith River, 10 Jun 1908, Macoun s.n. (s); Ucluelet, 7 May 1909, Macoun s.n. (s); E of Tofino, on Ucluelet Hwy, along Taylor River, Schofield 13478 (CANM, DUKE); ca 30 km E of Ucluelet, E end of Kennedy Lake, Goffinet 3166 (ALTA, NY); Kennedy River near entrance to Kennedy Lake, Schofield 43783 (CANM, DUKE); Beaver Lake, Macoun 55 (CANM); Kelsey Bay Ferry Terminal, Horton 5172 (ALTA); Elk Lake, Macoun 110 (CANM); Elk Falls, near Campbell River, Schofield 16199 (CANM, DUKE, S) and Schofield & Belland 85029 (DUKE); Brooks Peninsula, coast opposite Hackett and Guilliams Islands, Schofield 68691 (CANM, DUKE); Brooks Peninsula, W of Jacobson Point, Schofield 82635 (ALTA, CANM, DUKE, MO) & 82583 (ALTA, CANM, DUKE, KRAM); "Phyllodoce" Creek mouth, E of Clerke Point, Schofield 82612 (DUKE); Robson Bight, Tsitika River mouth, Schofield 85578 (ALTA, CANM, DUKE); Saanich Inlet, Rough Creek, 300 m, 12 Jan 1958, Boas s.n. (CANM); Wrentham on Brentwood Bay, Schofield 13610 (CANM, DUKE); Shirley area, near Sheringham Point road, Schofield 29387 (CANM); W of Shirley, Schofield 41483 (CANM, DUKE); Stamp Falls on Stamp River, Schofield 13573 (CANM, DUKE, S, WTU); Gary Oak Knob, near Ash Point on Pedder

Bay, Halbert 4558 (CANM, DUKE, NY, TENN); Ash Point, Pedder Bay, Schofield, Belland & Djan-Chekar 105183 (DUKE); ca 25 km W of River Jordan, Halbert & Price 2642A (DUKE); Jordan River near mouth, Schofield 41482 (DUKE); Thetis Lake, Flowers 7737 & 7745 (COLO, NY); Dock Island, Haro Strait, Schofield 20459 (CANM, DUKE); Nigei Island, NW of Browning Passage, Schofield 40759 (DUKE); Quadra Island, Gowlland Harbour, Schofield 59195 (DUKE); Raza Island, Raza Passage, Schofield 64096 (ALTA, CANM, DUKE); Sonora Island, Hall Point, Schofield 64160 (ALTA, CANM, DUKE); Springer Point, Wall Channel, Schofield 64240 (DUKE); Texada Island, Pocahontas Lookout, Schofield & Boas 18258 (CANM, DUKE, S).

USA. CALIFORNIA. Amador Co.: Sutter Creek Canyon, 1.5 km below Volcano on road to Sutter Creek village, 24 Mar 1974, Weber s.n. (COLO); above junction of East & West Fork Panther Creek, along Tiger Reservoir Road above Panther Creek Bridge and ca 16 km E of Tiger Flar Reservoir, ca 1050 m, Shevock & Norris 21746 (KRAM). Butte Co.: South Fork Feather River, Schofield 23212 (CANM, DUKE); Grizzly Creek, Schofield 23268 (CANM, DUKE). Del Norte Co.: Smith River Valley between Gasquet and Crescent-City near river mouth of South Fork River, Duell 441 (ALTA, KRAM, NY, UC): Griffin Creek at Smith River, Norris 8841 (UC); ca 16 km S of collier Tunnel on Smith River, Schofield 93101 (CANM, DUKE); Monumental, Eastwood 397 (CAS); North Fork of Smith River, S of Stony Creek, ca 150 m, Norris 9639 (NY, UC, US); Pappas Flat, ca 3.5 km W of Gasquet, ca 1400 m, Norris 7808 (UC); Stony Creek about 1.5 km N of Gasquet, 200 m, Norris 70746 (UC); Smith River at Middle Fork of the Jones River, Norris 46256 (UC); trail from Wilderness Fall to Doe Flat, ca 1200 m, Norris 67742 (UC); Six Rivers National Forest, 7.5 km S of Smith River Bridge, N of Darlingtonia, Schnooberger 10995 (NY); Hunter Creek ca 6 km NE of Hwy 199, Norris 9920, 9922 & 9944 (UC); Fieldbrook, Neilsen 2 (UC); junction of Siskiyou Fork and Hwy 199, Taylor 104 (UC). El Dorado Co.: Sly Park Creek, ca 1220 m, Norris 58614 (UC); south fork of American River at Bridal Veil Falls Campground, 1000 m, Norris 58331 (KRAM, UC). Humboldt Co.: North Fork of Mad River near Korbel, 100 m, Tracy 10909 (BM, CAS, FH, UC, US); the Trinity River along Highway 96 about 11 km N of Hoopa, Norris 22271 (ALTA, CANM, COLO, DUKE, FLAS, hb. Frahm, H, KRAM, MO, NY, PR, TENN, UC, WTU) & 22296 (UC); Quarry Road, ca 100 m, Norris 55105 (ALTA, KRAM, UC) & 55101 (UC); 5 km W of Willow Creek, Schofield 93147 (CANM, DUKE); West Fork of Willow Creek, Nelson 54 & 55 (UC); near East Fork of Willow Creek, Nelson 62 (UC); Cedar Creek, at junction with Willow Creek, ca 6 km E of Berry Summit, ca 700 m, Norris 10430 (UC); near Berry Summit, Nelson 50 (UC); Mad River, near Maple Creek, Schofield 28664 (CANM); Bridgeville, Schofield 28752 (CANM) and Frye 2108 (WTU); near Trinidad Bay, Duell 310 (ALTA); at College Cove, Norris 23597 (UC); North Fork of Bear Creek, ca 760 m, Norris 10852 (COLO, F, UC); at Mosquito Lake Road, S of Orleans, Norris 12173 (NY, UC): near Fish Lake above Weitchnec. Norris 22249 (UC); along Aikens Creek to Fish Lake, ca 240 m, Norris 56368 (UC); Humboldt State University, Arcata, Sommer 14 (UC); N of Ondianola, Norris 10262 (UC); near Kneeland, Norris 8582 (UC); Tish Tang Valley near Hoopa, ca 500 m, Duell & Norris 230 (NY) and Norris 11976 & 11989 (UC); Way County Park, ca 30 m, Norris 56292 (UC); N of Honeydew, Norris 10341 (UC); Emerald Creek E of Orick, Norris 24583 (UC); Norton Creek, ca 240 m, Norris 56651 (UC). Lake Co.: Adams, 25 Aug 1922, Frye s.n. (WTU). Mendocino Co.: Willits, upper Beachtal Canyon, Branscomb 22388 (MO); ca 12 km N of Legett, Schofield & Thomas 28860 (CANM, DUKE); Eel River, near Legett, Schofield & Thomas 28868 (DUKE); above the Eel River ca 5 km S of Piercy, ca 200 m, Norris 72114 (UC) & 72115 (KRAM, UC); ca 1.5 km S of Bridges Creek at confluence with Dora Creek and the South Fork Eel River, Frank & Bess Smithe Redwood Grove, ca 200 m, Shevock 20373 (KRAM); ca 11 km N of Branscomb, 400-1000 m, Bourell 349 & 1598 (CAS); Northern California Coast Range Preserve, 11 km NE of Branscomb, ca 425 m, Bourell 3778 (CAS, FLAS); off Redwood Hwy at Liggett, MacFadden 12261 (US) & 22261 (COLO, MO); along Middle Fork of Eel River ca 19 km N of Longvale on road to Dos Rios, Norris 48021 (UC); Covelo Road ca 5 km E of Longvale, Norris 21682 (COLO, F, NY, OSC, TENN, UC, US); Twin Rocks, Eastwood 368 (MO); 15 km N of Laytonville, Farr 63 (TENN); ca 3.5 km W of Yorkville adjacent to Beebe Creek Bridge, ca 260 m, Shevock 24644 (KRAM); Irvin Rocks, Eastwood 368 (CAS). Nevada Co.: Nevada City on Hwy to Downieville, MacFadden 9625 (CANM); Urtlon Valley, at Mosquito Creek, MacFadden 8949 (WTU); Tahoe National Forest, Washington Road, ca 915 m, Shevock 20723 (KRAM). Placer Co.: Tahoe National Forest, at North Fork Campground SSE of Emigrant Gap, 1400 m, 31 May 1996, Norris 88239 (UC); along Dutch Flat Reservoir at Dam Crossing, ca 820 m, Shevock & Norris 20698 (KRAM). Shasta Co.: Klamath Mountains, W of Shasta, 7.5 km from Buckhorn Summit, Schofield 23309 (CANM, DUKE); Whiskeytown National Recreation Area, at Brandy Creek Picnic Area, 350 m, Norris 73625 (COLO, DUKE, KRAM, MO, NY, UC); 8 km WNW of Lakehead, Chase Gulch, Dog Creek, Hermann 24720A (F); 1.5 km N of Mineral School at intersection of road to Oak Run, ca 400 m, Norris 68637 (UC). Siskiyou Co.: Salmon River near Summerville, ca 850 m, Norris 9475 (CANM, UC); White Mt, near Cook and Green Pass, ca 1700 m, Norris 50179 (UC); Idlewyld Campground, ca 15 km E of Sawyers Bar on road to Etna, Norris 11857 & 11876 (UC); Klamath National Forest, trail from Wilderness Falls toward Doe Flat, 800–950 m, Norris 67772 (UC); Klamath River at Oak Flat Creek, ca 300 m, Norris 72254 (UC); Butler Flat, Norris 10173 (UC); Crawford Creek, Ukonom Lake Quadrangle, Norris 10485 (UC); S of Happy Camp, ca 480 m, Norris 52221 (UC). Sonoma Co.: NE of Cazadero on Fort Ross Road, Keator & Mueller 6663 (COLO, S, UC); Gualala River near Lee Noble Road, 120 m, Norris 86966 (UC). Tehama Co.: Lassen Peak Quad, Battle Creek, ca 1100 m, Norris 52686 (UC). Trinity Co.: E of Del Loma, 350 m, Norris 70697 & 70698 (UC); Swede Creek, W of Del Loma, 17 Apr 1970, Kowalski s.n. (CANM); Trinity River at Barney Gulch, Norris 23570 (FLAS, UC); Swinging Bridge, 29 Apr 1972, Malachowski s.n. (MO); New River, betwen Denny and Mills Creek, ca 450 m, 21 Apr 1973, Norris s.n. (KRAM, NY, UC); Flame Gulch near Forest Glen, ca 760 m, Norris 22060 & 22073 (UC); Hayfork Creek about 12 km W of Hayfork, 650 m, Norris 56126 (UC); Big Canyon at Hayfork Creek, ca 670 m, Norris 56188 (UC). IDAHO. Clearwater Co.: Dworshak Reservoir, Silver Creek Arm, 490 m, Gray 1620 (NY). OREGON. Benton Co.: Oregon Route 34, Yew Creek, Illman 654 (CANM); S fork of Alsea River, Alsea Falls, Schofield & Lyford 59835 (DUKE) and Lyford 685 (OSC); Fall Creek, Merrifield 1688 (OSC); Coast Range, Corvallis City Watershed, 15 Apr 1978, Lyford s.n. (KRAM). Clackamas Co.: Mt Hood, Camp Creek, 1.5 mi SE of Rhododendron, ca 915 m, Hermann 18704 (DUKE, US, WTU); Salmon River, 18 Jun 1907, Foster s.n. (WTU); Oregon City, Mar 1885, Howell s.n. (BM, CANM, FH, MO, NY, US - type of Racomitrium oreganum); Estacada, Clackamus River, 20 Jul 1904, Foster s.n. (WTU). Clatsop Co.: Saddle Mt State Park, Saddle Mt, Schofield & Godfrey 67979 (DUKE). Columbia Co.: Columbia River, Goble, 25 Mar 1904, Bailey s.n. (WTU). Curry Co.: Humbug State Park, Schofield 21931 (DUKE); S of Humbug Mountain State Park, Norris 21875 (UC); near Bald Mt Creek bridge, Young 405 (WTU); Siskiyou National Forest, along Hunter Creek Road, SE of Gold Beach, ca 200 m, Norris 84590 (DUKE, UC) & 84628 (UC); 1.8 km W of Bill Moore Creek, Roque River Road, Schofield 93032 (DUKE); Agness, Rogue River above Lowery's Ranch, Henderson 11889 (OSC); Bear Creek, tributary of Winchuck, Henderson 11880 (OSC, WTU); Elk River, near McGribble Ranger Station, Henderson 11887 (OSC); Redwood State Park, Chetco River ca 12 km E of Brooking, Koch 3276 & 3292 (UC); Siskiyou National Forest, Elk River Road, E of Port Orford, ca 300 m, Norris 84663 (UC). Deschutes Co.: Metolius River, Lyford 915 (OSC). Douglas Co.: Canyon Creek, Canyonville, Schofield 22994 (CANM, DUKE); Curtin, Schofield 22933 (CANM, DUKE); Cow Creek Canyon, Henderson 12594 (OSC); Umpqua River, E of Reedsport, Lawton 3385 (S, WTU); Umpqua River at Susan Creek, E of Roseburg, 500 m, Norris 81838 (UC); Reedsport, 26 Mar 1935, Frye s.n. (ALTA, CANM, CAS, COLO, F, G, H, KRAM, MO, O, PR, S, TENN, US, WTU) [Moss Exs. No. 31] and Henderson 11881 (OSC); Bear Creek, ca 150 m, Norris 82542 (UC); S of Tiller, Young 203 (WTU); Canyonville, 15 Aug 1921, Frye s.n. (WTU). Hood River Co.: Columbia River Gorge, Starvation Creek, Schofield 68125 (ALTA, CANM, DUKE); ca 6 km E of Bridge of Gods and 4.5 km W of Wyeth, 2 May 1964, Simpson s.n. (F); Mt Hood, Tilly Jane Camp and Cloud Cap Inn, ca 1525 m, Miller 8407 (CAS, G, UC); Gorton Creek Falls near Wyeth, Weber 2868 (COLO). Jackson Co.: Elk Creek, Henderson 12112 (OSC). Josephine Co.: NW of Grants Pass, along Rogue River road to Galice Ranger Station and beyond to just N of Bailey Creek, Young 544 (KRAM, WTU); Sunny Valley, Schofield 38584 (ALTA, CANM, DUKE); Illinois River near Oak Flat, NE of Kalmiopsis Wilderness, ca 275 m, Norris & Stout 51123 & 51138 (UC). Lane Co.: Eugene, Leiberg 1335 (US); Eugene, Judkin's Point, Henderson 17087 (NY, OSC); Eugene, Spencer Butte, Henderson 17238 (NY, OSC); Hendrick's Park, Eugene, Schrader M-40 (UC); Dexter, Willamette River, Henderson 17168 (KRAM, NY, UC); Mapleton, Leiberg 1414 (US); Mapleton, Waterworks Creek, Henderson 17040 (DUKE, KRAM, NY, OSC, UC); Mapleton, Knowles Creek, Henderson 16972 (NY, WTU); Mapleton, Water Supply Creek, Henderson 17214 (osc); Oakridge Road, Willamette River, Henderson 17159 (KRAM, NY); 9 km SE of Oakridge, Lawton 3417 (FH, KRAM, UC, WTU); Willamette River, Lowell, Henderson 17295 (KRAM, NY); Swisshome, Henderson 16969A (KRAM, NY); near Swisshome, Indian Creek, Henderson 16846 (KRAM, NY, UC); McKenzie River near Indian Creek, Henderson 16910 (KRAM, NY, WTU); Belknap Springs, McKenzie River, Henderson 16914 (NY, OSC); McKenzie River above Leaburg Dam, Henderson 18048 (osc); Cape Perpetua, Schofield & Lyford 59688 (ALTA, CANM, DUKE, OSC); Austa, Schofield & Christy 82063 (CANM, DUKE); Lake Woahink, ca 60 m, Flowers 3968 (ALTA, COLO, NY); Springfield, Ben Pruett's place, 6 Feb 1951, Pruett s.n. (NY); Triangle Lake, Henderson 17489 (NY); Kitson Springs, Doty 3177 & 3178 (NY); S of Noti, 3 May 1935, Andrews s.n. (NY, OSC); Look-Out Creek, 580 m, Jonsson 229B/94 (OSC); Muriel Ponsler Memorial Wayside, S of Yachats, Norris 47381 (UC); Row River, just N of Cottage Grove, Schofield & Donovan 75968a (DUKE); Leaburg, Leiberg 1373 & 1744 (US). Lincoln Co.: N of Depue Bay (Boiler Bay), Schofield 92962 (DUKE); Wendling, 21 Mar 1936, Sipe s.n. (NY, OSC); Risley Creek, ca 30 m, Norris 78433 (UC). Linn Co.: Packers Gulch, Willamette National Forest, Norris 83917 & 83954 (UC); Willamette National Forest, Seven Mile Creek, ca 900 m, Norris 78478 (UC); E of Sweet Home, Santiam River, Lyford 884 (OSC); Canal Creek, Middle Fork Santiam River, Henderson 17965 (KRAM, NY, UC) & 17956 (OSC); Calapooya River, Brownsville, Henderson 12227 (KRAM, NY, OSC, WTU); Halsey, Schofield 82909 (CANM, DUKE); Quartzville Creek, upper Middle Fork Santiam River, Henderson 17966 (OSC); above Cascadia, S Santiam River, Henderson 18010 (OSC). Marion Co.: without closer locality, sine dato, Hall s.n. (F). Multnomah Co.: Latourell Falls, Columbia River E of Portland, ca 30 m. Ireland 7058 (CANM, FH); Shepperd's Dell, Ireland 6981 (CANM); Oneonta Gorge, Schofield 19824 (CANM); Oneota Falls, E of Portland, Anderson 14500 (DUKE); Larch Mt, 920-1200 m, Miller 8533 (G); Gordon Creek, Chapman 3179 (NY); Elk Rock, 17 Apr 1903, Sheldon s.n. (OSC); Portland, NW Cornell Road, Young 313 (UC, WTU); Portland, Foster 290 (WTU); Eagle Creek, Courtney & Tschopp 24 (WTU) and Culver & Namba 33 (WTU). Polk Co.: Siletz River, Norris 47356 (UC). Tillanook Co.: Oswald West State Park, Lyford 2150 (osc) and 8 m, Griffin III 16360 (FLAS). Wasco Co: Memaloose State Park, Memaloose Overlook ca 3 km NNE of Mosier, 120 m, Shevock, Harpel & Christy 19899 (KRAM). WASHINGTON. Clallam Co.: Olympic National Park, Elwha River near Lake Mills, Ireland 6328 (CANM); Whiskey Bend Trail, Ireland 6347 & 6359 (CANM); Hobo Creek, ca 11 km from junction of Clallam Bay to Neah Bay Road, Schofield & Spence 77671 (ALTA, CANM, DUKE); Elwha River, Svihla 951 (WTU) & 952 (MO, WTU); Elwha River valley, between Anderson's and Hume's, Frye 582 (WTU); Quinault River, Welch 20569 (MO); Port Angeles, Harthill 3A (ALTA, H, KRAM, O, S) [Moss. N. Am. No. 560]; Port Angeles, Elwa River, 210 m, Becking 5305P1093 (WTU); Lake Crescent, Barnes Point, Lawton 2452 (WTU) and 275 m, Harthill 334 (S); W of Sekiu, Kern 40 (NY); Olympic Hot Springs, Smith 2181 (E, MO) & 2032 (MO) and Svihla 761A (s); Mt Angeles, Svihla 1046 (WTU) and Foster 2699 (WTU); Bowman's Creek, Svihla 922 (WTU); Dungeness Forks Campground, ca 335 m, Wittmann B-111781 (hb. Frahm, KRAM); upper Olympic Hot Springs, ca 450-580 m, Wittmann B-111726 (KRAM); W of Soleduck Ranger Station, Soleduck River, Schofield & Iwatsuki 28290 (CANM, DUKE). Clark Co.: Camas, 30 Jul 1925, Frye s.n. (WTU). Cowlitz Co.: Trudle River, Eyerdam 3618 (NY); Kalama River, Young 325 (WTU). Grays Harbour Co.: Quinault River at mouth of Lake Quinault, Brinker 4336 (MO); South Olympic, along Quinault River beyond Lake Quinault, Schallert 1372 (F); Lake Quinault, Graves Creek Campground, Lawton 520520 (WTU). Island Co.: Langley, Nov 1920, Grant s.n. (O). Jefferson Co.: Quinalt River, Meyer 130 (FH, G, MO, TENN); Olympic Mountains, Elwha River, ca 5 km below Camp Elkhorn, 550 m, Frye 576 (WTU). King Co.: Green River Gorge, E of Black Diamond, Ireland & Schofield 9323 (CANM, DUKE, H, NY, S, TENN, US); Kent, 18 Dec 1927, Jones s.n. (CANM); Deception Creek Falls, 10 Oct 1964, Sharp s.n. (TENN); North Bend, Cedar Falls, 11 Mar 1932, Bailey s.n. (WTU); Seattle, Lake Washington, Piper 90 (FH, NY, WTU) & 157 (WTU) and Gardner 557 (NY); Seattle, Snoqualmie Falls, Parker 159 (FH) and Bailey 192 (DUKE, MO); Snoqualmie Falls, Coupeville, Gardner 30 (NY, UC); Fall City, Frye 12 (s, WTU); Renton, 15 Jul 1892, Piper s.n. (WTU); Lester, 5 Aug 1908, Frye s.n. (WTU). Klickitat Co.: S of Husum, Suksdorf 84 (UC, WTU); Klickitat River, Jun 1885, Suksdorf s.n. (NY, US); Salmon, 1885, Suksdorf s.n. (FH). Mason Co.: Olympic National Park, trail to Staircase Falls, Ireland 6401 (CANM, MO); Staircase Campground, Ireland 6431 (CANM); Lake Cushman, along Staircase Creek, Svihla 6417 (WTU); Shelton, Wynocchee Big Canyon, Tree Farm Camp, Becking 520806116 & 52080621B (WTU). Pacific Co.: Nemah River, Anderson 14650 (DUKE). Pierce Co.: Carbon River, above Fairfax, Brinker 4305 (BRNM, CANM, CAS, DUKE, hb. Frahm, MO, NY, PR); Mt Rainier National Park, S of Ohanapecosh, Hermann 19111 (COLO, US, WTU); Lagrande, Pack Forest, Becking 520275 (WTU); Fairfax, 12 Jul 1947, Frye s.n. (WTU); Carbonado, Flett 2086 (KRAM, NY, WTU); upper Valley of the Nesqually, Allen 30 (BM, CANM, COLO, DUKE, FH, H, MO, NY, TENN, UC, US); Silver Springs, Lawton W54 103 (WTU); Mt Rainier, Nesqually River, Allen 243 (WTU). San Juan Co.: Sportman's Lake, 7 Feb 1925, Roberts s.n. (MO); Friday Harbor, Cowles 320 (CANM, MO); Friday Harbor, South Bay, Foster 50 (NY, OSC); East Sound, Mt Constitution, 19 Jul 1923, Frye s.n. (WTU). Skagit Co.: Hamilton, South Fork of Nooksack River, Ireland 5913 & 5915 (CANM); Fidalgo Island, Pass Lake, road to Rosario Beach, Lawton 5790 (CANM, WTU); Hamilton, Merryette Creek, 18 Mar 1906, Foster s.n. (CANM, COLO, FH, MO, NY, S, UC, US) [Musci Acroc. Bor-Am. No. 419]; Iron Prospect, Hamilton, 12 Jan 1905, Foster s.n. (BM, CANM, F, FH, H, MO, NY, PC, PR, O, TENN, UC, US, WTU) [Musci Acroc. Bor-Am. No. 160]; Cumberland Falls, Hamilton, Foster 285 (NY); Mt Vernon, Carey 291 (WTU). Skamania Co.: Wind River, N of Carson on road to Lookout Mt, Ireland & Lawton 8464 (CANM, COLO, DUKE, H, US); Trout Creek, Weber 2652 (COLO); Stevenson, 26 Aug 1908, Frye s.n. (WTU). Snohomish Co.: W of Silverton, Ireland 5565 (ALTA, CANM, NY); road to Big Four, Coal Creek, Lawton 3904 (KRAM, OSC, UC, WTU); Stillaguamish River, near Wisconsin Creek, Lawton 3340 (WTU); Mt Pilchuck, Verlot Bridge, ca 300 m, 3 Dec 1947, Larrison s.n. (CANM); Mt Baker National Forest, on road to Pilchuck, Klett 23 (WTU); E of Verlot, S Fork Stillaguamish River, Ireland 17 (CANM); Fish Ladder E of Granite Falls, ca 110 m, 8 Oct 1977, Taylor s.n. (UC); E of Wisconsin Creek at Slide Camp, Lawton 5670 (UC); Sulphur Creek, Glacier Peak, Largent 244 (CANM); E of Elliott Creek Road, Schofield & Hermann 21868 (CANM, DUKE); Glacier Peak Wilderness Area, Suiattle River, ca 500 m, Jenkinson 8 (UC); Granite Falls, Skykomish River, Eyerdam 12018. (DUKE) and & Lawton 4615 (WTU); Monroe, Reynolds 48 (UC); Duvall, Lawton 5758 (WTU): E of Gold Bar, Lawton 3272 & 2369 (WTU): Ben Howard Road, Lawton 4585 (WTU). Thurston Co.: Deschutes River Park, Ireland 5721 (CANM); Nesqually River, Leiberg 1145 & 1146 (US); Gate, Foster 1951 (NY); Tumwater Falls, 10 Feb 1912, Foster s.n. (MO). Whatcom Co.: road to summit of Mt Baker, ca 9 km from Lodge, Ireland 7405 (CANM, NY, TENN); E of Glacier, road to Mt Baker Lodge, Ireland 7565 & 7568 (CANM); Glacier Creek, Glacier Point Overlook Rd., NW slope of Mt Baker, 3 km SE of Glacier, Hermann 22807A (BM, KRAM); Mt Baker Park, Glacier area, Schofield 92742 (CANM, DUKE); Mt Baker National Forest, Nooksack River above Falls, Glacier, Hermann 22746 (CANM, DUKE, H, WTU); Nooksack Falls Mt Baker, Ireland 7417 (CANM, H. S).

Chapter 8

NAMES WITH UNLOCATED TYPES AND TAXA EXCLUDED FROM CODRIOPHORUS

Only names which have been referred to the Racomitrium aciculare and R. fasciculare complexes and quite possibly belong to the treated taxa are listed here. Despite extensive search through the world herbaria it has proved impossible to find original material appropriate for typification and taxonomic assessment of the ten taxon names given below in which are included seven validly published names for varieties and forms and three nomina nuda. Among them is one name proposed by J. Röll, a German bryologist whose herbarium is preserved at the University of Würzburg (Frahm & Eggers 2001), but at present it is not available to students. In general, these names refer mostly to taxa which, judging from their descriptions, merely represent minor environmentally conditioned variants of no particular taxonomic importance. Additionally, five taxa are excluded from Codriophorus, including two varietal names which have been erroneously associated with the names of species correctly assigned to this genus. Taxon names are alphabetically arranged.

NAMES WITHOUT LOCATED TYPES

1. *Dicranum aciculare* Hedw. var. *fluitans* Turner, Musc. Hib.: 67. 1804. — TYPE CITATION: [Hibernia].

This variety is one of three varieties recognised by Turner (1804) within the protean Codriophorus acicularis but lacking closer locality data. The herbarium of Dawson Turner is now housed at BM as part of the Hooker herbarium which is incorporated in the general herbarium. It is marked "Herbarium Hookerianum 1867" and Turner's specimens are labelled "Herb. Dawson Turner'. There is one large sheet which comprises 13 specimens of Dicranum aciculare s. lato. Eleven of them are Codriophorus acicularis and the other two are C. aquaticus and Bucklandiella obtusa. The last two most probably refer to Turner's Dicranum aciculare [var.] y gracile and D. aciculare [var.] & pumilum. Frisvoll (1988: p. 225) stated that one of the eleven specimens of Codriophorus acicularis represents Turner's Dicranum aciculare [var.] ß fluitans but this is not explicitly indicated.

Turner (1804) described his [var.] β *fluitans* as follows: *foliis laxis ovato-lanceolatis nigro-viridibus; calyp*-

tris nigris and further commented on it: "var. β , quam pro diversa specie habuerunt Dillenius Brideliusque, caule fluitante foliorumque forma et colore insigniter differt". Specimen No. 6 on the aforementioned sheet in the Turner/ Hooker herbarium from "stones in a stream in Lough Bray 1802" certainly fits the characters of the plant described as var. *fluitans*. It is a typical aquatic moss growing in fast moving water as is evidenced by the entirely denuded lower parts of the stems. However, because the name of this variety is not definitely indicated on the sheet, this specimen cannot be indicated as the type, although it is very likely that Turner (1804) based his description on it. It is thus very likely that *Dicranum aciculare* var. *fluitans* merely represents a typical expression of *Codriophorus acicularis* growing in stream rapids.

2. *Racomitrium aciculare* (Hedw.) Brid. var. *angustifolium* Höhn., Sitzungsber. Akad. Wiss. Math.-Naturw. Cl. Abt. 1, 104: 325. 1895. — TYPE CITATION: Auf der Südseite der Sierra Nevada in der Höhe von circa 2600 m in oberen Trevelez–Thale.

This variety was described by Höhnel (1895) from the Sierra Nevada in southern Spain and he characterised it as follows: "Die Blätter sind relative schmäller, gegen die Spitze fast kieleg, an der Basis weniger faltig. Sie sind deutlicher papillös. Die Blattränder sind oft ganz flach und stets weniger stark umgerollt als bei der Normalform. Die Blattspitze ist nicht breit abgerundet, sondern mehr winiger spitz, oder mit weniger auffallenden, stumpflichen Sägezähnen versehen". No type material of this variety has been located during the present work, but Loeske (1930: p. 200) stated that "Ich sah ein Original" but without indication of the herbarium. He broadly commented on this taxon and it is evident from his discussion as well as the original description that this taxon represents a modification of otherwise typical plants of Codriophorus acicularis with narrower oblong-lanceolate, longer acuminate leaves with narrower rounded and often acute apices. Such phenotypes are not rare in the Iberian Peninsula and in western North America and certainly cannot be recognised as a separate taxon because all possible intermediates between it and plants with broadly rounded leaves and obtuse leaf apices can be found. Nonetheless, without examination of the original material, formal reduction of this name to synonymy cannot be made.

3. *Racomitrium aciculare* var. *angustifolium* Röll, Hedwigia 46: 201. 1907, *hom. illeg.* — ORIGINAL COLLECTION: [Erzgebirge] am Filzteich bei Schneeberg.

Röll (1907) characterised briefly this variety as follows: "klein, zart, schlaff, mit schmäleren, often fast spitzen Blättern". This diagnosis clearly indicates that the plant closely resembles that described by Höhnel (1895) from Spain and in all likelihood represents the same phenotype of *Codriophorus acicularis*.

4. *R. aciculare* [var.] β *aquaticum* Poech *in* Keil, Lotos (Prag) 1: 177. 1851. — TYPE CITATION: [Böhmen] [...] um Liebwerda, wo es von Wasser bespülte Granitblöcke überzieht.

This taxon was recognised by Poech whose manuscript was used by Keil (1851) for publication of an account of Bohemian mosses. It is an unranked taxon described within *Racomitrium aciculare* and diagnosed as follows: "caule fluitante, foliis patente-recurviusculis, laxis, atroviridibus". No type material was located at PR where the main set of his collection (J. Váňa, *pers. comm.*) is housed. The diagnosis provides no more precise data on leaf shape and therefore any suggestion as to the identity of this plant is impossible, unless it is truly an aquatic plant of *Codriophorus acicularis*, growing submerged on rocks in fast moving water.

5. *R. aciculare* var. *brevicaule* Meyran, Ann. Soc. Bot. Lyon 39: 53. 1916, *nom. nud.* — ORIGINAL COLLECTION: [France] Forez: le mont Pilat (D.)[ebat].

This taxon was mentioned by Meyran (1916) and is a typical *nomen nudum* but no original material has been located. No suggestion as to the identity of this plant is given, although its name may suggest a short-stemmed plant.

6. *R. aciculare* fo. *purpurascens* Zodda, Ann. Bot. 11: 263. 1913. — TYPE CITATION: [Sicily] Presso gli stillicidii sugli schisti cristallini al Pizzo Polo a 1200 m. insieme ad una forma porporina scura di *Bryum alpinum*.

Zodda (1913) briefly characterised this taxon as follows: "Differisce dal tipo per I frusti gracili, flessuosi, la foglie rossicce, almeno lungo la metà basale del nervo, I denti fogliari ridotti o nulli e spesso scolorati". No material of this taxon has been located at MES but other specimens collected by Zodda in this region have been seen which somewhat resemble those described as *Racomitrium aciculare* fo. *purpurascens*. The reddish colour of the plants with reduced dentation of the leaf margins at the apex and fairly gracile capsules are certainly not unusual for *Codriophorus acicularis* and it can be confidently stated that this taxon is scarcely even an ecological variant of that species which does not deserve any taxonomic recognition.

7. *R. aciculare* var. *viride* Hampe, Flora **20**: 281. 1837, *nom. nud.* – TYPE CITATION: Germania [without closer locality data].

Hampe (1837) mentioned this variety in his checklist of the German mosses as a *nomen nudum* since no description was provided. No original material of this taxon was located at BM in the Hampe herbarium, nor has any material been traced in other herbaria which could univocally be ascribed to this author. In the Schliephacke herbarium at JE there is a specimen labelled as follows: "Racomitrium acicular v. viride <u>Bridl.</u> Erzgebirge am Katzenstein" and it represents *Bucklandiella affinis* (F.Weber & D.Mohr) Bednarek-Ochyra & Ochyra, but there is no evidence that it could have been seen by E. Hampe. Hence the identity of this name must remain unresolved.

8. *R. fauriei* Cardot fo. *irrigatum* Cardot, Bull. Herb. Boissier Sér. 2, 8: 333. 1908. – TYPE CITATION: Japon: Hakkoda, pierres arrosées, à 1300 m. (n. 2939 in parte); Iwagisan (n. 325 in parte).

Cardot (1908*a*) provided the following diagnosis of this form: "Obscure viridis, foliis mollioribus, cellulis parietibus minus incrassatis" and cited two specimens from Japan in the protologue. Neither of these has been located either in the herbarium of J. Cardot at PC or in any other herbaria consulted, so the true identity of this taxon must remain unknown. However, when considering the remarkable variability of *Codriophorus carinatus*, it is quite possible that this form falls well within the range of variation of this species.

9. *R. fasciculare* (Hedw.) Brid. fo. *gracile* Boulay, Musci. France 1: 357. 1884. — Type CITATION: ... des Vosges et du Mt-Blanc.

Boulay (1884) characterised this taxon as follows: "Dans certaines conditions, les tiges se redressent, s'allongent et montrent les rameux courts plus espacés; le pedicelle peut atteindre 1 centim. Cette variété plus grêle (*forma gracilis*), resemble jusqu'à un certain point à certaines formes du *Rh. heterostichum* v. *microcarpum*; elle en differe par ses feuilles toutes dépourvues de poil, d'une contexture plus molle, à cellules supérieures papilleuses rendant le contour sinuolé, etc.". The herbarium of A. J. N. Boulay is housed at LILLE but this material has not been available for study. Judging from the description, this is merely a gracile plant of otherwise typical *Codriophorus fascicularis* with erect stems and more distant lateral tuft-like branchlets.

10. *Trichostomum aciculare* (Hedw.) P.Beauv. var. *acutifolium* Arn., Disp. Méth. Mousses: 23. 1825, *nom. nud.* — TYPE CITATION: Écosse.
Arnott (1825) briefly commented on this variety ("J'ai trouvé, mais rarement, cette variété en Écosse : peut-être est-elle une espèce distincte?) but gave not the slightest suggestion as to its diagnostic characters. Therefore the identity of this name has to remain unresolved and no specimen bearing this name could be located in any herbarium consulted.

11. *T. fasciculare* Hedw. var. *secundum* Ahnf. *in* Fries, Stirp. Agr. Femsj.: 28. 1825. — TYPE CITATION: [Sweden, Småland Province, parish Femsjö] ad rupes udas abunde.

Fries (1825) described this taxon as follows: "Caules longi, simplices, decumbentes. Folia secunda. Ad T. patens accedit". No original material of this taxon was located at UPS. The resemblance to *Dryptodon patens* (Hedw.) Brid. may suggest a plant with a narrow leaf apex, so possibly this taxon is identical to *Codriophorus aquaticus* which is a very common plant in Femsjö, a parish in Småland Province in southern Sweden where Elias Fries lived.

TAXA EXCLUDED FROM CODRIOPHORUS

1. *Dicranum aciculare* var. *pumilum* Turner, Musc. Hib.: 67. 1804. = *Racomitrium aciculare* (Hedw.) Brid. var. *pumilum* (Turner) Brid., Bryol. Univ. 1: 221. 1826. = *R. heterostichum* (Hedw.) Brid.) var. *pumilum* (Turner) Moore, Proc. R. Irish Ac. Sc. 1: 361. 1873. — TYPE CITATION: [Ireland] prope Derry, D. Brown legit. [Holotype: "91. Bryum curtum. From a large stone beside a Munting house way between Strabane and Derry Mr Brown" – BM-Turner/ Hooker!]. = *Bucklandiella obtusa* (Brid.) Bednarek-Ochyra & Ochyra. First synonymised by Lindberg (1875: p. 542, 553).

2. *Racomitrium aciculare* (Hedw.) Brid. fo. *excurrens* Mönk., Hedwigia 50: 338. 1911. — TYPE CITATION: [Bornholm] bei Hammersö.

Mönkemeyer (1911) described this form as having "Blätter nach der Spitze zu verschmälert, Rippe kraftig, oft austretend". It would be a curious and the only known case of the excurrency of the costa in *Codriophorus acicularis*, but recognition of this taxon was based upon an error as stated by Loeske (1930).

3. *R. cucullatifolium* Hampe, Linnaea 32: 143. 1863. — TYPE CITATION: Bogota LaPenna et Chapinero ad saxa rorida riparia, 2700 – 3000 metr., Octobr. [Lectotype (*selected here*): "Racomitrium cucullatifolium Hpe Nova Granada, Bogota Penna 3000 metres ad rivulos in saxis roridis August 1859 nº 2032 leg Linding" – BM-Hampe!; isolectotype: BM-Hampe!, M!, s-Ångström!; syntype: "Racomitrium cucullatifolium Hpe Nova Granada, Bogota Chapinero 2700 metres ad rivul in rorid Octob. 1859 nº 2049 leg Linding" – BM-Hampe!; isosyntype: BM-Hampe!, M!, s-Ångström!]. *Racomitrium cucullatifolium* was originally described by Hampe (1863) from Colombia and the author compared it to *R. fasciculare* in the original diagnosis. Bednarek-Ochyra (1995) placed this species in *Racomitrium* subg. *Cataractarum* and established a separate section to accommodate it, subsect. *Cucullaria* Bednarek-Ochyra. The species was subsequently transferred to *Bucklandiella* as *B. cucullatifolia* (Hampe) Bednarek-Ochyra & Ochyra (Ochyra *et al.* 2003). Actually it is closely related to, or possibly conspecific with, *B. subsecunda*.

4. *R. fasciculare* (Hedw.) Brid. var. *minus* Mitt. & Wilson, Hooker's J. Bot. Kew Gard. Misc. 9: 324. 1857 ['minor'], *nom. nud.* — ORIGINAL MATERIAL: Sikkim-Himalaya alpine; Lachen, alt. 13,000 ped., J. D. H. [No. 321] – BM-Hooker!, NY-Mitten!. = *Bucklandiella himalayana* (Mitt.) Bednarek-Ochyra & Ochyra.

This variety was mentioned by Mitten & Wilson (1857) in the list of mosses collected by J. D. Hooker in India but no description was given. Two years later Mitten (1859) cited this specimen as one of several syntypes in the protologue of his newly described species, *Grimmia himalayana* Mitt. It represents an epilose ecad of this species (Frisvoll 1988) which is currently known as *Racomitrium himalayanum* (Mitt.) A.Jaeger or *Bucklandiella himalayana* (Mitt.) Bednarek-Ochyra & Ochyra.

5. *R. fasciculare* var. *compactum* Röll *ex* Podp., Consp. Musc. Eur.: 297. 1954, *nom. inval. in synon. err. pro* Racomitrium microcarpon var. compactum Röll.

Röll (1886) described this taxon as a variety of *Racomitrium microcarpon* (Hedw.) Brid. and Podpěra (1954) erroneously ascribed it to *R. fasciculare*.

6. *R. fasciculare* var. *gracilescens* Molendo, Ber. Naturh. Ver. Augsburg 18: 148. 1865, *nom. inval. err. pro* R. lanu-ginosum (Hedw.) Brid.

7. *R. grimmioides* Herzog, Darwinia 11: 218. 1957. — TYPE CITATION: República Argentina: Tronador, Filo Bariloche, "en rocas sombrias", 1.400 m (nº 180); ibidem, "Campamento, en rocas", 1.500 m (nº 192), leg. A. Donat, 1.6.37. [Lectotype (*selected here*): "Herbarium Haussknecht, Jena Rhacomitrium grimmioides Herz. n. sp. Argentina Parque Nac. de Nahuelhuapi Tronador, Filo Bariloche, Campam rocas 1500 m leg. A. Donat, 6.I.37 n. 192" – JE-Herzog!; isolectotype: JE-Herzog! (2 specimens), s! (2 specimens); syntype:): "Herbarium Haussknecht, Jena Rhacomitrium grimmioides Herz. n. sp. Parque Nac. Argentino Nahuelhuapi No. 180 p.p. Tronador, Filo Bariloche, en rocas sombrías 1400 m leg. A. Donat, 6.I.37 det. Herzph II.43" – JE-Herzog!; isolectotype: JE-Herzog!].

This species was placed by Bednarek-Ochyra (1995) in the separate section *Grimmiiformia* Bednarek-Ochyra in *Racomitrium* subg. *Cataractarum*. However, it correctly belongs within *Bucklandiella* and was actually given the name, *B. grimmioides* (Herzog) Bednarek-Ochyra & Ochyra (Ochyra *et al.* 2003). It appears to be a distinct species from the Andes of Argentina but actually is known only from the type collection from the Nahuelhuapi National Park (Herzog 1957).

8. *R. lepervanchei* Besch, Ann. Sc. Nat. Bot. Sér. 6, 9: 351. 1880. — TYPE CITATION: La Réunion: sur les bois pourris, 1839, Lépervanche, nº 15 (herb. Thuret); pas Belcombe, 1877, Paul Lépervanche. [Lectotype (*selected here*): "Herb. Bescherelle Rhacomitrium Lepervanchei Besch. Pas de Belcombe – 146 La Réunion Lepervanche legit" – BM-Bescherelle!; isolectotypes: H-Brotherus!, PC!, PC-Thériot!, s-Roth/Möller!, w-Förster!].].

Bednarek-Ochyra (1995) placed this species in sect. *Pilifera* within *Racomitrium* subg. *Cataractarum* but in fact it is a member of *Bucklandiella* to which it was transferred as *B. lepervanchei* (Besch.) Bednarek-Ochyra & Ochyra (Ochyra *et al.* 2003). The species is known only from Réunion in the Indian Ocean (Bescherelle 1880; De Sloover 1977) and Lawton (1973) considered it to be identical to *Racomitrium crispulum* var. *tasmanicum* (Hampe) E.Lawton. This identity appears to be correct, although according to unpublished data this variety really represents a distinct species, *Bucklandiella emersa* (Müll. Hal.) Bednarek-Ochyra & Ochyra.

9. *Trichostomum obtusifolium* P.Beauv., Prodr. Aethéogam.: 91. 1805. = *Racomitrium obtusifolium* (P.Beauv.) Brid., Mant. Musc.: 80. 1819. = *Trichostomum aciculare* (Hedw.) P.Beauv. α [var.] *obtusifolium* (P.Beauv.) Arn., Disp. Méth. Mousses: 23. 1825, *nom. illeg. incl. typ. spec.* — TYPE CITATION: Amérique Septentrionale [Lectotype (*vide* Bednarek-Ochyra 2001: 45): "Racomitrium obtusifolium. Trichostomum obtusifolium j'en fais un nouveau genre avant les Dicranum aciculare, pulvinatum et autres espèces à dents fendues Palis de Beauvois" – B-Bridel!] = *Anomodon minor* (Hedw.) Lindb. (*fide* Bednarek-Ochyra 2001: 45).

This species was described by Palisot de Beauvois (1805) from material from North America. It was subsequently transferred to *Racomitrium* by Bridel (1819) and Arnott (1825) reduced this species to a variety of *Trichostomum aciculare*. Because he placed *Trichostomum aciculare* in synonymy with this variety, the combination *T. aciculare* var. *obtusifolium* is illegitimate because it includes the type and correctly this taxon should be called *T. aciculare* var. *aciculare*. In other words, Arnott (1825) reduced *T. obtusifolium* to synonymy with *T. aciculare*. The identity of this species was studied in detail by Bednarek-Ochyra (2001) who found that it has nothing to do with *Codriophorus acicularis* but is conspecific with *Anomodon minor* (Hedw.) Lindb.

SUMMARY

The genus *Codriophorus* P.Beauv. is one of four segregates of the traditionally conceived genus *Racomitrium* Brid. which has proved to be an artificial and heterogeneous taxon. *Codriophorus* is easily distinguished, principally by the presence of large, flat papillae distributed over the longitudinal cell walls which cover the major part of the lumina. In this character is very much resembles the genus *Racomitrium s. str.* but differs in having a densely papillose calyptra, a costa often ending well below the leaf apex, epilose innermost perichaetial leaves, smooth setae that are twisted to the right on drying, lack of a hyaline hair-point in the vast majority of species, a capsule which is never ventricose and mostly shorter peristome teeth that are divided to the middle or base.

Codriophorus species have usually been classified in sect. *Papillosa* (Kindb.) Nog. or subg. *Cataractarum* Vilh. within *Racomitrium*. In total, 42 species, 25 varieties and 13 forms have been described which may be referred to the latter genus. The types or original material of 69 names (86%), including the types of all species names, have been located and taxonomically assessed. As a result of these critical taxonomic studies 15 species have been recognised within *Codriophorus*. They are defined by a combination of gametophyte and sporophyte characters, the most important of which are to be found in the morphological and anatomical structure of the costa, leaf areolation, leaf apex, recurvature of the leaf margin, branching pattern and alar cells.

Codriophorus is here divided into two sections, sect. *Codriophorus* and sect. *Fascicularia* Bednarek-Ochyra. They are subsequently subdivided into four and three subsections respectively.

The type subsection is characterised by having isodiametric upper laminal cells and a broad and robust costa lying at the bottom of a shallow and wide-angled furrow. It is further characterised by a costa that is multistratose and strongly dorsally convex in the median and lower parts, irregular branching of the stems which always lack short lateral tuft-like branchlets, leaf margins variously recurved on one or both sides in the lower half (rarely three quarters), lingulate to broadly ovate or ovate-lanceolate, concave to broadly canaliculate-concave leaves and dextrorse setae. Sect. *Codriophorus* contains nine species which are placed in four subsections. The type subsection consists of four species, *Codriophorus acicularis*, *C. aduncoides*, *C. mollis* and *C. norrisii*, possessing lingulate, elliptical to broadly ovate-lanceolate leaves which are broadly rounded-obtuse or subacute to acute, have entire to irregularly toothed leaf apices, distinct alar cells and lack a basal marginal border. *C. acicularis* is the most widespread species in this subsection, whereas the remaining ones are narrow endemics of western (*C. norrisii*) and eastern (*C. aduncoides*) North America with *C. mollis* having a wider northern trans-Pacific range.

Subsect. *Hydrophilus* contains three species, *Codriophorus aquaticus*, *C. ryszardii* and *C. carinatus* that are characterised by ovate-lanceolate or lanceolate leaves which are concave below and canaliculate-concave to obtusely keeled, narrowly rounded-obtuse, muticous to shortly hyaline tipped and have an entire to eroso-dentate apex. The leaf apices are either consistently entire and muticous (*Codriophorus aquaticus*), entire and muticous to shortly hyaline-tipped (*C. carinatus*) or eroso-dentate and muticous (*C. ryszardii*). They also possess a robust costa which is distinctly convex on the dorsal side. The three species are highly isolated endemics of three continents of the Northern Hemisphere, namely western North America (*C. ryszardii*), Europe and Macaronesia (*C. aquaticus*) and the Far East of Asia (*C. carinatus*).

The monotypic subsect. *Depressi* is diagnosed by its entirely smooth laminal cells that are only weakly papillose on young leaves, very broad and strongly flattened costa and the acute to obtuse, entire to bluntly irregularly dentate leaf apex and obloid or cylindrical capsules that are straight or often somewhat curved and gibbous. *Codriophorus depressus*, the only species of this subsection, is endemic to California.

Subsect. *Andicola* is also monotypic and consists of only *Codriophorus dichelymoides*, endemic to the Northern Andes of Colombia. It is characterised by having strongly falcato-secund to circinate leaves that are concave to subtubular, smooth to slightly papillose laminal cells, entirely chlorophyllous innermost perichaetial leaves and strongly flattened costa not lying in a furrow.

Sect. *Fascicularia* is characterised by cells elongate throughout the lamina and narrow costae situated at the bottom of deep and narrow-angled furrows. The costae are bistratose throughout, not or weakly convex dorsally

though occasionally they may be tristratose and prominent on the dorsal side in the lower half. Additional characteristic features are the frequent presence of many short, lateral, tuft-like branchlets, narrowly lanceolate to lanceolate and muticous to hair-pointed leaves, setae that are basically sinistrorse but have a single torsion to the right immediately below the urn. The section consists of six species that are placed in three subsections.

Subsect. *Fasciformes* comprises species that lack a hyaline hair-point and have entire to dentate or erosodentate and cristate leaf apices, unfolded or scarcely plicate leaf bases, weakly developed auricles and weakly plicate to unfolded innermost perichaetial leaves. The subsection contains four species of which *Codriophorus fascicularis* has the widest geographical pan-Holarctic range. The remaining three species, *C. brevisetus*, *C. anomodontoides* and *C. corrugatus* are principally East Asiatic, extending only occasionally to Alaska (*C. corrugatus*) and Oceania (*C. anomodontoides*).

Subsect. *Chrysei* is diagnosed by having hyaline or yellowish-hyaline, denticulate leaf hair-points, plicate leaves with distinct, coloured auricles composed of cells with strongly incrassate walls, and convolute, chlorophyllous and plicate innermost perichaetial leaves that are

truncate and notched or cuspidate at the apex. The sporophyte characters of this subsection are largely unknown since in its only species, *Codriophorus laevigatus*, only immature sporophytes have been found. This species is widely distributed in the Southern Hemisphere in southern South America with some extensions to the Subantarctic (South Georgia) and Tristan da Cunha.

Subsect. *Piliferi* contains a single species, *Codriophorus varius*, which stands out from others in the genus by its piliferous leaves with distinctly plicate bases and a costa 3–4-stratose and strongly convex dorsally in the lower half of the leaf. It also possesses long cylindrical capsules and very long peristome teeth divided to the base into two filiform prongs. It is a highly isolated endemic of western North America.

Aspects of the ecology and phytogeography of the *Codriophorus* species have been studied and global and regional distribution maps for each species are provided. Every species is illustrated with many line drawings, showing all morphological and anatomical details and SEM micrographs for some species are also included. The phytogeography of *Codriophorus* is analysed and its species are placed in generally recognised phytogeographical elements.

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TAXONOMIC AND NOMENCLATURAL NOVELTIES

New taxa and combinations:

- Codriophorus subsect. Depressi Bednarek-Ochyra, subsect. nov. (p. 151)
- Codriophorus subsect. Fasciformes Bednarek-Ochyra, subsect. nov. (p. 168)
- Codriophorus subsect. Piliferi Bednarek-Ochyra, stat. et comb. nov. (p. 236)

New synonyms:

- Racomitrium aciculare (Hedw.) Brid. var. brachypodium Besch. = Codriophorus carinatus (p. 142)
- *R. aciculare* var. *denticulatum* Bruch. & Schimp. = *Codriophorus acicularis* (p. 55)
- *R. aciculare* var. *falcatum* Grav. = *Codriophorus acicularis* (p. 55)
- *R. aciculare* fo. *falcatum* Jaap = *Codriophorus acicularis* (p. 55)
- *R. aciculare* fo. *fluviatile* Vilh. = *Codriophorus acicularis* (p. 55)
- *R. aciculare* fo. *humile* Vilh. = *Codriophorus acicularis* (p. 55)
- *R. bandaiense* Sakurai = *Codriophorus anomodontoides* (p. 204)
- R. bandaiense var. ramosum Sakurai = Codriophorus anomodontoides (p. 206)
- *R. brevipes* Müll.Hal. = *Codriophorus anomodontoides* (p. 204)
- *R. canaliculatum* Mitt. *ex* Cardot = *Codriophorus anomodontoides* (p. 204)
- *R. canescens* (Hedw.) Brid. var. *yezoalpinum* Sakurai = *Codriophorus brevisetus* (p. 195)
- *R. fasciculare* (Hedw.) Brid. var. *atroviride* Cardot = *Codriophorus fascicularis* (p. 170)
- *R. fasciculare* var. *haplocladon* Kindb. = *Codriophorus fascicularis* (p. 169)
- R. fasciculare var. hayachinense Nog. = Codriophorus brevisetus (p. 195)
- *R. fasciculare* fo. *nigrescens* H.Winter = *Codriophorus fascicularis* (p. 170)
- *R. fasciculare* var. *nigricans* Warnst. = *Codriophorus fascicularis* (p. 169)

- *R. fasciculare* var. *orientale* Cardot = *Codriophorus brevisetus* (p. 195)
- *R. fasciculare* var. *perrobustum* Broth. = *Codriophorus anomodontoides* (p. 204)
- *R. fasciculare* fo. *rivulare* J.E.Zetterst. = *Codriophorus fascicularis* (p. 169)
- *R. fasciculare* fo. *submersum* H.Winter = *Codriophorus fascicularis* (p. 170)
- *R. fasciculare* fo. *validius* H.Winter = *Codriophorus fascicularis* (p. 170)
- *R. fauriei* Cardot = *Codriophorus carinatus* (p. 142)
- *R. hedwigioides* Sakurai = *Codriophorus anomodontoides* (p. 206)
- R. hedwigioides var. chrysophyllum Sakurai = Codriophorus anomodontoides (p. 206)
- *R. hespericum* Sérgio, Muñoz & Ochyra = *Codriophorus acicularis* (p. 55)
- *R. hypnoides* Lindb. fo. *chrysophyllum* Sakurai = *Codriophorus brevisetus* (p. 195)
- *R. nipponicum* Sakurai = *Codriophorus anomodontoides* (p. 204)
- *R. papeetense* Besch. = *Codriophorus fascicularis* (p. 169)
- *R. papillosum* Sakurai = *Codriophorus brevisetus* (p. 195)
- *R. protensum* (Duby) Bruch & Schimp. fo. *robustum* Loeske = *Codriophorus aquaticus* (p. 111)
- *R. sawadae* Cardot = *Codriophorus brevisetus* (p. 195)
- *R. sudeticum* (Funck) Bruch & Schimp. var. *subellipticum* Cardot = *Codriophorus carinatus* (p. 142)

New lectotypes and epitypes:

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