Endemic genera of bryophytes of North America (north of Mexico)

Endemické rody mechorostů Severní Ameriky

Wilfred Borden S c h o f i e l d

D e d i c a t e d t o t h e m e m o r y o f E m i l H a d a č

Department of Botany, University Boulevard 3529-6270, Vancouver B. C., Canada V6T 1Z4, e-mail: wilfs@interchange.ubc.ca

Schofield W. B. (2004): Endemic genera of bryophytes of North America (north of Mexico). – Preslia, Praha, 76: 255–277.

There are 20 endemic genera of mosses and three of liverworts in North America, north of Mexico. All are monotypic except *Thelia*, with three species. General ecology, reproduction, distribution and nomenclature are discussed for each genus. Distribution maps are provided. The Mexican as well as Neotropical genera of bryophytes are also noted without detailed discussion.

K e y w o r d s : bryophytes, distribution, ecology, endemic, liverworts, mosses, reproduction, North America

Introduction

Endemism in bryophyte genera of North America (north of Mexico) appears not to have been discussed in detail previously. Only the mention of genera is included in Schofield (1980) with no detail presented. Distribution maps of several genera have appeared in scattered publications. The present paper provides distribution maps of all endemic bryophyte genera for the region and considers the biology and taxonomy of each.

When compared to vascular plants, endemism in bryophyte genera in the region is low. There are 20 genera of mosses and three of liverworts. The moss families *Andreaeobryaceae*, *Pseudoditrichaceae* and *Theliaceae* and the liverwort family *Gyrothyraceae* are endemics; all are monotypic. A total of 16 families of mosses and three of liverworts that possess endemic genera are represented. Only the moss families *Brachytheciaceae*, *Hypnaceae* and *Leucodontaceae* have more than one endemic genus.

Although previously considered a North American endemic, *Donrichardsia* H. A. Crum et L. E. Anderson, has a second species in China, *D. patulifolia* (Cardot et Thér.) Ignatov et Huttunen as reported by Ignatov & Huttunen (2002).

The endemic genera of mosses are: *Alsia* Sull., *Andreaeobryum* Steere et B. M. Murray, *Aphanorrhegma* Sull., *Bestia* Broth., *Brachelyma* Schimp. ex Cardot, *Bryoandersonia* H. Rob., *Bryocrumia* L. E. Anderson, *Bryolawtonia* Norris et Enroth, *Dendroalsia* E. Britton, *Leucolepis* Lindb., *Meiotrichum* (G. L. Sm.) Merrill, *Neomacounia* Ireland, *Platylomella* A. L. Andrews, *Pseudobraunia* (Lesq. et James) Broth., *Pseudoditrichum* Steere et Z. Iwats., *Rhytidiopsis* Broth., *Roellia* Kindb., *Thelia* Sull., *Trachybryum* (Broth.) W. B. Schofield, *Tripterocladium* (A. Jaeger) A. Jaeger. The endemic genera of liverworts include: *Geothallus* Campb., *Gyrothyra* M. Howe, *Schofieldia* J. D. Godfrey. All genera except *Thelia* are monotypic.

The majority of the genera, 15 of the 23, are essentially woodland or forest-dwelling, either as epiphytes, on the forest floor or on shaded rock surfaces. Of these, in western North America, the moss genera *Meiotrichum, Rhytidiopsis* and *Roellia* are predominantly in higher elevation forest. *Andreaeobryum* is mainly on damp calcareous rock in tundra habitats, but occasionally is in open coniferous forest. *Pseudoditrichum* is also a calcicole, on soil in open *Populus* thickets (Steere & Iwatsuki 1974). Genera confined mainly to summer-dry, winter-wet climates, usually near the coast, are the moss genera *Alsia*, *Bestia, Bryolawtonia*, *Dendroalsia*, *Pseudobraunia* and, to a degree, *Trachybryum* (also in subalpine forest). The liverwort *Geothallus* is also in this climatic region. In the western coniferous rainforest the moss genus *Leucolepis* and liverwort genus *Gyrothyra* are mainly confined. The liverwort genus *Schofieldia* is subalpine to alpine. The moss genus *Tripterocladium* is most frequent on outcrops, often near water courses within forest away from the coast.

In the eastern North American deciduous forest region the moss genera *Bryoandersonia* and *Thelia* are widespread, as is the genus *Aphanorregma,* the latter on fine-textured damp soils. *Brachelyma* is a strict aquatic in this region, while *Platylomella* and *Bryocrumia* are found on wet rock surfaces. Of the moss genera, epiphytic mosses include *Alsia* (occasionally), *Bryolawtonia* (occasionally), *Denroalsia, Leucolepis* (occasionally), *Neomacounia*, *Thelia* and *Tripterocladium* (occasionally). Epilithic mosses include *Alsia*, *Andreaeobryum*, *Bestia*, *Bryocrumia*, *Bryolawtonia*, *Dendroalsia* (occasionally), *Pseudobraunia*, *Thelia* (occasionally) and *Tripterocladium.* Mainly soil dwellers are the mosses *Aphanorrhegma*, *Bryoandersonia*, *Leucolepis*, *Meiotrichum*, *Pseudoditrichum, Rhytidiopsis, Roellia*, T*rachybryum* and the liverworts *Geothallus*, *Gyrothyra* and *Schofieldia*. As can be noted in the listing above, a number of genera are found as both epiphytes and epiliths.

Sexuality is predominantly dioicous, including all of the liverworts and 16 genera of mosses. In spite of this, sporophytes are occasional to frequent in most genera: 17 of the 20 mosses and 2 of the 3 liverworts.

As shown by the maps (Figs 1–22), most of the genera are widely distributed. The frequency of sporophytes probably accounts for this to a large extent. The moss genera in eastern North America are often restricted to southeastern United States, extending sometimes into southeastern Canada. *Thelia*, the most widespread of the genera, is found rarely in Mexico and Hispaniola, thus, strictly speaking, is not a North American endemic, but the southernmost populations are clearly outliers where *Thelia hirtella* is rare.

The majority of the endemic genera of mosses and all of the endemic liverwort genera are western North American, occurring mainly west of the Rocky Mountains. The moss genera include *Alsia*, *Andreaeobryum*, *Bestia*, *Bryolawtonia*, *Dendroalsia*, *Leucolepis*, *Meiotrichum*, *Pseudobraunia, Pseudoditrichum*, *Rhytidiopsis*, *Roellia*, *Trachybryum* and *Tripterocladium.* Of these, *Pseudoditrichum* is known only from the type collection and the liverwort *Geothallus* very local in southern California. *Bestia* is confined to California, and *Andreaeobryum* is restricted to calcareous rock from Alaska to northern British Columbia. The remainder of the western North American genera are widely distributed. The endemic genera of eastern North America include *Aphanorrhegma*, *Brachelyma*, *Bryoandersonia*, *Bryocrumia*, *Neomacounia*, *Platylomella* and *Thelia.* Of these, *Neomacounia* is known only from the type locality, and the trees on which it was epiphytic were destroyed soon after it was collected. *Bryocrumia* is confined to a relatively limited area in the southern Appalachians and is never common; the type locality was destroyed. The remainder of the genera are widespread.

The higher number of endemic genera in western North America is possibly attributable to the isolation of that area from eastern North America for millions of years before the prairie climates of the present isolated it. Southward the semi-arid climates as well as physical separation, have excluded a corridor for exchange of Neotropical genera that were able to enter eastern North America via a relatively continuous climatic and vegetational corridor.

Extracted from information in "The moss flora of Mexico" (Sharp et al. 1994), the following genera are endemic to Mexico: *Acritodon* Robinson (*Sematophyllaceae*), *Anomobryopsis* Cardot (Bryaceae), *Breedlovea* H. A. Crum (*Dicranaceae*), *Curviramea* H. A. Crum (*Hookeriaceae*), *Cygniella* H. A. Crum (*Ditrichaceae*), *Elharveya* (H. A. Crum) H. A. Crum (*Hookeriaceae*), *Hymenolomopsis* Thér. (*Seligeriaceae*), *Nematocladia* W. R. Buck (*Myriniaceae*).

These genera show, in most cases, a very restricted range – in many instances known only from the type collection. Ecologically the genera exhibit a wide range of habitats. All genera are monotypic and most have been described recently. Several genera, not restricted to Mexico, are confined to the Neotropics, but extend to South America and/or the Caribbean islands. Many others are widespread in the Neotropics, sometimes extending northward to southeastern United States, e.g. *Donnellia* Austin, *Homalotheciella* (Cardot) Broth., *Pireella* Cardot, *Pseudocryphaea* E. Britton and *Zelometeorium* Manuel. No endemic liverwort genera are in Mexico (Gradstein et al. 2001).

It is of interest to compare the bryofloras of temperate North America and tropical South America (including Mexico and the West Indies). This is made possible with the recent publication of "Guide to the bryophytes of tropical America" (Gradstein et al. 2001).

In the Neotropics the moss flora contains 99 endemic genera, of which 70 are monotypic. Greatest generic endemism is in the *Pilotrichaceae*, with 14 endemic genera (4 monotypic), *Pottiaceae* with 16 endemic genera (13 monotypic) and *Sematophyllaceae* with 11 endemic genera (9 monotypic). The total Neotropic moss flora is approximately 76 families, 400 genera and 3,000 species.

For North America (exclusive of Mexico) there are 74 families, 317 genera and approximately 1320 species. It is of particular interest that the family diversity is extremely similar between this area and the Neotropics, with generic endemism differing more and species endemism more than doubled in the tropics compared to North America. With further careful exploration and documentation in the Neotropics, the numbers are likely to increase, while those in North America likely to change only modestly.

For the liverworts the Neotropics has 57 endemic genera, of which 33 are monotypic. The largest number of endemic genera (30) is in the *Lejeuneaceae*, of which 13 are monotypic. In the hornworts only the monotypic *Leiosporoceros* Hässel is endemic to the Neotropics.

A further observation is that 95% of the endemic bryophyte genera in North America are monotoypic, while in the Neotropics the proportion is closer to 58%.

Before discussing each of the genera in detail, it should be noted that acceptance or rejection of the distinctiveness of a genus is often based on personal bias. My own acceptance demands morphological distinctiveness as well as a well-defined geographic range. I have endeavoured to reflect this diversity of opinion in the following discussions. The definitive answer to the controversy will rest on an extensive field-experience with the species, with molecular data of secondary importance.

Overview of endemic genera

M o s s e s

Alsia Sull. (*Leucodontaceae*) Fig. 1

This genus is mainly an epiphyte on broad-leafed trees, but found occasionally on cliffs. On trees, especially in near-coastal California, it can form extensive colonies, richly sporophytic, while northward, especially in its extreme northern range in southernmost British Columbia, where epilithic populations are mainly sterile and epiphytic populations infrequent.

Manuel (1974) has illustrated and discussed this genus in detail, including the problems in typification. He notes an Alaskan specimen, but lacking a locality. It seems probable that this specimen did not originate in Alaska. The distribution of the genus shows it to extend barely into British Columbia. Sporophytes are frequent through most of its range. Lawton (1971) provides an illustration of details, but no habit sketch, but Brotherus (1925) provides one.

Andreaeobryum Steere et B. M. Murray (*Andreaeobryaceae*) Fig. 2

Murray (1988) presents a very thorough study of this genus based on her wide field experience as well as her careful microscopic analysis of material. She places it in the class *Andreaeopsida* and builds a case for considering it to belong to its own order, *Andreaobryales* B. M. Murray. She considered the genus to share ancestry with *Takakia* Hatt. et Inoue, but this was based entirely on gametophytic features. The antheridial and sporophytic features now noted (Smith & Davison 1993, Schuster 1997, Renzaglia et al. 1997) could be used to support this suggestion, rather than any relationship with the hepatic genus *Haplomitrium* Nees as has been followed in the past (Schuster 1966, Schofield 1985). Details of both sporophyte and gametophyte, however, argue against a close relationship with the Takakiopsida. This includes, in *Andreaeobryum*, detailed structure of the sex organs, nature of leaves, detailed structure of presumptive mucilage cells and absence of rhizomatous systems, as well as presence of rhizoids. A single species, *A. macrosporum* Steere et B. M. Murray is represented. Although dioicous, sporophytes are relatively frequent (Murray 1988). The genus is restricted to calcareous rock subject to irrigation. Murray (1988) provides exceptional illustrations.

Aphanorrhegma Sull. (*Funariaceae*) Fig. 3

The genus contains a single species, *A. serratum* (Hook. et Wilson ex Drumm.) Sull. The plants are very small, are ephemeral and confined to mineral soil that is moist, "especially in places subject to flooding" (Crum & Anderson 1981). It produces sporophytes late in the year, a feature that has probably led to its under-collection. Sporophytes are common; the species is unlikely to be collected without them. *Physcomitrella patens* (Hedw.) Bruch et Schimp. was treated within *Aphanorrhegma* by Lindberg in 1865, a decision not generally accepted since then. A beautiful illustration and description are provided by Sullivant (1864).

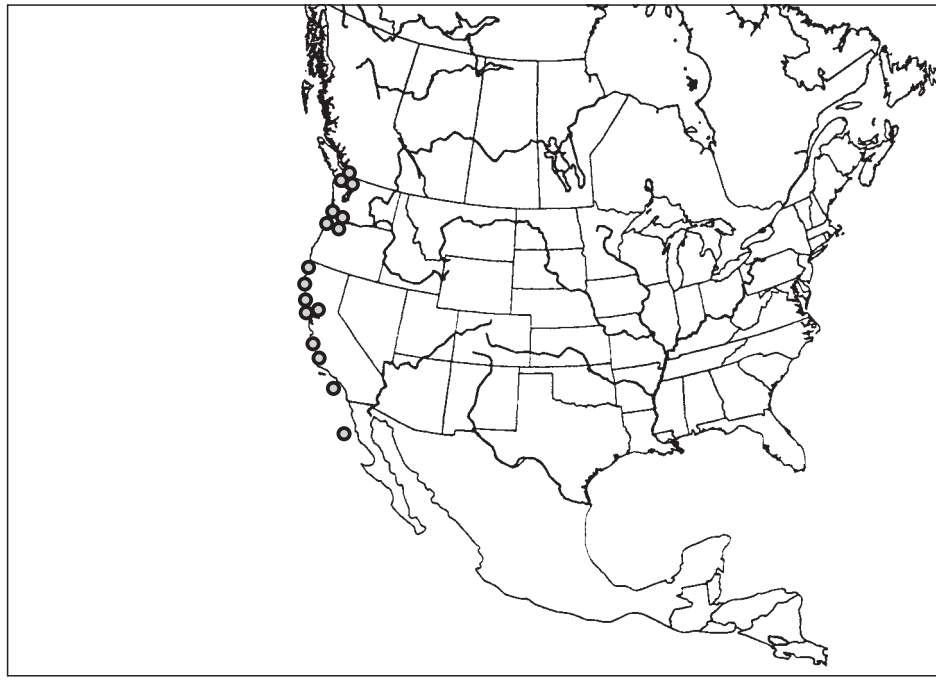

Fig. 1. – Distribution of the moss genus *Alsia* Sull. (*Leucodontaceae*).

Fig. 2. – Distribution of the moss genus *Andreaeobryum* Steere et B. M. Murray (*Andreaeobryaceae*).

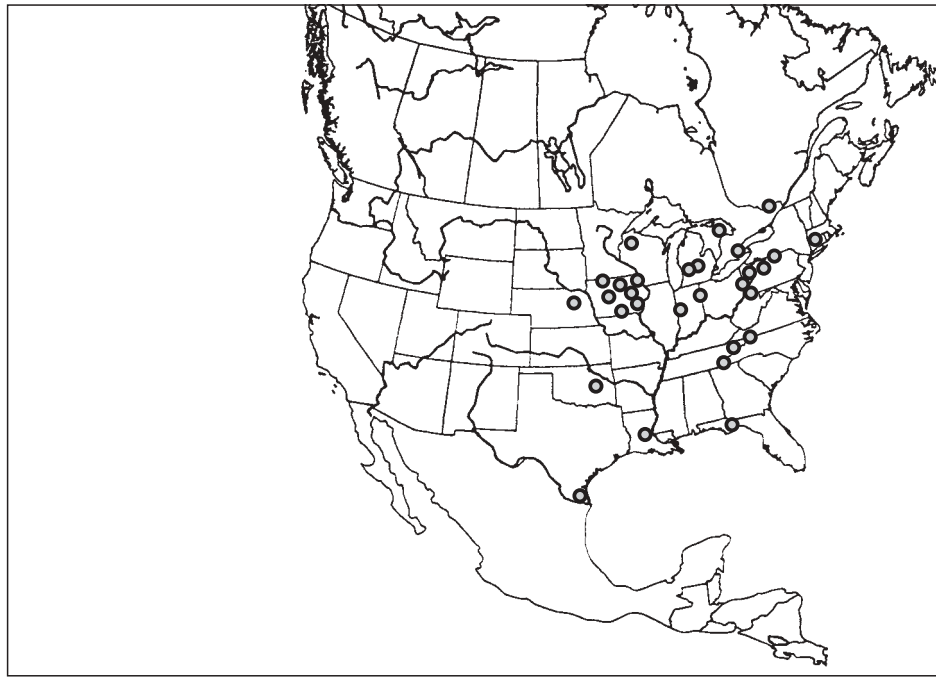

Fig. 3. – Distribution of the moss genus *Aphanorrhegma* Sull. (*Funariaceae*).

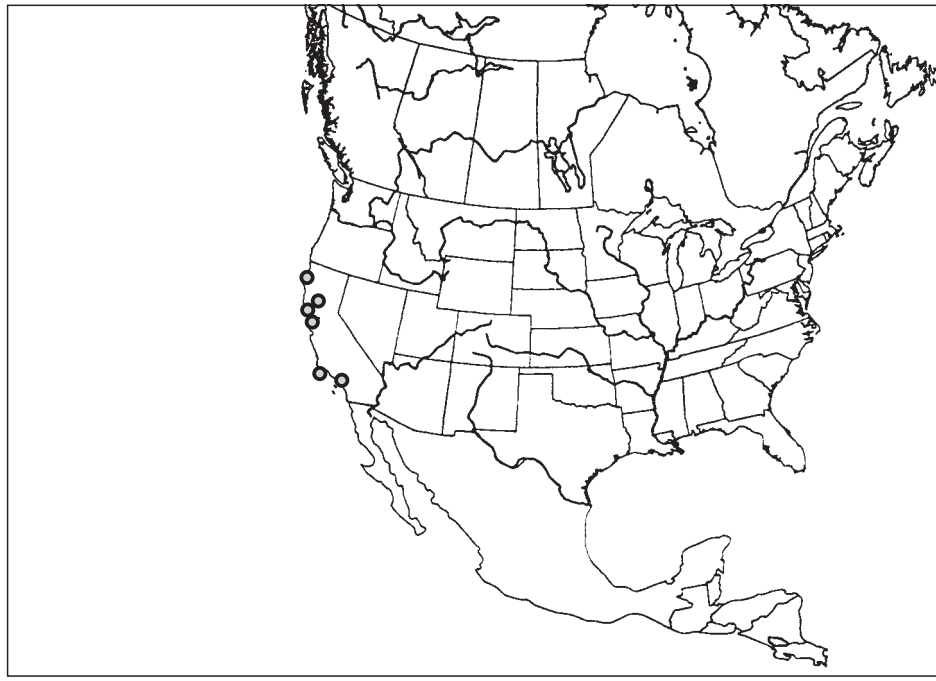

Fig. 4. – Distribution of the moss genus *Bestia* Broth. (*Leucodontaceae*).

Bestia Broth. (*Leucodontaceae*) Fig. 4

Bestia is confined to California, but should be expected in Baja California, based on its distribution and habitat. It can be expected to occur on Guadeloupe Island, where the genera *Dendroalsia* and *Alsia* have their only Mexican localities. *Bestia* is predominantly on cliffs, usually in areas that retain humidity longer than the general terrain. Occasionally it is found on the bases of trees, especially *Umbellularia*. It is dioicous, and sporophytes are rare.

Crum (1991) asserted that *Bestia longipes* (Sull. et Lesq.) Broth. is a mere form of *Isothecium myosuroides* Brid. a decision that is rapidly refuted by the sporophytes as well as details of the gametophyte. On his assumption, he reduced the genus *Bestia* out of existence. Although Buck & Goffinet (2000) recognized the genus and, presumably influenced by the reference of *Isothecium* to the *Brachytheciaceae* [again an error in attribution: it belongs to the *Neckeraceae* (*Porotricheae*)], placed it in the *Brachytheciaceae*. Grout (1928) possibly contributed to the problem by expanding the concept of *Bestia* beyond its original bounds, adding to it what is now considered *Bryolawtonia* as well as what is now treated as *Isothecium cristatum* (Hampe) H. Rob. In consequence, he had placed in a single genus taxa that belong to two families (*Neckeraceae* and *Leucodontaceae*). The family placement of *Bestia* remains unresolved. Its relationship with *Alsia* and *Dendroalsia* strongly supports its placement in the *Leucodontaceae*, rather than the *Cryphaeaceae*, where Brotherus (1925) placed all three genera. A beautiful illustration is provided, under the name *Alsia longipes* Sull. et Lesq., by Sullivant (1874).

Brachelyma Schimp. ex Cardot (*Fontinalaceae*) Fig. 5

This genus was treated by Welch (1960, 1963) as possessing two species: *B. robustum* (Card.) E. Britton and *B. subulatum* (P. Beauv.) Schimp. ex Cardot, but Crum & Anderson (1981) consider *B. robustum* to fit within the concept of *B. subulatum*. The genus is, therefore, monotypic. As is common for aquatic and dioicous species, sporophytes are produced erratically. Crum & Anderson (1981) note a Brazilian specimen, but doubt its provenance. It is predominantly a Coastal Plain species and is confined to eastern United States. A detailed description and illustration are provided by Crum & Anderson (1981), and an attractive plate is provided by Bruch et al. (1842) under the name *Dichelyma subulatum* Myrin.

Bryoandersonia H. Rob. (*Brachytheciaceae*) Fig. 6

The widespread genus *Bryoandersonia* was described by Robinson (1962) to include a single species, *B. illecebra* (Hedw.) H. Rob. The genus is readily recognized and of considerable attractiveness, as noted in the species name. The species is dioicous, and sporophytes are of erratic presence. The species is predominantly terrestrial in broadleafed forest. It is beautifully figured and described in Crum & Anderson (1981).

Bryocrumia L. E. Anderson (*Hypnaceae*) Fig. 7

The genus *Bryocrumia* was proposed for a single species, *B. andersonii* (E. C. Bartram) L. E. Anderson. The species was originally placed in *Glossadelphus* Fleisch., but Crum (1965) transferred it to *Taxiphyllum* M. Fleisch. Since neither genus was satisfactory, An-

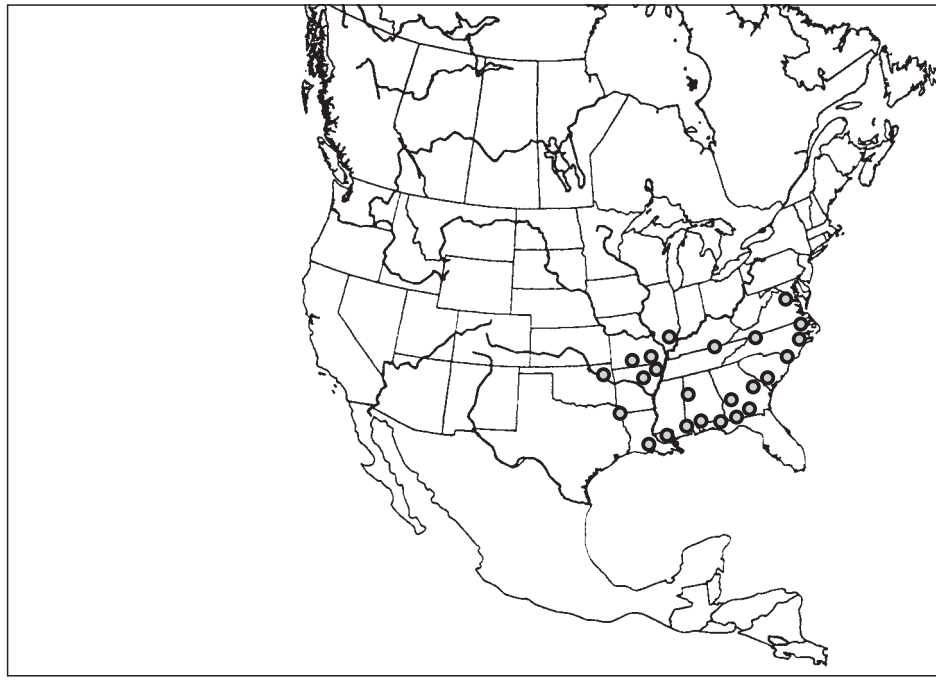

Fig. 5. – Distribution of the moss genus *Brachelyma* Schimp. ex Card. (*Fontinalaceae*).

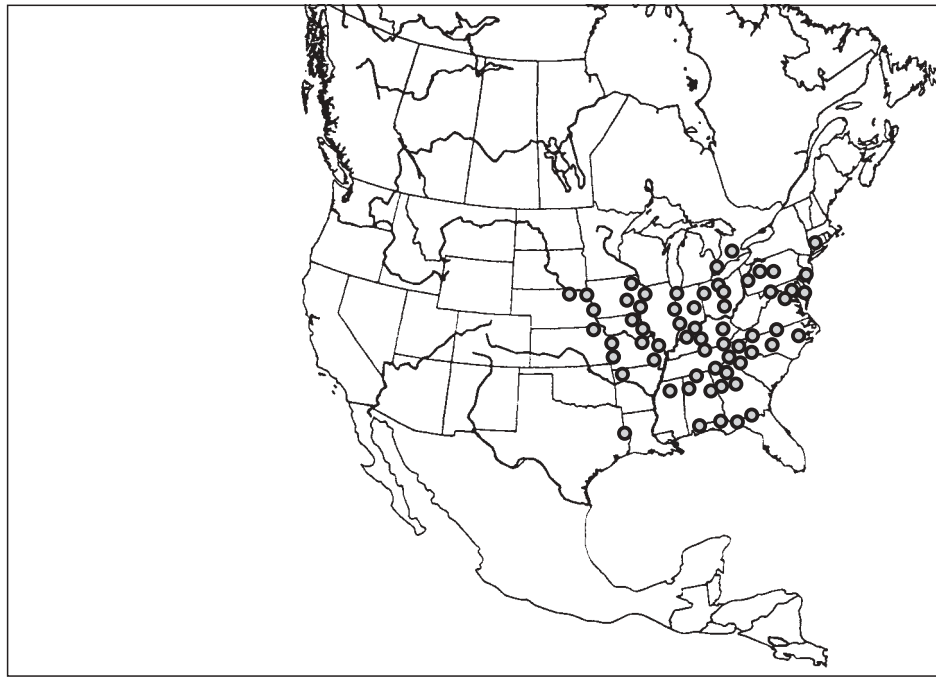

Fig. 6. – Distribution of the moss genus *Bryoandersonia* H. Rob. (*Brachytheciaceae*).

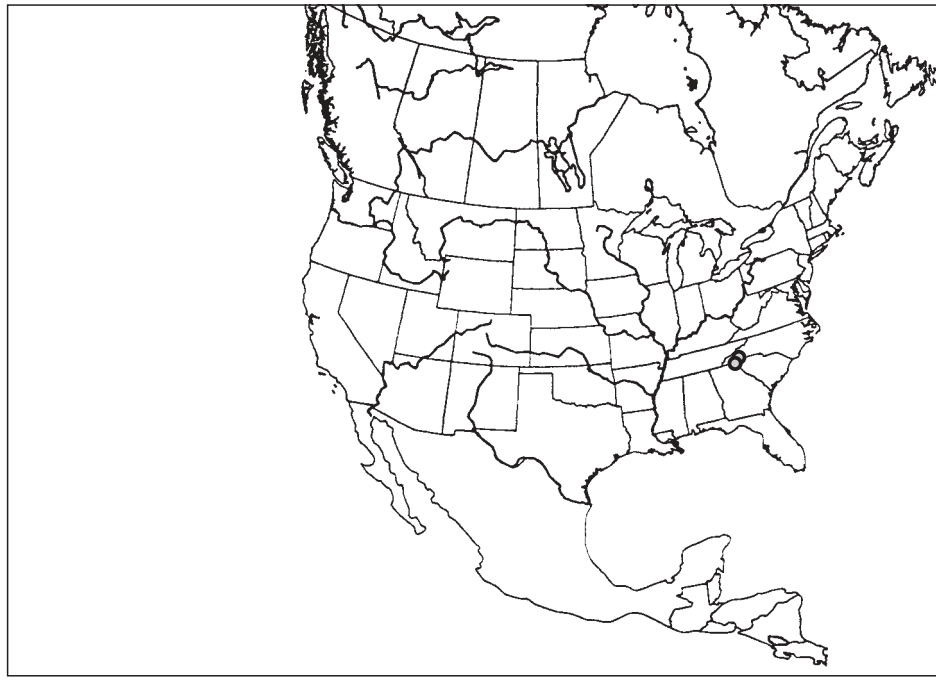

Fig. 7. – Distribution of the moss genus *Bryocrumia* L. E. Anderson (*Hypnaceae*).

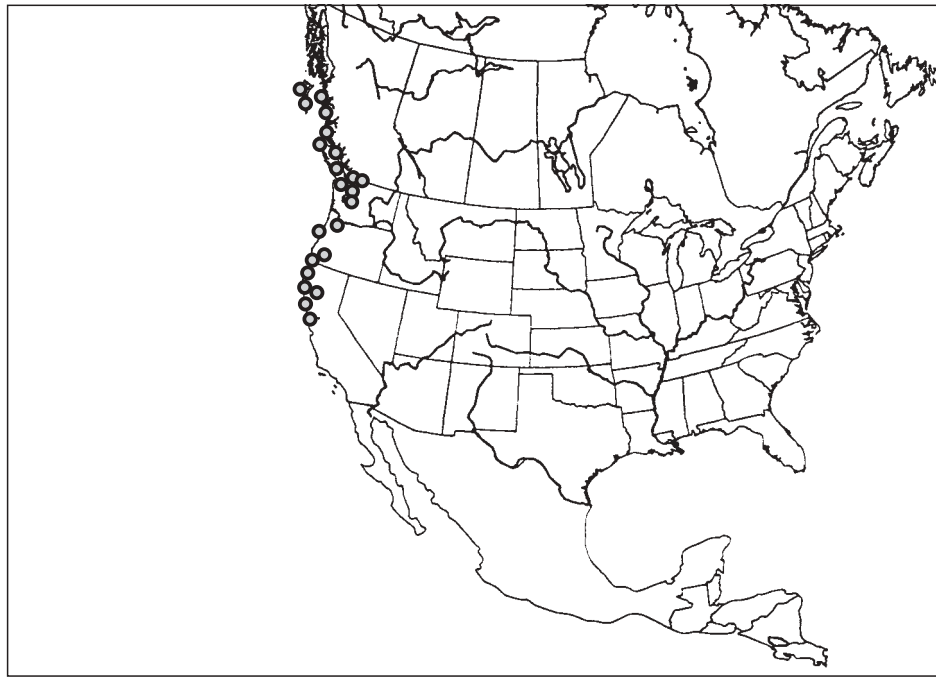

Fig. 8. – Distribution of the moss genus *Bryolawtonia* Norris et Enroth (*Neckeraceae*).

derson (1980) proposed *Bryocrumia*. It is always found as shoots among other mosses on perpendicular, wet surfaces. Its range is restricted to a few gorges in the southern Appalachian mountains (Anderson 1980). Unfortunately the type locality has been destroyed by flooding. An illustration is also provided by Crum & Anderson (1981). A valuable discussion is that of Anderson (1980).

Bryolawtonia Norris et Enroth (*Neckeraceae*) Fig. 8

The genus *Bryolawtonia* was proposed by Norris & Enroth (1990) to include a single species, *B. vancouveriensis* (Kindb.) Norris et Enroth. This taxon had been placed in six different genera, indeed in several families, preceding that time. Several specific epithets further confounded the problems. It is clearly neckeraceous, where Lawton (1971) placed it. Crum (1987) considered it to belong to the genus *Porotrichum* (Brid.) Hampe. It is an epilithic species, for the most part, but can stray to tree trunks and persist on logs. Sporophytes are occasional. Sullivant (1874) provides a fine illustration and description under the name *Hypnum occidentale* Sull. et Lesq.

Dendroalsia E. Britton (*Leucodontaceae*) Fig. 9

Manuel (1974) described and mapped the distribution of this genus and provided illustrations of sporophytic features. The single species, *Dendroalsia abietina* (Hook.) E. Britton, is most frequently an epiphyte of broad-leafed trees, but occurs occasionally on cliffs. It is dioicous, but sporophytes are relatively frequent, except in epilithic populations. There is considerable variability in stature, seemingly influenced mainly by the duration of the dry season and exposure of the population. The "Alaskan" specimen is unlikely to have been collected from Alaska, and as with *Alsia*, probably is based on a mix-up in locality data. The distribution map here, differing little from that of Manuel (1974) shows its predominantly near-coastal range in summer-dry climates. The specimen from Colorado is also unlikely to have originated from that state. An attractive illustration is provided by Schofield (1992).

Leucolepis Lindb. (*Mniaceae*) Fig. 10

This genus is so distinctive that it seems extraordinary that its single species was treated as belonging to *Mnium* Hedw., long after Lindberg (1868) proposed *Leucolepis*. Steere et al. (1954) noted the cytological distinctiveness, already remarked by Lowry (1948), who also considered *L. acanthoneuron* (Schwaegr.) Lindb. to be the correct name, not *L. menziesii* (Hook.) Steere. It is dioicous, but sporophytes are frequent in spring. The plant is generally terrestrial but can stray to trunks, especially of maples (*Acer*) and alders (*Alnus*). It occurs mainly at lower elevations in coniferous or mixed forest. An attractive illustration is in Schofield (1992).

Meiotrichum (G. L. Sm.) Merrill (*Polytrichaceae*) Fig. 11

This name was originally proposed by Smith (1971) to indicate clearly that the species *M. lyallii* (Mitt.) Merrill was isolated from the Southern Hemisphere genus *Polytrichadelphus* (C. Müll.) Mitt., where it had been placed. It was raised to generic level by Merrill (1992). Without sporophytes, the species strongly resembles *Polytrichastrum alpinum* (Hedw.) G. L.

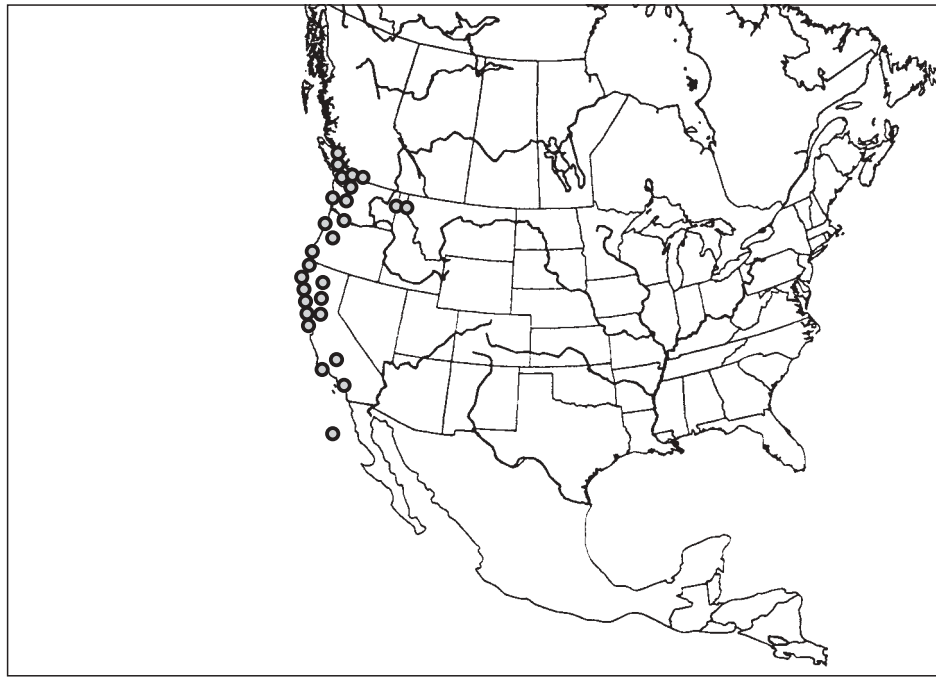

Fig. 9. – Distribution of the moss genus *Dendroalsia* E. Britton (*Leucodontaceae*).

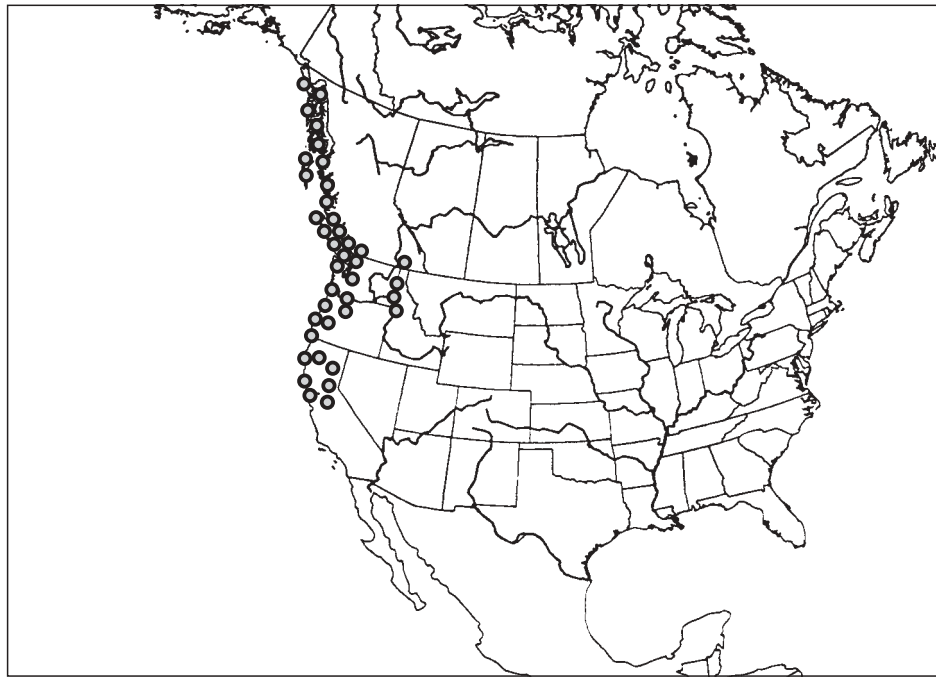

Fig. 10. – Distribution of the moss genus *Leucolepis* Lindb. (*Mniaceae*).

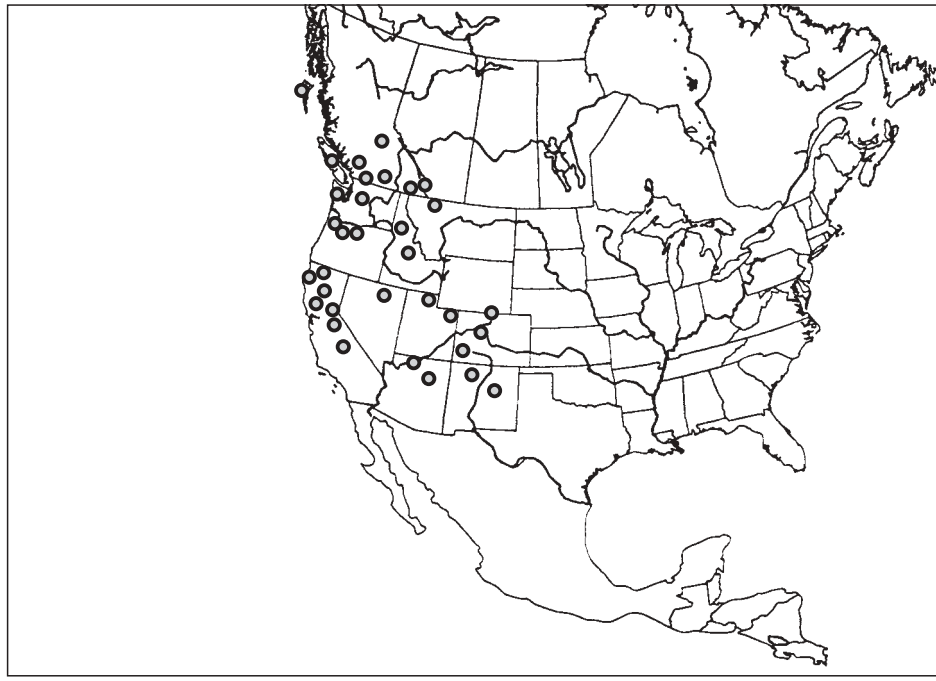

Fig. 11. – Distribution of the moss genus *Meiotrichum* (G. L. Sm.) Merrill. (*Polytrichaceae*).

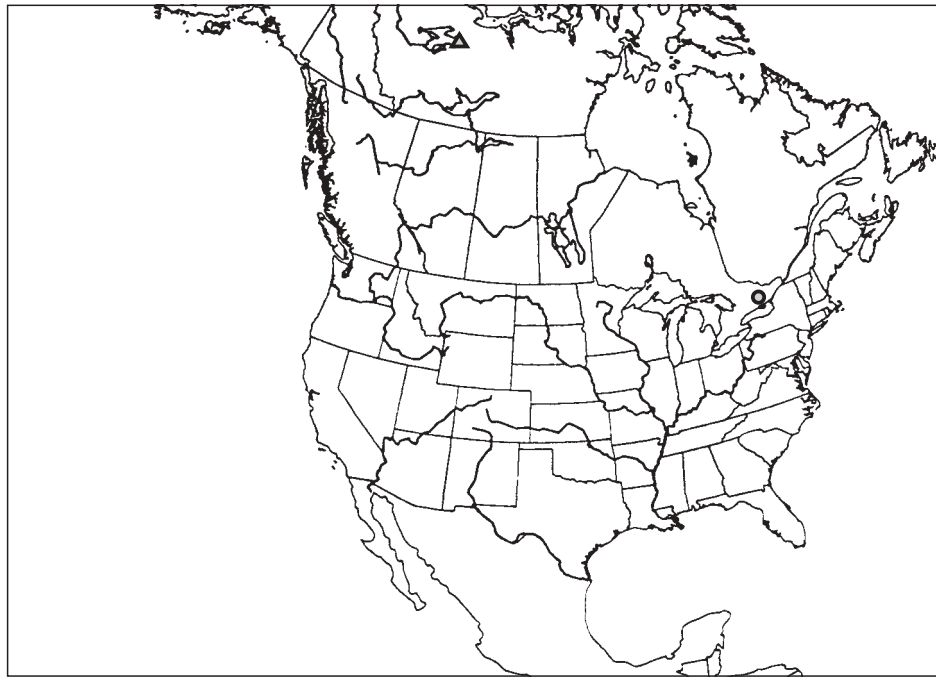

Fig. 12. – Distribution of the moss genera *Neomacounia* Ireland (circle), and *Pseudoditrichum* Steere et Z. Iwats. (*Pseudoditrichaceae*) (triangle).

Sm., a widerspread and variable species in western North America, where *Meiotrichum* is endemic. *M. lyallii* is a terrestrial species in subalpine forest. The four-angled and bilaterally compressed sporangium, broad at the base and tapering to its apex, is unlike any other Polytrichaceous genus in North America, but was probably significant in its placement in *Polytrichadelphus*. It is dioicous, but sporophytes are relatively common. An illustration of critical details is provided by Lawton (1971) under the name *Polytrichadelphus lyallii* Mitt.

Neomacounia Ireland (*Cryphaeaceae*) Fig. 12

The genus *Neomacounia* was proposed by Ireland (1974) to include the single species *N. nitida* (Lindb.) Ireland. Crum & Anderson (1981) do not accept the genus, but retain the species in *Forsstroemia* Lindb., in which it was originally placed. It is known only from the type locality east of Belleville, Ontario. Sporophytes were present. It was an epiphyte on *Ulmus*. In spite of considerable exploration, it has not been collected since the two original collections of 1864 and 1866. As Crum & Anderson (1981) remarked, "That area is so unexceptional phytogeographically that one wonders if the specimen actually came from some other place." The fact that it was collected in two different years from the same habitat and the same geographic locality, however, is strong evidence that the provenance is accurate. According to Ireland (1974) the elm trees from which it was collected had been destroyed soon after Macoun had collected the material, and had returned to the site to enrich its documentation. The plant is remarkably distinctive and relatively large (to 6 cm long). Ireland (1974) provides excellent illustrations and a fine description and discussion of the species. It is presumed to be extinct.

Platylomella A. L. Andrews (*Amblystegiaceae*) Fig. 13

The genus was proposed by Andrews (1950) to include the single eastern North American species *P. lescurii* (Sull.) Andrews. The species is discussed in detail by Andrews (1945). It is a species of wet rocks, but not a submerged aquatic. In spite of its autoicous condition, sporophytes are absent in most populations. Crum & Anderson (1981) argue that the genus is unnecessary and that the species should be treated as *Sciaromium lescurii* (Sull.) Broth., but Buck (1998) has shown that the generic name *Sciaromium* (Mitt.) Mitt. cannot be applied; thus the genus *Limbella* (Broth.) E. B. Bartram would be correct if *Platylomella* is rejected. A fine illustration and description are provided by Sullivant (1864) under the name *Hypnum lescurii* Sull.

Pseudobraunia (Lesq. et James) Broth. (*Hedwigiaceae*) Fig. 14

The genus *Pseudobraunia* was proposed by Brotherus (1905) to include a single species *P. californica* (Lesq.) Broth. Originally placed in the genus *Braunia* Schimp., *Pseudobraunia* is readily recognized in the field, even when without sporophytes. Its colour is normally reddish brown; the plant grows on exposed rock surfaces, and the leaves are ecostate. It is autoicous, thus sporophytes are frequent with eperistomate subspherical sporangia on a long seta. Its distribution is confined mainly to summer-dry climates. It is elegantly figured and described (under the name *Braunia californica*) in Sullivant (1874).

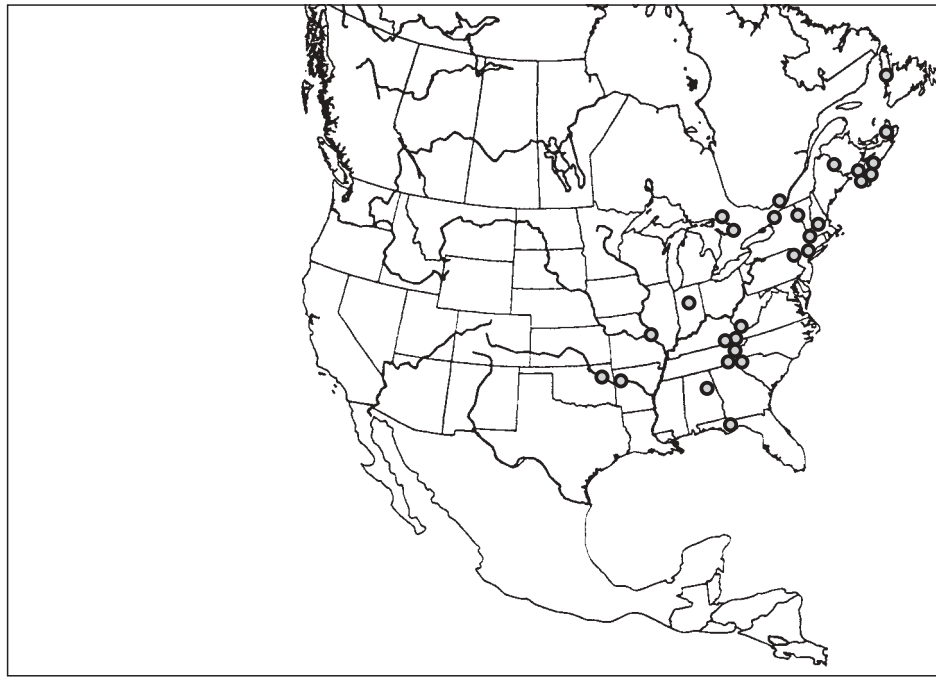

Fig. 13. – Distribution of the moss genus *Platylomella* A. L. Andrews (*Amblystegiaceae*).

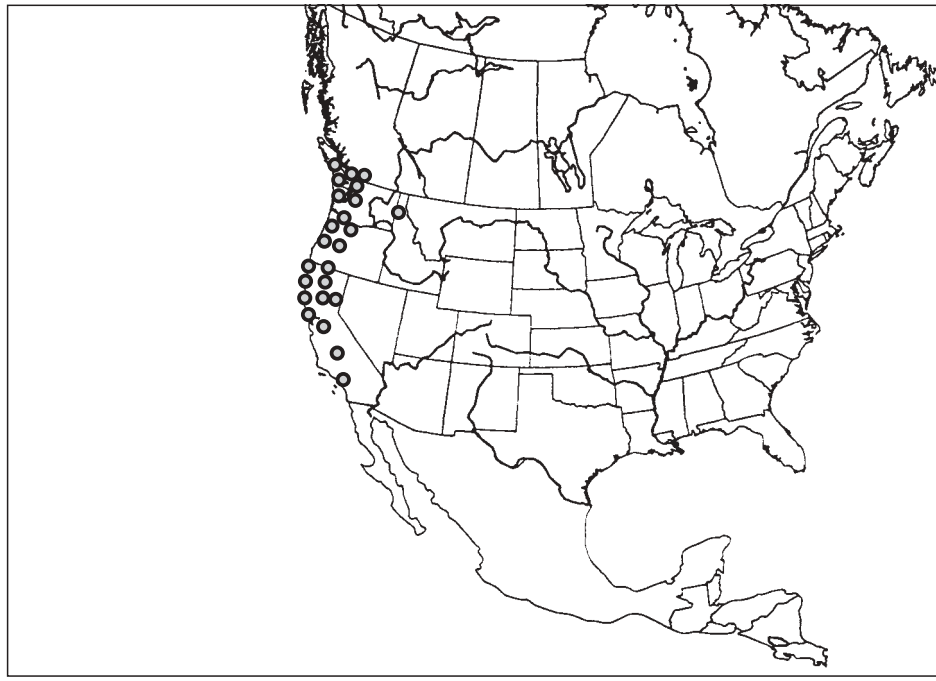

Fig. 14. – Distribution of the moss genus *Pseudobraunia* (Lesq. et James) Broth. (*Hedwigiaceae*).

Pseudoditrichum Steere et Z. Iwats. (*Pseudoditrichaceae*) Fig. 12

The unusual, and extremely rare, genus *Pseudoditrichum* was described and figured by Steere & Iwatsuki (1974) to accommodate a single species, *P. mirabile* Steere et Z. Iwats. from a single collection made by Steere from Great Bear Lake area. As the name indicates, it strongly resembles *Ditrichum* in gross appearance, but the double peristome immediately dispels that relationship. Since it could not be placed satisfactorily in any known family, the authors described the monotypic family *Pseudoditrichaceae* for it.

Buck & Goffinet (2000) place the family in the order *Bryales*. A thoroughly glaciated area is an unlikely source for a monotypic family that remains as mystifying as when Steere and Iwatsuki described it. A thorough discussion and fine illustration are given by Steere & Iwatsuki (1974).

Rhytidiopsis Broth. (*Hylocomiaceae*) Fig. 15

This is a striking genus, easily recognized at a glance in the field. Sometimes it can resemble *Rhytidium* (Sull.) Kindb., or *Rhytidiadelphus triquetrus* (Hedw.) Warnst., superficially. It often forms extensive carpets in subalpine coniferous forests, but rarely strays as isolated small populations in near sea-level forest, where it tends to be restricted to rotten logs. A detailed description is found in Rohrer (1985). Noguchi (1972) considered the single species of *Rhytidiopsis, R. robusta* (Hook.) Broth., to belong to *Hylocomium* Schimp., but this transfer has not been generally accepted. The species is dioicous and sporophytes are infrequently produced in abundance. Lawton (1971) provides a fine illustration and description.

Roellia Kindb. (*Bryaceae*) Fig. 16

The genus *Roellia* was originally proposed by Kindberg (1897) to include what had been named *Bryum lucidum* E. Britton in 1891. The name *Mnium roellii* Broth. ex Röll applied to the same species and was an earlier acceptable name. These names indicate the ambiguity of the familial placement of the genus. Crum (1967) provides a clear discussion of the nomenclature and morphology of this genus. It is an elegant moss, readily recognized in the field and isolated morphologically from all other genera. It is a moss of subalpine coniferous forest, and, although dioicous, sometimes forms extensive stands of richly sporophyte-bearing plants. An attractive illustration is provided by Schofield (1992).

Thelia Sull. (*Theliaceae*) *Fig. 17*

The genus *Thelia* is widely distributed in eastern North America and is represented by three species: *T. asprella* Sull., *T. hirtella* (Hedw.) Sull., and *T. lescurii* Sull. (Crum 1966) *T. hirtella* is the most widespread of the species, extending rarely into northern Mexico and Hispaniola (Buck 1989, 1998). It is generally an epiphyte, but is occasionally on rock. All species are phyllodioicous (Crum 1966) and except for *T. hirtella* produce sporophytes infrequently. It has been accorded its own family, *Theliaceae* (Broth.) M. Fleisch., accepted as recently as 2000 (Buck & Goffinet 2000), but has been placed in the *Leskeaceae* by Crum & Anderson (1981) and the *Anomodontaceae* by Buck (1998). The family *Theliaceae* is monotypic. Sullivant (1864) provides descriptions and illustrations of all species.

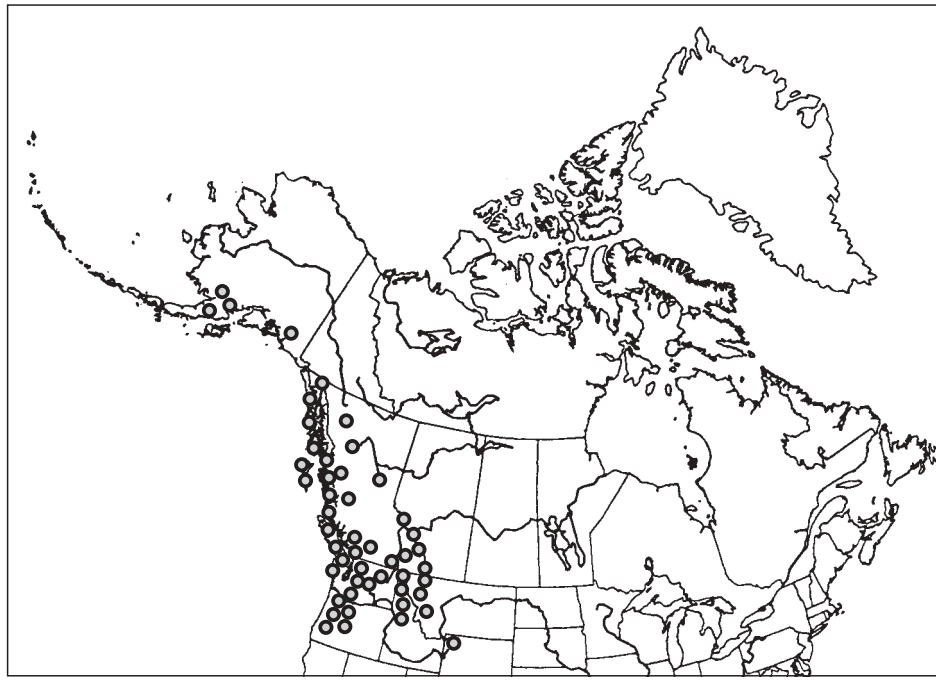

Fig. 15. – Distribution of the moss genus *Rhytidiopsis* Broth. (*Hylocomiaceae*).

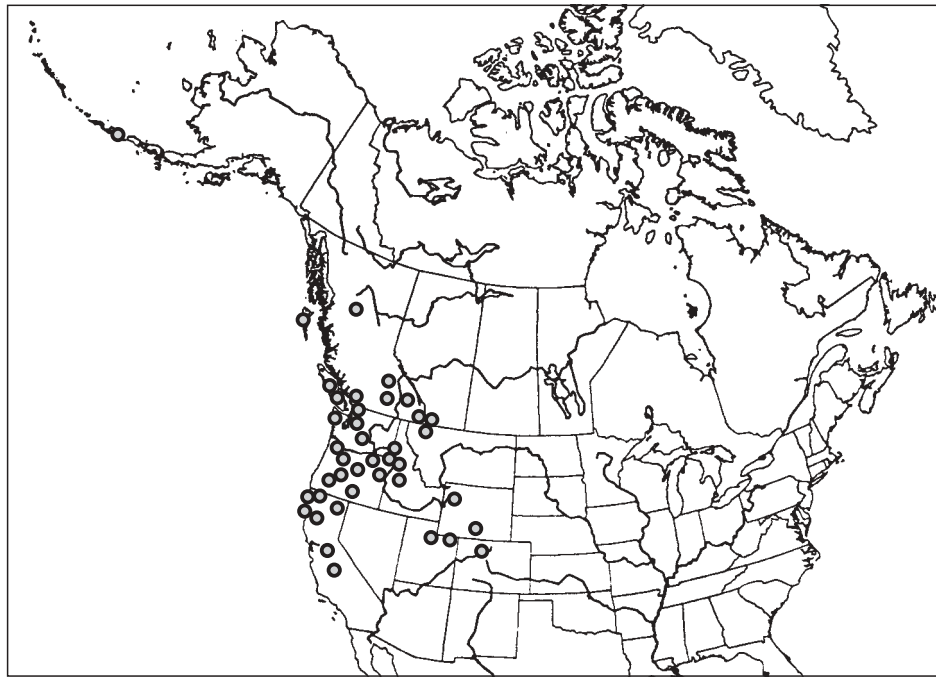

Fig. 16. – Distribution of the moss genus *Roellia* Kindb. (*Bryaceae*).

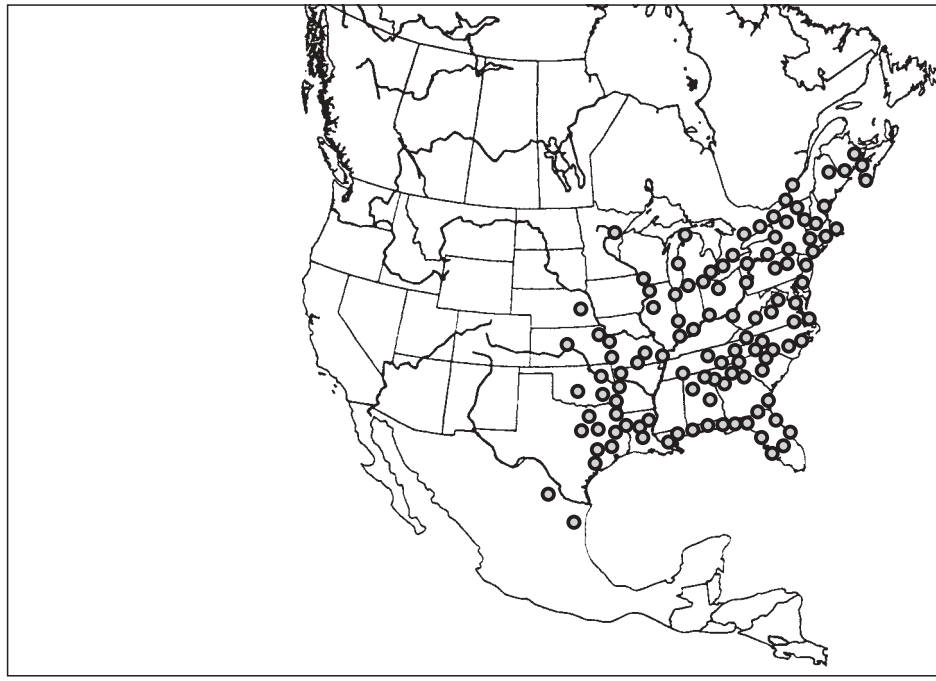

Fig. 17. – Distribution of the moss genus *Thelia* Sull. (*Theliaceae*). All three species are combined.

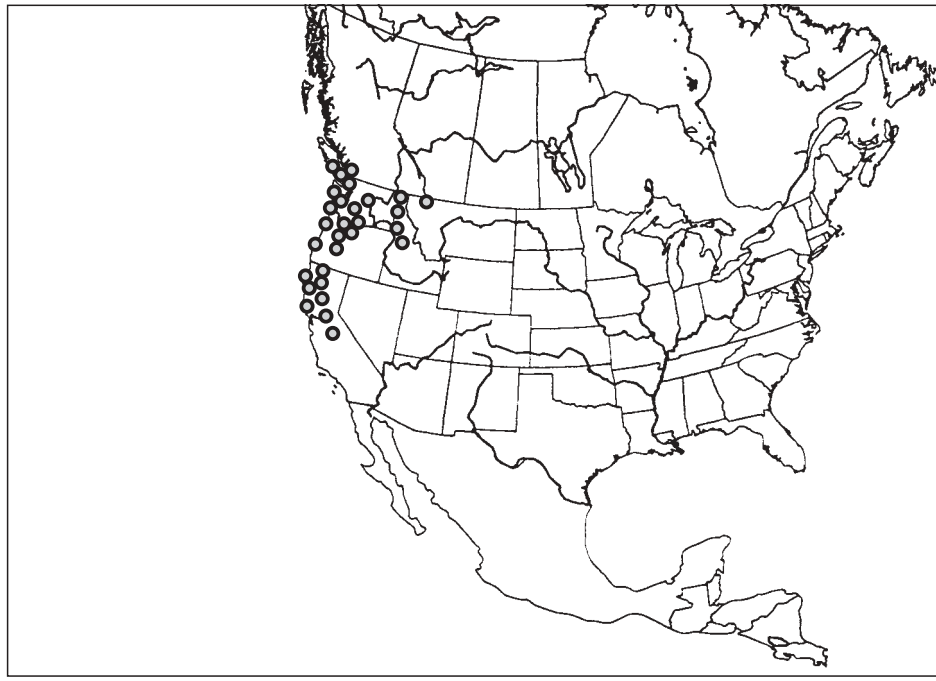

Fig. 18. – Distribution of the moss genus *Trachybryum* (Broth.) W. B. Schofield (*Brachytheciaceae*).

Trachybryum (Broth.) W. B. Schofield (*Brachytheciaceae*) Fig. 18

This genus was treated as a section of the genus *Camptothecium* Schimp. by Brotherus (1925) and then as a subgenus of *Homalothecium* Schimp. by Robinson (1962). It was raised to generic level by Schofield (1968). Its relationship to *Homalothecium* is obvious, but its distinctiveness from all known species is so apparent, that generic placement is reasonable for the single species *H. megaptilum* (Sull.) W. B. Schofield. Ignatov & Huttunen (2002), however, based on their analyses, would treat *Trachybryum* within *Homalothecium*. It is a terrestrial species, found near sea-level and on subalpine forest floor, but generally absent from intermediate elevations. It is dioicous or phyllodioicous and sporophytes are occasional and locally abundant, especially in subalpine forests. Sullivant (1874) provides a fine illustration and description under the name *Camptothecium megaptilium* Sull.

Tripterocladium (A. Jaeger) A. Jaeger (*Hypnaceae*) Fig. 19

This genus has had a chequered history as clearly detailed by Crum (1987). The family placement has also been problematic. *T. leucocladulum* (C. Müll.) A. Jaeger is the only species. There exists no satisfactory habit sketch of the species, although the illustrated details provided by Lawton (1971) are the best available. The species is predominantly epilithic, but does stray to the trunks of trees. Sporophytes are infrequent, reflecting its dioicous condition. The species has a relatively restricted range, but it can be locally abundant. In the field it is most likely to be confused with *Pterigynandrum filiforme*. Even then the sharply acuminate leaves and the usually abundant flagellate branches separate it immediately.

Liverworts

Geothallus Campb. (*Sphaerocarpaceae*) Fig. 20

The type specimen of this genus was collected near San Diego, California, by Katherine Brandegee and described by Campbell (1896a, b). The genus is now known from five localities in San Diego County and Riverside County (A. Whittemore 1999, unpublished). Resembling many hornworts, *Geothallus* has perennating tubers that are not known in the allied genus *Sphaerocarpos* Boehm. The genus is ecologically restricted to soil around vernal pools and other wet depressions (A. Whittemore 1999, unpublished). Although this habitat is widespread in California, *Geothallus* is never abundant. Urbanization has undoubtedly reduced its potential range and the role of perennial grasses in invading sites of known populations further restricts the extent of the population (Doyle 1962).

A concerted exploration of Kearney Mesa, the main range of the genus, was made (Wolery & Doyle 1969) when several new populations were discovered. They note that the genus superficially resembles *Fossombronia* Raddi rather than *Sphaerocarpos*. They present a detailed treatment of its ecology, including its constant liverwort associates. They conclude that the genus *Geothallus* "is uncommon but widespread in the San Diego region of California".

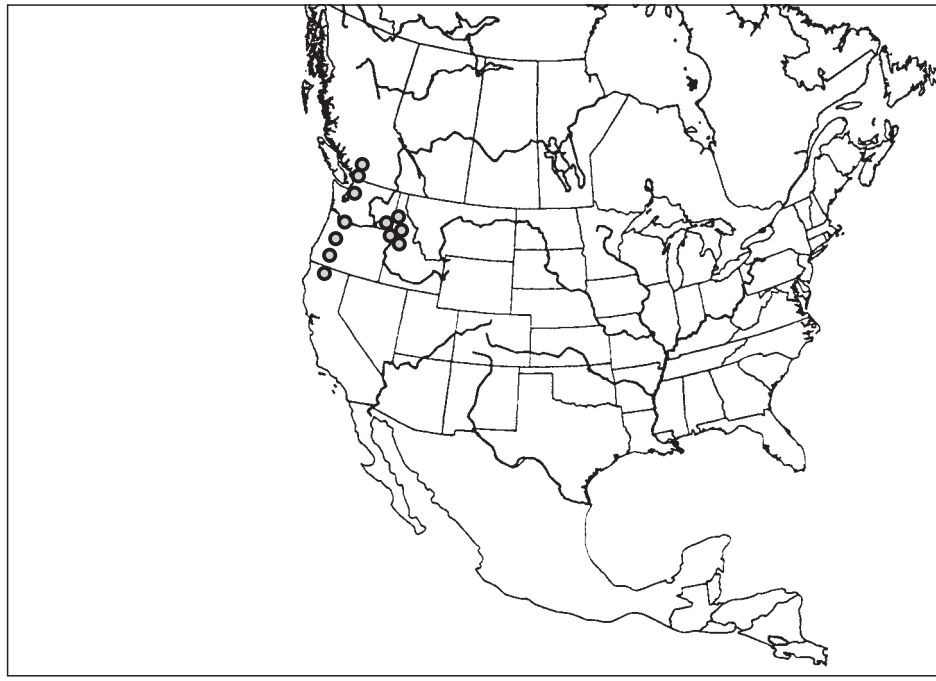

Fig. 19. – Distribution of the moss genus *Tripterocladium* (A. Jaeger) A. Jaeger (*Hypnaceae*).

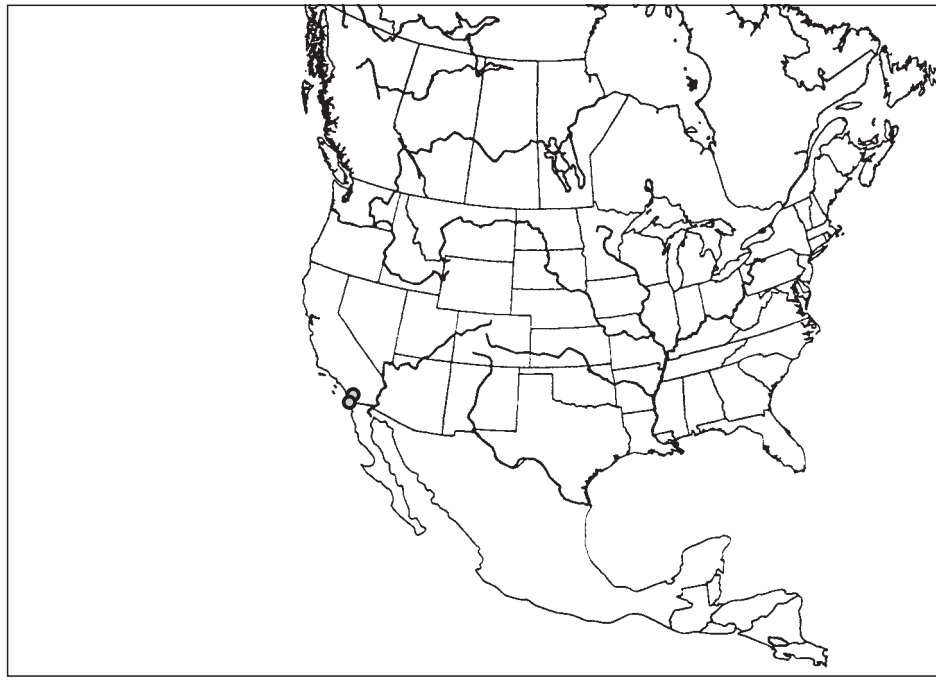

Fig. 20. – Distribution of the liverwort genus *Geothallus* Campbell (*Sphaerocarpaceae*).

The detailed study of Doyle (1962) makes a convincing argument that the genus should be maintained, and should not be included in *Sphaerocarpos* as Schuster (1958) recommended.

Although dioicous, as in *Sphaerocarpos*, sporophytes are frequent in the few populations. Once established, however, persistence is assured as long as the habitat is not invaded by flowering plants. Both "tubers" and spores assure local persistence.

A detailed description and illustrations are also provided by Doyle (1962). The line drawing in Schofield (2002) is also valuable.

Gyrothyra M. Howe (*Gyrothyraceae*) Fig. 21

This highly distinctive genus was discovered and described by M. Howe (1897) and considered in detail by him later (Howe 1899). This genus appears to be favoured by disturbance; raw mineral soil of banks created by human activity have allowed the species to extend the length of the Aleutian Islands. When human disturbance disappears, however, the plant appears to diminish in extent. In clear-cut forest, too, the species abounds for several years, then decreases as the habitat is occupied by more aggressive species.

Schuster (1955) erected the family *Gyrothyraceae*, based on an enumeration of "numerous isolating features" of both sporophyte and gametophyte.

Sporophytes are frequent in spring, but vanish very quickly. Gemmae are also formed, but never abundantly. Howe (1899) provides a fine illustration and Schofield (2002) provides another.

Schofieldia J. D. Godfrey (*Cephaloziaceae*) Fig. 22

Godfrey (1976) described this genus to accommodate a single species, *S. monticola* J. D. Godfrey. Surprisingly, this relatively widespread subalpine to alpine species had been overlooked before this time. It is dioicous, and sporophytes are extremely rare. Gemmae are produced. It is found in upper subalpine to low alpine sites, always in non-forested areas, but where snow persists late, often shaded by heaths. It superficially resembles a large *Lophozia* (Dumort.) Dumort. (subgenus *Schistochilopsis*), as Schuster (1995) has noted and illustrates beautifully. It is most closely related to *Pleurocladula* (Godfrey 1976, Schuster 1995). Fine illustrations are also provided by Godfrey (1976), Schuster (1995), and Schofield (2002).

Acknowledgments

I am indebted to Carl J. Marken, U.S. Geological Survey (Anchorage) for preparing the base maps, to the Botany Department of the University of British Columbia for their generosity since I have retired, and to the Natural Sciences and Engineering Research Council of Canada for many years of financial support for field-work. To these I express my gratitude. Margaret I. Schofield has typed the manuscript from a hand-written text and has patiently inserted revisions. I owe her gratitude for this as well as for her patience with my preoccupation in bryology.

Souhrn

V Severní Americe (severně od Mexika) se vyskytuje 20 endemických rodů mechů (*Alsia*, *Andreaeobryum*, *Aphanorrhegma*, *Bestia*, *Brachelyma*, *Bryoandersonia*, *Bryocrumia*, *Bryolawtonia*, *Dendroalsia*, *Leucolepis*,

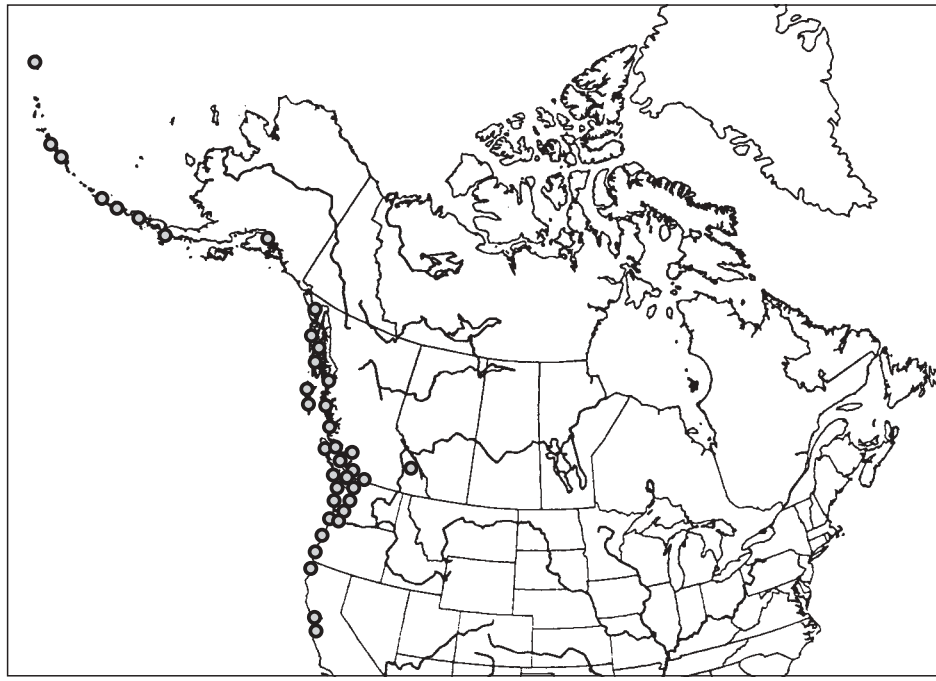

Fig. 21. – Distribution of the liverwort genus *Gyrothyra* M. Howe. (*Gyrothyraceae*).

Fig. 22. – Distribution of the liverwort genus *Schofieldia* J. D. Godfrey (*Cephaloziaceae*).

Meiotrichum, *Neomacounia*, *Platylomella*, *Pseudobraunia*, *Pseudoditrichum*, *Rhytidiopsis*, *Roellia*, *Thelia*, *Trachybryum* a *Tripterocladium*) a 3 endemické rody jatrovek (*Geothallus*, *Gyrothyra* a *Schofieldia*). Všechny tyto rody jsou monotypické, výjimkou je pouze *Thelia* se třemi druhy. Práce je přehledem těchto rodů a shrnutím ekologie, rozšíření a způsobu reprodukce jejich zástupců. Stručně zmiňuje též rody mexické a neotropické.

References

Anderson L. E. (1980): *Bryocrumia*, a new genus of *Hypnaceae* (*Musci*). – Phytologia 45: 63–66.

Andrews A. L. (1945): Taxonomic notes IV. *Sciaromium lescurii*. – The Bryologist 48: 100–103.

Andrews A. L. (1950): Additions and corrections. – The Bryologist 58: 57–58.

Brotherus V. F. (1905): *Hedwigieae*. – In: Engler A. & Prantl K. (eds.), Die Natürlichen Planzenfamilien, p. 713–718, W. Engelmann Verlag, Leipzig.

Brotherus V. F. (1925): *Musci* (Laubmoose). – In: Engler A. & Prantl K. (eds.), Die Natürlichen Planzenfamilien, Ed. 2, Vols. 10 & 11, W. Engelmann Verlag Leipzig.

Bruch P., Schimper W. P. & Gümbel T. (1842): Bryologia Europaea. Fasc. XVI. – E. Schweizerbart, Stuttgart.

Buck W. R. (1989): Miscellaneous notes in Antillean mosses 1. *Thelia* (*Anomodontaceae*) and *Acaulon* (*Pottiaceae*) new to the West Indies. – Moscosoa 5: 186–188.

Buck W. R. (1998): Pleurocarpous mosses of the West Indies.– Mem. New York Bot. Garden. 82: 1–400.

Buck W. R. & Goffinet B. (2000): Morphology and classification of mosses. – In: Shaw A. J. & Goffinet B. (eds.), Bryophyte biology, p. 71–123, Cambridge Univ. Press, Cambridge.

Campbell D. H. (1896a): A new Californian liverwort. – Bot. Gaz. 23: 9–13.

Campbell D. H. (1896b): The development of *Geothallus tuberosus* Campbell. – Ann. Bot. 10: 489–510.

Crum H. A. (1965): A re-evaluation of *Glossadelphus andersonii*. – The Bryologist 68: 219–220

Crum H. A. (1966): A taxonomic account of the genus *Thelia*. – Contrib. to Botany IV, Nat. Mus. Canada Bull. 216: 123–127.

Crum H. A. (1967): Studies in North American *Bryaceae*. – The Bryologist 70: 107–110.

Crum H. A. (1987): *Bestia, Tripterocladium*, and *Isothecium*: An explication of relationships. – The Bryologist 90: 40–42.

Crum H. A. (1991): A partial clarification of the *Lembophyllaceae*. – J. Hattori Bot. Lab. 69: 313–322.

Crum H. A. & Anderson L. E. (1981): Mosses of eastern North America. Vols. 1–2. – Columbia University Press, New York.

Doyle W. T. (1962): The morphology and affinities of the liverwort *Geothallus*. – Univ. California Publ. Bot. 33: 185–268.

Godfrey J. D. (1976): *Schofieldia*, a new hepatic from the Pacific Northwest. – The Bryologist 79: 314–320.

Gradstein S. R., Churchill S. P. & Salazar-Allen N. (2001): Guide to the bryophytes of tropical America. – Mem. New York Bot. Garden 86: 1–577.

Grout A. J. (1928): Moss flora of North America north of Mexico. Vol. 3, Part 1. – [Published by author, I. Vine St., New Brighton, Staten Island, New York City.]

Howe M. A. (1897): *Gyrothyra*, e new genus of *Hepaticae*. – Mem. Torrey Bot. Club. 24: 201–205.

Howe M. A. (1899): The *Hepaticae* and *Anthocerotes* of California. – Mem. Torrey Bot. Club 7: 1–208.

Ignatov M. S. & Huttunen S. (2002): *Brachytheciaceae* (*Bryophyta*) – a family of sibling genera. – Arctoa 11: 245–296.

Ireland R. R. (1974): *Neomacounia,* a new genus in the *Neckeraceae* (*Musci*) from Canada. – The Bryologist 77: 453–459.

Kindberg N. C. (1897): Species of European and North American *Bryineae* (Mosses), Part 2. – Lindköpings Lithographfiska.

Lawton E. (1971): Moss flora of the Pacific Northwest. – The Hattori Botanical Laboratory, Nichinan.

Lindberg S. O. (1868): Observationes de Mniaceis europaeis. – Notiser Sällsk. Fauna & Flora Fenn. Förh. 9: 39–88.

Lowry R. J. (1948): A cytotaxonomic study of the genus *Mnium.* – Mem. Torrey Bot. Club 20/2: 1–42.

Manuel M. G. (1974): A revised classification of the *Leucodontaceae* and a revision of the subfamily *Alsioideae*. – The Bryologist 77: 531–550.

Merrill G. L. S. (1992): Notes on North American *Polytrichaceae*: *Polytrichastrum.* – The Bryologist 95: 270–272.

Murray B. M. (1988): Systematics of the *Andreaeopsida* (*Bryophyta*): two orders with links to *Takakia*. – Nova Hedwigia Beih. 90: 289–336.

Noguchi A. (1972): On the delimitation of the genera of *Hylocomiaceae* and *Rhytidiaceae*. – J. Hattori Bot. Lab. 59: 241–278.
Norris D. H. & Enroth J. (1990): Description of *Bryolawtonia* Norris & Enroth. (*Thamnobryaceae*) with observations on the genus *Bestia*. – The Bryologist 93: 328–331.
Renzaglia K. S., McFarland K. D. & Smith D. K. (1997): Anatomy and ultrastructure of the sporophyte of *Takakia ceratophylla* (*Bryophyta*). – Amer. J. Bot. 84: 1337–1350.
Robinson H. E. (1962): Generic revision of North American *Brachytheciaceae*. – The Bryologist 65: 73–146.
Rohrer J. R. (1985): A generic revision of the *Hylocomiacae*. – J. Hattori Bot. Lab. 59: 241–278.
Schofield W. B. (1968): Bryophytes of British Columbia I. Mosses of particular interest. – J. Hattori Bot. Lab. 31: 205–226.
Schofield W. B. (1980): Phytogeography of the mosses of North America (north of Mexico). – In: Taylor R. J. & Leviton E. A. (eds.), The mosses of North America, p. 131–170, Pacific Division AAAS, San Francisco.
Schofield W. B. (1985): Introduction to bryology. – Macmillan Publ. Co., New York.
Schofield W. B. (1992): Some common mosses of British Columbia. Ed. 2. – Royal B. C. Museum Handbook, UBC Press, Vancouver.
Schofield W. B. (2002): Field guide to liverwort genera of Pacific North America. – Global Forest Society at University of Washington Press, Seattle.
Schuster R. M. (1955): Notes on nearctic *Hepaticae* IX. The relationships of the genus *Gyrothyra*. – The Bryologist 58: 137–141.
Schuster R. M. (1958): Annotated key to the orders, families and genera of *Hepaticae* of America north of Mexico. – The Bryologist 61: 1–66.
Schuster R. M. (1966): The *Hepaticae* and *Anthocerotae* of North America east of the Hundredth Meridian. Vol. I. – Columbia University Press, New York.
Schuster R. M. (1995): Notes on nearctic *Hepaticae* XX. On *Schofieldia* and evolution in the *Cephaloziaceae*. – Fragm. Flor. Geobot. 40: 39–46.
Schuster R. M. (1997): On *Takakia* and the phylogenetic relationships of the *Takakiales*. – Nova Hedwigia 64: 281–310.
Sharp A. J., Crum H. A. & Eckel P. M. (eds.) (1994): The moss flora of Mexico. Vol. 1–2. – Mem. New York Bot. Garden 69: 1–1113.
Smith D. K. & Davison P. G. (1993): Antheridia and sporophytes in *Takakia certophylla* (Mitt.) Grolle: Evidence for reclassification among the mosses. – J. Hattori Bot. Lab. 73: 263–271.
Smith G. L. (1971): A conspectus of the genera of *Polytrichaceae*. – Mem. New York Bot. Garden 21/3: 1–83.
Steere W., Anderson L. E. & Bryan V. S. (1954): Chromosome studies in Californian mosses. – Mem. Torrey Bot. Club 20/4: 1–75.
Steere W. C. & Iwatsuki Z. (1974): *Pseudoditrichum mirabile* gen. et. sp. nov. (*Musci*, *Pseudoditrichaecae* fam. nov.) a unique moss from Great Bear Lake, Northwest Territories. – Can. J. Bot. 52: 701–706.
Sullivant W. S. (1864): Icones Muscorum (of mosses peculiar to eastern North America). – Sever & Francis, Cambridge, Massachusetts.
Sullivant W. S. (1874): Icones Muscorum (Supplement) (of mosses peculiar to North America). – Charles W. Sever, Cambridge, Massachusetts.
Welch W. H. (1960): A monograph of the *Fontinalaceae*. – M. Nijhoff, The Hague.
Welch W. H. (1963): *Fontinalaceae*. – In: North American Flora, ser. 2, pars 3: 1–51, New York Botanical Garden.
Wolery M. G. & Doyle W. T. (1969): The distribution of *Geothallus tuberosus*. – The Bryologist 72: 413–417.

Received 16 March 2004
Revision received 5 April 2004
Accepted 4 May 2004