

AN EVALUATION OF FAMILIAL LIMITS AMONG THE GENERA TRADITIONALLY ALIGNED WITH THE THUIDIACEAE AND LESKEACEAE

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INTRODUCTION

The definitions of moss families, and the genera that constitute them, have been undergoing tremendous change. This is particularly true of the pleurocarps, perhaps because the phenetic distances between genera traditionally have been perceived as less than in acrocarps. This seeming disparity between generic concepts is reflected throughout the history of moss taxonomy. In Hedwig's *Species Muscorum* (1801), 35 moss genera were recognized, only 4 of them, or 11%, pleurocarpous, *Fontinalis*, *Leskea*, *Neckera*, and *Hypnum*. In the *Bryologia Europaea* (1836–1855), Schimper and his colleagues recognized 130 genera of mosses, and of those 35% were pleurocarpous. The small percentage of pleurocarps recognized reflected the Eurocentric view of the day. The tropical latitudes, where pleurocarps abound, were only spottily collected and largely unknown bryologically. However, with the advent of tropical exploration in the last half of the 19th century, as well as the advancement of bryology to a respected scientific discipline, the number of recognized pleurocarpous genera increased as did their percentage within the Musci. Bryologists of the period, especially Mitten, Hampe, Müller, and Bescherelle, and later Fleischer, Brotherus, Cardot, and Dixon, described new genera all too willingly.

By the time Fleischer finished his *Musci der Flora von Buitenzorg* (1904–1923) and Brotherus produced the second edition of *Die natürlichen Pflanzenfamilien* (1924–1925), the number of moss genera had risen to about 660, with pleurocarps accounting for 57% of the total. Since then the number of genera has increased to about 850 (Crosby & Magill, 1981), but the percentage of pleurocarpous genera has scarcely changed.

Because so many of the newly described genera were crowded into already existent families whose concepts were initially based on European taxa, it is not surprising that familial limits were strained and once natural-seeming assemblages took on heterogeneity. Since bryologists primarily have been occupied with the description of new genera and species, the delimitation of intangible categories based on relationships and phylogenies has been left to the few. Today, in an era of extreme specialization, one finds the trend continuing. However, with the increase in the number of bryologists, phylogenetic speculation above the level of genus is

now ascendant. Indeed, it has been of special interest to us (Buck & Crum 1978; Buck 1980a, 1987; Buck & Ireland 1985; Buck & Vitt 1986). That interest has often led us to discussions of the genera of Thuidiaceae and their relationships to the Leskeaceae.

The families of mosses used during the first half of the last century correspond to our modern concept of subclass or other higher category. Schimper in his *Corollarium Bryologiae Europaeae* (1855) was the first to use families in a modern sense. He was also the first to recognize families for the pleurocarps, a group he recognized at the ordinal level. He described eleven families of pleurocarpous mosses, and segregated *Leskea* and *Thuidium* into the Leskeaceae and Hypnoleskeaceae, respectively. In the Leskeaceae he placed only *Leskea* and *Anomodon*, while the Hypnoleskeaceae accommodated *Pseudoleskea*, *Heterocladium* and *Thuidium*. In his 1860 *Synopsis*, Schimper further refined his concepts of this group (designated as a tribe), and added *Myrinia* and *Myurella* to the Leskeaceae and split the Hypnoleskeaceae into the Thuidiaceae embracing *Heterocladium* and *Thuidium* (inclusive of *Helodium*) and the monotypic Pseudoleskeaceae. In the second edition of the *Synopsis*, Schimper (1876) further developed his familial concepts and moved *Myrinia* into its own family in a tribe with the Fabroniaceae; the leskeoid tribe was otherwise unaltered.

Schimper, although largely unrecognized for his contributions, truly was the father of modern moss classification. All subsequent familial speculation was based on his work and at least as late as Grout's *Moss Flora of North America*, Schimper had a profound influence on the taxonomy of mosses. His system of classification, based primarily on gametophytic resemblances, is now largely superseded by the Fleischer/Brotherus system, which places a greater emphasis on sporophytic features as indicators of relationships. In the first edition of *Die natürlichen Pflanzenfamilien*, Brotherus (1907–1908) conserved what Schimper had considered a tribe as a broadly based Leskeaceae of five "Gruppen," the Heterocladiaceae, Thelieae, Anomodonteae, Leskeae and Thuidieae. Brotherus' Leskeae encompassed Schimper's Leskeaceae and Pseudoleskeaceae. Fleischer (1923), on the other hand, defined the Leskeaceae more narrowly as consisting of the Leskeoideae (including in it Schimper's Pseudoleskeaceae) and the Regmatodontoideae. He considered the Leskeaceae derived from the Fabroniaceae. The Thuidiaceae were expanded to include the Heterocladioideae, Anomodontoideae, and Helodioideae, as well as the Thuidioideae. Fleischer's disposition of the leskeoid/thuidioid genera was followed by Brotherus in 1925 and by virtually all bryologists since that time.

PHYLOGENETIC SPECULATIONS

We are basically dissatisfied with the Fleischer/Brotherus concepts because of the gametophytic and sporophytic disparities of the Leskeaceae and Thuidiaceae. We think this is due in part to the inclusion of extraneous genera in the two families, but also because some genera do not seem closely allied to either *Leskea* or *Thuidium*, but indeed belong in a general relationship. We have thus looked upon the two primary genera as nomenclatural cores around which satellite genera are accreted.

We agree with some of the more modern treatments in which genera morphologically distant from this leskeoid assemblage have been moved to other associations. These are either proposed in or followed by Buck and Vitt (1986). The

Regmatodontaceae are allied with the Myriniaceae: the peristome, areolation, alar development, and distribution have little in common with the Leskeaceae. The Anomodontaceae are excluded from a relationship with either the Leskeaceae or Thuidiaceae and are placed in the Leucodontales (=Isobryales) near the Cryphaeaceae and its relatives on the basis of the peristomial morphology, the primary creeping stem, and the leaf areolation. This still leaves several genera which we would like realigned with other families, as discussed below.

THUIDIACEAE

Grout, in the *Moss Flora of North America* (1928–1940), included in the Leskeaceae the Thuideae, Leskeae, Thelieae, and Anomodontae. More recently, Noguchi (1972) treated the Leskeaceae separately from the Thuidiaceae on the basis of gametophytic characters, as follows: the Leskeaceae have paraphyllia few, unbranched, and non-papillose and leaf cells smooth or unipapillose. The Thuidiaceae have, by contrast, abundant, branched, papillose paraphyllia and leaf cells commonly pluripapillose. Crum and Anderson (1981) defined the same two families in terms of sporophytic distinctions. Their concept of the Leskeaceae called for smooth setae, erect and symmetric capsules, and peristomes variously developed, but not clearly hypnaceous; the branching is irregular; the stem and branch leaves are similar, and the leaf cells are short throughout, even near the costa at base. Their unifying features of the Thuidiaceae were the perfect hypnaceous peristome and, almost consistently, the inclined and asymmetric capsules. The branching is regularly pinnate, usually compoundly so, with dimorphic leaves. The leaves have short, papillose cells, and the costa in almost all cases is single. The terminal cells of branch leaves are almost always truncate and pluripapillose. The paraphyllia are abundant on the stems and usually on the branches as well, and multiform, with papillose cells and transverse cell walls.

We, though, have problems with a strict sporophytic definition of these families. If followed unwaveringly, some plants with extreme gametophytic similarities are segregated into separate families. Such broad-based gametophytic convergence seems unlikely. Rather, in the same way that we must be prepared to expect gametophytic adaptation to habitat, we must also accept that the sporophyte, and particularly the peristome because of its important functions, can be influenced by environment. This is most easily observed in association with the epiphytic lifestyle. Repeatedly one can observe a syndrome of morphological adaptations when a lineage of primarily terrestrial organisms adopts an epiphytic existence. These adaptations, with only minor modification, can be seen in many unrelated taxonomic groups. They can be observed in the Bryaceae when comparing *Bryum* to *Brachymenium*, in the Hookeriales with *Distichophyllum* and *Leskeodon* or *Crosbya* and *Daltonia*, and in the Hynaceae with *Homomallium* and *Pylaisiella* or *Platygyrium*. Epiphytic adaptations include a reduction in the regularity of branching, an erect capsule, the insertion of the peristome below the capsule mouth, a reduced or modified exostomial ornamentation associated with a paler color and reduced hygroscopic activity, and reduced endostome, sometimes to the point of absence. Thus, if a classification system is to reflect phylogeny, the beginning and end points of a single reduction series should not be placed in different families.

Accepting the above-cited reduction series and its nomenclatural consequences, our scheme may appear in some ways retrogressive. However, we cannot otherwise dispose of genera that we think of as closely related even though their peristomes may

not be morphologically similar. This may appear to go against the time-honored Philibert concept of peristome-dominated phylogeny, but in fact, it only refines it and recognizes that some seemingly disparate peristomes may be nothing more than simple reductions of more complicated or "perfect" peristomes.

We have made a detailed study of *Thuidium* and the genera traditionally associated with it, and to a lesser extent, the taxa aligned with the Leskeaceae. Because of our greater attention to the Thuidiaceae, we are proposing a subfamilial classification, an action we are unprepared to follow in the Leskeaceae. Our two subfamilies, the Thuidioideae and Cyrtohypnoideae, are carved from the Thuidioideae sensu Brotherus (1925). The other subfamilies of Brotherus are shuttled into different alliances. As mentioned above, we are following Buck and Vitt (1986) in their realignment of the Anomodontoideae as a family of the Leucodontales. Our new proposals follow.

The bulk of the Helodioideae are misplaced in the Thuidiaceae, despite the early inclusion of *Helodium* itself within *Thuidium*. *Helodium*, *Hylocomiopsis*, *Actinothuidium* and *Tetracladium* (= *Bryonoguchia*), the genera placed by Brotherus (1925) in the subfamily, do not all seem particularly closely related. *Bryonoguchia* is totally unlike the other genera and is treated below under the Thuidioideae s. str. The other three genera, unlike a restricted Thuidiaceae, have paraphyllia of elongate, nonpapillose cells, axillary hairs of 4–6 cells, leaf cells that are mostly not papillose over the cell lumina (except some species of *Helodium*), and branching that is not regularly pinnate. (Although *Actinothuidium* is usually illustrated as regularly pinnate, in fact the branches emerge not just from two sides of the stem, but from all around it.) *Hylocomiopsis* and *Actinothuidium*, both genera of mesic forest habitats, also have a tendency to have leaves that are fairly strongly serrate at the apex. Each of these characters, especially the morphology of the paraphyllia and axillary hairs, are rather in accord with the Hylocomiaceae. Further in support of this placement are the erect, frondose habit of *Actinothuidium* (which incidentally has smooth leaf cells, neither prorulose nor pluri-papillose as illustrated by Watanabe, 1972, p. 296) and the leaves of *Hylocomiopsis* with scattered teethlike prorulae at back like those found in *Rhytidiadelphus*. Admittedly these two genera have single costae, rather than the typical double costae usually encountered in the Hylocomiaceae. However, even within *Hylocomium* itself (s.l., *Hylocomiastrum* s.str.) some species have a single costa. Therefore, despite a recent attempt to purify the Hylocomiaceae (Rohrer 1985a), we are transferring *Hylocomiopsis* and *Actinothuidium* to that family.

Helodium itself, though, is another problem. The genus was described and illustrated by Abramova and Abramov (1972), but they failed to provide insights into its relationships. As mentioned above, the paraphyllia and leaf areolation are incompatible with those of the Thuidiaceae s.str. Now that the Helodioideae of Brotherus (1925) have been purged, *Helodium* stands alone, without any close generic allies in the Thuidiaceae. The wet habitats of the plants also preclude serious consideration of the Thuidiaceae, but suggest rather the Amblystegiaceae. However, the paraphyllia and papillose leaf cells are incongruent in the Amblystegiaceae. Therefore, we see no alternative but to recognize it in its own family, the Helodiaceae.

The Heterocladioideae are of special interest since the short, double costa and sparse to absent paraphyllia seem unlike *Thuidium* and its satellites. Brotherus (1925) included in the subfamily only *Heterocladium* and *Leptopterigynandrum*. The latter genus belongs in the Leskeaceae and has no similarity to *Heterocladium*.

The peristome of *Heterocladium* is hypnoid in every respect and gives no clue to the relationships of the genus. On the other hand, the gametophytes show a remarkable resemblance to several others never previously associated with it. These genera, *Pterigynandrum*, *Habrodon*, *Iwatsukiella*, and *Myurella*, all share a similar areolation, costal development, sexuality and distribution, but most have decidedly more reduced peristomes than does *Heterocladium*. This reduction we relate to adaptation to an epiphytic habitat. *Heterocladium*, the only genus in the alliance which is truly terricolous, has the asymmetric capsule and perfect peristome associated with the Hypnales, and a regularly branched habit. *Myurella*, primarily inhabiting vertical rock walls and rock crevices, has reduced branching and erect capsules, with only minimal endostomial reduction. The other genera, all strict epiphytes, have scarcely branching stems, erect capsules, modified exostomes, and greatly reduced endostomes. Thus, a reduction series of peristomes can be demonstrated as a result of life style adopted by the plants. *Pterigynandrum* can be related to both *Habrodon* and *Iwatsukiella*. With the former it has almost identical stem-borne gemmae, and with the latter prorulose leaf cells. Therefore, we place this united assemblage of genera in a family of its own, the Pterigynandraceae. Although related to the Leskeaceae and Thuidiaceae, the morphological modifications indicate a long and separate evolution that we think deserves familial recognition.

While examining *Pterigynandrum* in connection with this study, we re-evaluated *P. sharpii* Crum & Anderson, a species whose placement has been questioned even by the combining authors. The species was first described by Sharp (1933), at Dixon's suggestion, as *Hylocomium splendens* var. *tenue*. Crum and Anderson (1967) raised the taxon to the species level and transferred it to *Pterigynandrum*. Although the species has also been transferred to *Taxiphyllum* (Robinson 1974) and *Mitlenothamnium* (Buck 1980b), none of these placements has been very satisfactory. At last a comfortable resting place for the taxon has come to light. It appears to be a species of *Leptohymenium*. The characters that distinguish this genus (Rohrer 1985b) are sympodial branching, decurrent leaves with differentiated alar cells, and obscurely and casually prorulose leaf cells. All these characters, but the branching pattern, which may have been modified in a small-statured, reduced plant, are in *P. sharpii*, although the decurrencies have been overlooked, and it does not seem too distant from the type of the genus, the Mexican-Southeast Asian *L. tenue* (Hook.) Schwaegr. Therefore, without hesitation we transfer this Southern Appalachian endemic into *Leptohymenium*.

Thus, the Thuidiaceae are left with only the Thuidioideae. Our detailed analysis of the genera included those of the Thuidioideae with the addition of those excluded from the Anomodontaceae, i.e., *Claopodium* and *Bryohaplocladium* (*Haplocladium* sensu Brotherus, 1925, nom. illeg.). The genera we have studied, in addition to those two just listed, are *Thuidium*, *Bryonoguchia*, *Raiiella*, *Orthothuidium*, *Pelekium*, *Thuidiopsis*, *Abietinella*, and *Boulaya*. Since our initial interest was in the relationships of *Thuidium* itself, we segregated the small, autoicous species from the large, dioicous ones (*Thuidium* s.str.); this group of species is here called *Cyrtohypnum*, the oldest name at the generic level. (The oldest name as a subgenus is *Microthuidium* and as a section, *Minutula*; the nomenclature is presented in more detail below.) The characters which we found to be of most use in defining the Thuidiaceae and in sorting out the genera within it are sexuality, placement of the leaf cell papillae on both general laminal cells and branch leaf terminal cells, papillosity of the cells of the paraphyllia, morphology of the axillary hairs, and ornamentation of the seta. If these characters seem trivial, it is because

most of the genera are very close to one another, and even in recent years some of the genera, such as *Rauarella*, *Abietinella*, *Thuidiopsis*, and *Cyrtohypnum* have been included in *Thuidium* (e.g., Scott & Stone 1976; Smith 1978; Crum & Anderson 1981). This is due in part to a general aspect similarity (what we think of as a familial aspect) and also to a lack of appreciation of some of the characters that are not easily ascertained. Some genera contain discrepancies, i.e., some species within them have one state of a given character, whereas others have another character state. For example, both autoicy and dioicy are found in *Pelekium*. This, however, is the exception. Most genera are quite uniform for characters that are significant indicators of phylogenetic relatedness.

Because *Cyrtohypnum* is the one genus that has failed to gain acceptance since its description (Hampe 1869), except by Hampe himself, we would first like to argue for its recognition. This requires that *Thuidium* itself be typified to avoid future confusion. *Thuidium* was described in the *Bryologia Europaea* (1852) for five European species, only three of which are still kept in the genus, *T. minutulum*, *T. tamariscinum*, and *T. delicatulum*. The first typification was made by E. G. Britton in the *Flora of Bermuda* (1918, pp. 445–446), and she chose *T. minutulum*. Here, as throughout that work, she chose the first species listed in the original work, i.e., she mechanically chose the lectotype. Grout in his *Moss Flora of North America* (3: 174. 1932) chose *T. tamariscinum* as the generic type, and this was followed by Watanabe (1972) in his revision of the Japanese Thuidiaceae. Although these authors specifically cited a type species, several earlier works give indirect indications of typification. For example, Bescherelle, in his Mexican *Prodromus* (1872), divided *Thuidium* into three subgenera, *Orthothuidium*, *Thuidiella*, and *Thuidium*, citing Schimper, the pleurocarp author in the *Bryologia Europaea*, and Bescherelle's "compatriote" in his *Prodromus*, as the authority for the first two. Within subgen. *Thuidium* only two species were included, *T. tamariscinum* and *T. schlumbergii*. The small, autoicous *T. minutulum* was relegated to subgen. *Thuidiella*. This same scheme was followed, with modification, by Brotherus (1907–1908). Also of significance is the citation of *Hypnum* sect. *Tamariscina* Brid. and *H.* subsect. *Tamariscella* C. Müll. in the protologue of *Thuidium*. Therefore, we accept *T. tamariscinum* as the type of *Thuidium* and ignore Britton's typification as she ignored her predecessors'.

Thus, *Thuidium* is typified by a species of large stature, with dioicous sexuality, three-celled axillary hairs, abundant, strongly branched paraphyllia, leaf cells papillose only at back of the leaf, and smooth setae. This same suite of characters is held by scores of other species within the genus. Variation in the genus of potential interest is the number of papillae over each cell, usually one but occasionally several (never in North America, Africa, or Europe, rare in Central and South America, not uncommon in Asia), and the fact that the type species has a smooth branch leaf apical cell (all other species have a pluripapillose branch leaf apical cell).

In comparison, *Cyrtohypnum*, typified by *C. brachythecium*, is a genus of small statured plants with autoicous sexuality; the axillary hairs are two-celled; the stems are sparsely clothed with unbranched or weakly branched paraphyllia; the leaf cells are papillose on both surfaces; and the setae are often roughened. Although the leaf cells are usually pluripapillose, sometimes they are unipapillose (as in the type), and the setae are sometimes smooth.

The combination of so many unrelated characters amply justifies the recognition of *Cyrtohypnum*. Considering how different the two genera are in aspect alone,

one could have suspected the widespread recognition of their segregation long ago. The correlation of so many microscopic differences, though, readily reinforce macroscopic intuition.

Norris and Koponen (1985) recently described a new genus, *Orthothuidium*, for a single New Guinea species. They provided few characters worthy of generic consideration, but rather were more impressed by the plant's aspect and ramicolous habitat. In fact, *O. curtisetum* shows no differences from typical *Cyrtohypnum*. The species appears distinctive due to the short setae but all other characters can be found in other *Cyrtohypna*. It is an interesting coincidence that the generic name *Orthothuidium* was chosen for the plant (the capsules are in fact only suberect), since the name was already used as an undescribed subgenus for a Mexican plant, *Thuidium mexicanum*, that also has suberect capsules, unipapillose leaf cells, and frequently a ramicolous habitat.

Raiiella has needlessly been confused with other genera in this assemblage. Crum and Anderson (1981) placed the type species, *R. scita* in *Thuidium*, and Crum (1984) transferred *R. praelonga* into *Bryohaplocladium*. Because of its autoicous inflorescences and papillae on both surfaces of the leaves, the genus comes closest to *Cyrtohypnum*. However, it is separated from the latter genus by once-pinnate branching, leaves not incurved when dry, strongly bulging leaf cells, three-celled axillary hairs, and smooth setae. From *Bryohaplocladium*, *Raiiella* differs in having papillose paraphyllia and cells papillose on both surfaces of the leaf. We are tempted to speculate that *Raiiella* is an ancient genus because of its current distribution. The North American *R. scita* is closely related to the East Asian *R. fujisana*; *R. subcatenulata* is a tropical American endemic; and *R. praelonga* (with the "African" *R. subfilamentosa* as a synonym) ranging from Mexico to Patagonia and throughout much of sub-Saharan Africa. Although we have not seen all the types, most of the other species assigned to the genus seem either to be synonyms or misplaced in the genus (as treated below).

Boulaya is very similar to *Raiiella* and may best be considered part of that genus. It differs in its dioicous condition and the erect capsule with a somewhat reduced endostome.

Pelekium is the other genus related to *Cyrtohypnum*, *Raiiella*, and *Boulaya*. Like those genera, it has leaf cells papillose on both surfaces; and like *Cyrtohypnum* it has two-celled axillary hairs and a roughened seta. It is the only genus in the Thuidiaceae that has both autoicous and dioicous species. Additionally, it is morphologically unique in the family for its mitrate, spinose calyptrae. Although the calyptral difference may seem significant, we view it as only a generic marker. In some species of *Cyrtohypnum* the calyptra is roughened and when immature is mitrate-like, only splitting up one side as the capsule expands. Therefore, we prefer to think of the mitrate calyptra, a condition that sometimes stands as a familial character state, to represent a minor divergence from the cucullate calyptra more typically encountered in the family.

Unfortunately, the generic name *Pelekium* needs to be replaced by a less familiar one, but with only four species recognized in the genus the nomenclatural changes are not excessive. The reason for the change in names is that Hampe (1867) published the generic name *Lorentzia*, but assigned no species to it. Although somewhat odd, this procedure does not invalidate the generic name. In 1868 Mitten published *Pelekium* with a single species, *P. velatum*. Finally, in 1872 Hampe published a species in his *Lorentzia*, *L. longirostris*. This species is synonymous with the type species of *Pelekium*. Therefore, although Mitten's specific name stands, his

generic name should be replaced by Hampe's. The nomenclatural novelties are presented below.

These four genera just discussed, *Cyrtohypnum*, *Rauarella*, *Boulaya*, and *Lorentzia*, form a natural group characterized by autoicous sexuality (except *Boulaya* and some species of *Lorentzia*), small-statured plants, leaf cells mostly pluripapillose on both surfaces, and a strong tendency for roughened setae. We think of them as a subfamily of the Thuidiaceae, the Cyrtohypnoideae.

The Thuidioideae s.str. are characterized by dioicous, large plants with abundant, branched paraphyllia. The leaf cells are mostly unipapillose, either just at back (in *Thuidium*) or on both surfaces (in *Abietinella* and *Thuidiopsis*); the setae are never roughened. Axillary hair morphology varies from the typical 3-celled condition in *Thuidium*, i.e., with a single short, brown basal cell and two elongate hyaline ones, to 3-4-celled in *Abietinella* but with all cells brown, to 3-celled in *Thuidiopsis* but with two short brown basal cells and a single elongate hyaline apical one.

As discussed above, *Thuidium* is characterized by large-statured, dioicous plants with abundant paraphyllia; the leaf cells are papillose only on the back of the leaf; and the axillary hairs are 3-celled. This identical condition is found in *Bryonoguchia*. The single species in the genus, *B. molkenboeri*, is striking for the extremely large papillae over the leaf lumina, but they are not particularly large in comparison to some South American species of *Thuidium*. Also, recognition of the species at the generic level implies that its origin is independent from that of *Thuidium*, whereas it is almost surely derived from *Thuidium* itself, but has undergone specialized modification.

Thuidiopsis has frequently been synonymized with *Thuidium*, probably because of the similarity in stature and sexuality. However, the leaf cells are papillose on both surfaces rather than just at back, and the papillae are almost always smaller than those in *Thuidium*. Additionally there is the axillary hair difference described above. The austral dispersal of *Thuidiopsis* is additional evidence, albeit circumstantial, of phylogenetic distance.

Abietinella, like *Thuidiopsis*, is distinguished from *Thuidium* by leaf cells papillose on both surfaces and different axillary hairs. At first glance *Abietinella* and *Thuidiopsis* may seem to be best merged. However, the former is once-pinnate and boreal in distribution, whereas the latter is mostly twice-pinnate and austral. The differences in axillary hair morphology are outlined above.

Two genera have been left out of the above scheme, the two previously rejected from the Anomodontaceae, *Bryohaplocladium* and *Claopodium*. These differ from the Thuidiaceae s.str. in different paraphyllia (nonpapillose in the former, absent in the latter) and the nonpapillose apical cell of branch leaves. Both have perfect, hypnoid peristomes. They are placed in an expanded Leskeaceae that we justify below.

LESKEACEAE

Leskea and its immediate allies, with erect capsules and peristomes pale, somewhat reduced, and only weakly cross-striolate, form the nomenclatural nucleus of the Leskeaceae. This is in marked contrast to the unreduced hypnoid peristomes of *Pseudoleskea* and its relatives. However, despite peristomial differences, these two clusters of genera are both characterized by leaf cells mostly mammillose or low papillose at back. The cells are short throughout the leaf, and alar cells are mostly

not differentiated in shape but often in orientation; the apical cell of the branch leaves is neither truncate nor pluripapillose. Like the Thuidiaceae, the plants are mostly adapted to exposed habitats, but in the Leskeaceae the branching pattern is irregular and the paraphyllia, when present, are short, unbranched, and not papillose. The setae are mostly smooth and the capsules often suberect. In the same way that we have postulated a peristomial reduction series for the Pterigynandraceae, we see a similar trend in the Leskeaceae. In the terrestrial taxa, such as *Bryohaplocladium* and *Pseudoleskea*, branching is more extensive, paraphyllia more common, leaf cells more strongly papillose, capsules more strongly inclined, and peristomes attached at the mouth of the urn and well developed. As plants evolved into corticolous habitats, branching became more irregular, paraphyllia fewer, leaf cells less conspicuously papillose or even smooth, capsules suberect to erect, and peristomes paler, attached below the mouth, and reduced. *Leskea* itself exemplifies this reductionary extreme. Therefore, we recognize the Leskeaceae primarily on the basis of gametophytic characters (as families throughout the Hypnales are) and perceive a habitat-driven, sporophytic reduction series.

Although we do not think that peristomial reduction series should be accorded familial status, we do think they are valid markers of lineage at the generic level. Therefore, we do not follow the recent treatment by Wilson and Norris (1989) in which *Leskeella* is submerged into *Pseudoleskeella*.

NOMENCLATORIAL CONCLUSIONS

LESKEACEAE Schimp., Coroll. Bryol. Eur. 109. 1855 [1856]. Pseudoleskeaceae Schimp., Syn. Musc. Eur. 491. 1860.

Leskea Hedw., *Leskeadelphus* Herz., *Leskeella* (Limpr.) Loeske, *Lescuraea* Schimp. in B.S.G., *Leptopterigynandrum* C. Müll., *Schwetschkea* C. Müll., *Mamillariella* Lazarenko, *Fabronidium* C. Müll., *Bryobartlettia* Buck, *Pseudoleskea* Schimp. in B.S.G., *Pseudoleskeella* Kindb., *Pseudoleskeopsis* Broth., *Okamuraea* Broth., *Orthoamblystegium* Dix. & Sak., *Rigodiadelphus* Dix., *Bryohaplocladium* Watanabe & Iwatsuki, ? *Claopodium* Schimp. in B.S.G., *Lindbergia* Kindb.

Note: Two species, previously placed in *Raiiella*, differ significantly from that genus. Both have nonpapillose paraphyllia, leaf cells papillose only at back, erect capsules and pale, reduced peristomes. We place them back in *Leskea*, where Mitten (1869) originally had them:

Leskea plumaria Mitt., J. Linn. Soc., Bot. 12: 568. 1869. *Raiia plumaria* (Mitt.) Broth., Nat. Pfl. 1(3): 1005. 1907; *Raiiella plumaria* (Mitt.) Wijk & Marg., Taxon 11: 222. 1962.—TYPE: ECUADOR. Andes Quitenses, Pangor, 10,000 ft, *Spruce 1450* (NY!).

Leskea teretiuscula Mitt., J. Linn. Soc., Bot. 12: 567. 1869. *Raiia teretiuscula* (Mitt.) Broth., Nat. Pfl. 1(3): 1005. 1907; *Raiiella teretiuscula* (Mitt.) Wijk & Marg., Taxon 11: 222. 1962.—TYPE: ECUADOR. Andes Quitenses, Baños, 6000 ft, *Spruce 1466*; Tunguragua, 7000–8000 ft, *Spruce 1467*; Leito, 8000 ft, *Spruce 1468*; Chimborazo, 10,000 ft, *Spruce 1469*; Carguairazo, 11,000 ft, *Spruce 1470*; Pinchincha, 10,500 ft, *Spruce 1470*; Guayrapata, 9000 ft, *Spruce 1473*; Quito ex Jameson, *Spruce 1472*. Lectotype, *Spruce 1466* (NY!).

PTERIGYNANDRACEAE Schimp., Syn. Musc. Eur., ed. 2, CXIII, 618. 1876, "Pterigynandreae."

Pterigynandrum Hedw., *Myurella* Schimp. in B.S.G., *Habrodon* Schimp., *Iwatsukiella* Buck & Crum, *Heterocladium* Schimp. in B.S.G.

Note: As mentioned in the discussion above, a species previously included in *Pterigynandrum*, *P. sharpii*, needs to be transferred to the Hylocomiaceae as follows:

Leptohymenium sharpii (Crum & Anderson) Buck & Crum, comb. nov.

Hylocomium splendens var. *tenue* Sharp, Bryologist 36: 21. 1933; *Pterigynandrum sharpii* Crum & Anderson, Bryologist 70: 99. 1967; *Taxiphyllum sharpii* (Crum & Anderson) Robinson, Phytologia 28: 66. 1974; *Mitlenothamnium sharpii* (Crum & Anderson) Buck, Bryologist 83: 461. 1980.

Helodiaceae (Fleisch.) Buck & Crum, stat. et comb. nov. Thuidiaceae subfam. Helodioideae Fleisch., Musci Fl. Buitenzorg 4: 1499. 1923, "Helodieae."

Helodium Warnst.

THUIDIACEAE Schimp., Syn. Musc. Eur. 493. 1860. "Thuidieae."

Thuidiaceae subfam. Thuidioideae.

Thuidium Schimp. in B.S.G. (incl. *Bryonoguchia* Iwatsuki & H. Inoue, syn. nov.), *Thuidiopsis* (Broth.) Fleisch., *Abietinella* C. Müll.

Thuidiaceae subfam. **Cyrtohypnoideae** Buck & Crum, subfam. nov. Thuidiaceae subfam. Microthuidioideae Podp., Consp. Musc. Eur. 25, 540. 1954, nom. nud.

A Thuidioideis plantis autoicis parvis, paraphylliis sparsis pauciramosis nonpapillosis, cellulis foliorum utrinque papillosis et setis saepe papillosis differt.—TYPE: *Cyrtohypnum* (Hampe) Hampe & Lor. in Hampe.

Lorentzia Hampe (incl. *Pelekium* Mitt., syn. nov.).—TYPE: *L. longirostris* Hampe.

Lorentzia bifaria (Bosch & Lac.) Buck & Crum, comb. nov. *Thuidium bifarium* Bosch & Lac., Bryol. Jav. 2: 123. 1865; *Pelekium bifarium* (Bosch & Lac.) Fleisch., Musci Fl. Buitenzorg 4: 1513. 1923.

Lorentzia calcicola (Fleisch.) Buck & Crum, comb. nov. *Pelekium calcicola* Fleisch., Musci Fl. Buitenzorg 4: 1511. 1923.

Lorentzia tenue (Fleisch.) Buck & Crum, comb. nov. *Pelekium tenue* Fleisch., Musci Fl. Buitenzorg 4: 1515. 1923; *Thuidium bifarium* var. *pertenue* Bosch & Lac., Bryol. Jav. 2: 123. 1865.

Lorentzia velata (Mitt.) Buck & Crum, comb. nov. *Pelekium velatum* Mitt., J. Linn. Soc., Bot. 10: 176. 1868.

Lorentzia longirostris Hampe, Nuovo Giorn. Bot. Ital. 4: 288. 1872.

Raiiella Reimers (incl. *Rauia* Aust., nom. illeg.)

Boulaya Card.

Cyrtohypnum (Hampe) Hampe & Lor. in Hampe. *Hypnum* sect. *Cyrtohypnum* Hampe, Ann. Sci. Nat. Bot. V, 5: 310. 1866, nom. nud.; *Hypnum* subgen. *Cyrto-hypnum* Hampe, Flora 50: 78. 1867; *Cyrto-hypnum* (Hampe) Hampe & Lor. in Hampe, Bot. Zeitung (Berlin) 27: 455. 1869.—TYPE: *C. brachythecium* (Hampe & Lor.) Hampe & Lor.

Thuidium sect. *Minutula* Schimp. in B.S.G., Bryol. Eur. 5(fasc. 49/51): 161. 1852.—TYPE: *T. minutulum* (Hedw.) Schimp. in B.S.G.

Thuidium subgen. *Microthuidium* Limpr. in Rabenh., Kryptog.-Fl. Deutschl., ed. 2, 4(Laubm. Deutschl. 2): 822. 1895; *T.* sect. *Microthuidium* (Limpr.) Kindb., Eur. N. Amer. Bryin. 1: 54. 1897, nom. illeg.; *Microthuidium* (Limpr.) Warnst., Kryptog. Fl. Brandenburg 2: 677. 1905.—TYPE (selected here): *T. minutulum* (Hedw.) Schimp. in B.S.G.

Thuidium subgen. *Thuidiella* Schimp. ex Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 235. 1872, nom. nud., Schimp. ex Broth. in Engler & Prantl, Nat. Pfl. 1(3): 1012. 1908, nom. illeg.—TYPE: *T. minutulum* (Hedw.) Schimp. in B.S.G.

Orthothuidium Norris & Koponen, Acta Bot. Fennica 131: 23. 1975, syn. nov.—TYPE: *O. curtisetum* Norris & Koponen.

Cyrtohypnum bonianum (Besch.) Buck & Crum, comb. nov. *Thuidium bonianum* Besch., Bull. Bot. Soc. France 34: 98. 1887.

Cyrtohypnum brotheri (Salmon) Buck & Crum, comb. nov. *Thuidium brotheri* Salmon, J. Bot. 39: 153. 1901.

Cyrtohypnum byssoideum (Besch.) Buck & Crum, comb. nov. *Thuidium byssoideum* Besch., Ann. Sci. Nat. Bot. VII, 2: 95. 1885.

Cyrtohypnum chenagonii (C. Müll ex Ren. & Card.) Buck & Crum, comb. nov. *Thuidium chenagonii* C. Müll. ex Ren. & Card., Bull. Soc. Roy. Bot. Belgique 33(2): 129. 1895.

Cyrtohypnum curtisetum (Norris & Koponen) Buck & Crum, comb. nov. *Orthothuidium curtisetum* Norris & Koponen, Acta Bot. Fennica 131: 23. 1985.

Cyrtohypnum gratum (P.-Beauv.) Buck & Crum, comb. nov. *Hypnum gratum* P.-Beauv., Prodr. aethéogam. 64. 1805; *Thuidium gratum* (P.-Beauv.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 256. 1878.

Cyrtohypnum gratum ssp. *subscissum* (Besch.) Buck & Crum, comb. nov. *Thuidium subscissum* C. Müll. ex Besch., Ann. Sci. Nat. Bot. VI, 10: 290. 1880; *T. gratum* ssp. *subscissum* (Besch.) Touw, Lindbergia 3: 158. 1976.

- Cyrtohypnum haplohymenium** (Harv.) Buck & Crum, comb. nov. *Hypnum haplohymenium* Harv., London J. Bot. 2: 21. 1843.
- Cyrtohypnum intricatum** (Jaeg.) Buck & Crum, comb. nov. *Thuidium intricatum* Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 251. 1878; *Leskea intricata* Mitt., J. Linn. Soc., Bot. 7: 161. 1863, nom. illeg., non Hartm., Handb. Skand. Fl., ed. 5, 336. 1849.
- Cyrtohypnum investe** (Mitt.) Buck & Crum, comb. nov. *Hypnum investe* Mitt., Kew J. Bot. 8: 355. 1856.
- Cyrtohypnum involvens** (Hedw.) Buck & Crum, comb. nov. *Leskea involvens* Hedw., Sp. Musc. 218. 1801; *Thuidium involvens* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 575. 1869.
- Cyrtohypnum involvens** ssp. **thomeanum** (Broth.) Buck & Crum, comb. nov. *Thuidium involvens* var. *thomeanum* Broth., Bol. Soc. Brot. 8: 183. 1890; *T. involvens* ssp. *thomeanum* (Broth.) Touw, Lindbergia 3: 168. 1976.
- Cyrtohypnum kiasense** (Williams) Buck & Crum, comb. nov. *Thuidium kiasense* Williams, Bull. New York Bot. Gard. 8: 363. 1914.
- Cyrtohypnum koelzii** (Robinson) Buck & Crum, comb. nov. *Thuidium koelzii* Robinson, Bryologist 71: 92. 1968.
- Cyrtohypnum kuripanum** (Dozy & Molk.) Buck & Crum, comb. nov. *Thuidium kuripanum* Dozy & Molk. in Zoll., Syst. Verz. 1: 32. 1854.
- Cyrtohypnum lepidoziaeum** (Sak.) Buck & Crum, comb. nov. *Thuidium lepidoziaeum* Sak., Bot. Mag. (Tokyo) 60: 88. 1947.
- Cyrtohypnum leptocladum** (Tayl.) Buck & Crum, comb. nov. *Leskea leptoclada* Tayl., London J. Bot. 6: 339. 1847; *Thuidium leptocladum* (Tayl.) Mitt., J. Linn. Soc., Bot. 12: 573. 1869.
Hypnum brachythecium Hampe & Lor. in Lor., Bot. Zeitung (Berlin) 26: 819. 1868; *Cyrto-hypnum brachythecium* (Hampe & Lor.) Hampe & Lor. in Hampe, Bot. Zeitung (Berlin) 27: 455. 1869; *Thuidium brachythecium* (Hampe & Lor.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 254. 1878, syn. nov.
- Cyrtohypnum mexicanum** (Mitt.) Buck & Crum, comb. nov. *Thuidium mexicanum* Mitt., J. Linn. Soc., Bot. 12: 577. 1869.
Thuidium pellucens Ren. & Card., Bull. Soc. Roy. Bot. Belgique 32(1): 198. 1894, syn. nov.
- Cyrtohypnum minusculum** (Mitt.) Buck & Crum, comb. nov. *Leskea minuscula* Mitt., J. Linn. Soc., Bot. Suppl. 1: 134. 1859.
- Cyrtohypnum minutulum** (Hedw.) Buck & Crum, comb. nov. *Hypnum minutulum* Hedw., Sp. Musc. 260. 1801; *Thuidium minutulum* (Hedw.) Schimp. in B.S.G., Bryol. Eur. 5(fasc. 49/51); 161. 1852.

Thuidium exasperatum Mitt., J. Linn. Soc., Bot. 12: 576. 1869, syn. nov.
Thuidium glaucescens Schimp. ex Besch., Mém. Soc. Sci. Nat. Cherbourg 16:
235. 1872, syn. nov.

Cyrtohypnum pelekinoïdes (Chen) Buck & Crum, comb. nov. *Thuidium pelekinoïdes* Chen, Sunyatsenia 6: 190. 1941, non *T. pelekioïdes* Broth., Bot. Jahrb. Syst. 17: 479. 1893.

Cyrtohypnum pseudo-involvens (C. Müll.) Buck & Crum, comb. nov. *Hypnum pseudo-involvens* C. Müll., Linnaea 40: 285. 1876; *Thuidium pseudo-involvens* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 254. 1878.

Cyrtohypnum pygmaeum (Schimp.) Buck & Crum, comb. nov. *Thuidium pygmaeum* Schimp. in B.S.G., Bryol. Eur. 5(fasc. 49/51): 162. 1852.

Cyrtohypnum ramusculosum (Mitt.) Buck & Crum, comb. nov. *Leskea ramusculosa* Mitt., J. Linn. Soc., Bot. 7: 161. 1863; *Thuidium ramusculosum* (Mitt.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 254. 1878.

Cyrtohypnum rubiginosum (Besch.) Buck & Crum, comb. nov. *Thuidium rubiginosum* Besch., Ann. Sci. Nat. Bot. VII, 15: 80. 1892.

Cyrtohypnum scabrosulum (Mitt.) Buck & Crum, comb. nov. *Thuidium scabrosulum* Mitt., J. Linn. Soc., Bot. 12: 574. 1869.
Thuidium complanum Mitt., J. Linn. Soc., Bot. 12: 575. 1869, syn. nov.

Cyrtohypnum schistocalyx (C. Müll.) Buck & Crum, comb. nov. *Hypnum schistocalyx* C. Müll., Syn. 2: 691. 1851; *Thuidium schistocalyx* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 575. 1869.

Cyrtohypnum sharpii (Crum) Buck & Crum, comb. nov. *Thuidium sharpii* Crum, Bryologist 87: 211. 1984.

Cyrtohypnum sparsifolium (Mitt.) Buck & Crum, comb. nov. *Leskea sparsifolia* Mitt., J. Linn. Soc., Bot. Suppl. 1: 135. 1859.

Cyrtohypnum squarrosulum (Ren. & Card.) Buck & Crum, comb. nov. *Thuidium squarrosulum* Ren. & Card., Bull. Soc. Roy. Bot. Belgique 38(1): 31. 1900.

Cyrtohypnum stevensii (Ren. & Card.) Buck & Crum, comb. nov. *Thuidium stevensii* Ren. & Card., Bull. Soc. Roy. Bot. Belgique 38(1): 33. 1900.

Cyrtohypnum synoicum (Touw) Buck & Crum, comb. nov. *Thuidium synoicum* Touw in Touw & Falter-van den Haak, J. Hattori Bot. Lab. 67: 146. 1989.

Cyrtohypnum talongense (Besch.) Buck & Crum, comb. nov. *Thuidium talongense* Besch., Ann. Sci. Nat. Bot. VII, 15: 81. 1892.

Cyrtohypnum tamariscellum (C. Müll.) Buck & Crum, comb. nov. *Hypnum tamariscellum* C. Müll., Bot. Zeitung (Berlin) 12: 573. 1854; *Thuidium tamariscellum* (C. Müll.) Bosch & Lac., Bryol. Jav. 2: 20. 1865.

Cyrtohypnum tenuissimum (Welw. & Duby) Buck & Crum, comb. nov. *Thuidium tenuissimum* Welw. & Duby in Duby, Mém. Soc. Phys. Genève 21: 442. 1871.

Cyrtohypnum varians (Welw. & Duby) Buck & Crum, comb. nov. *Thuidium varians* Welw. & Duby in Duby, Mém. Soc. Phys. Genève 21: 440. 1871.

Cyrtohypnum venustum (Besch.) Buck & Crum, comb. nov. *Thuidium venustum* Besch., Ann. Sci. Nat. Bot. VII, 15: 78. 1892.

Cyrtohypnum versicolor (C. Müll.) Buck & Crum, comb. nov. *Hypnum versicolor* Hornsch. ex C. Müll., Syn. 2: 494. 1851; *Thuidium versicolor* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 249. 1878.

Cyrtohypnum vestitissimum (Besch.) Buck & Crum, comb. nov. *Thuidium vestitissimum* Besch., Ann. Sci. Nat. Bot. VII, 15: 79. 1892.

Note: We have not made all the appropriate combinations in *Cyrtohypnum*. Rather we have made those for taxa that we have personally examined and those monographed by Robinson (1968), Watanabe (1972), Touw (1976), Gangulee (1978), Norris and Koponen (1985), and Touw and Falter-van den Haak (1989). We have intentionally not transferred those listed by Gier (1980), because the work is so uncritical that mass transferring of species would only result in superfluous nomenclature. We have, though, transferred some names with which we are unfamiliar, because it is more likely that our taxonomy will be followed by others if they have the appropriate nomenclature available to them.

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LITERATURE CITED

- Abramova, A. L., & I. I. Abramov. 1972. On the span of the genus *Helodium* (Sull.) Warnst. J. Hattori Bot. Lab. 35: 371–381.
- Bescherelle, E. 1872. Prodromus bryologiae mexicanae ou énumération des mousses du Mexique avec description des espèces nouvelles. Mém. Soc. Sci. Nat. Cherbourg 16: 145–256.
- Britton, E. G. 1918. Musci. Mosses. In: N. L. Britton, *Flora of Bermuda*, 430–448. New York: Charles Scribner's Sons.
- Brotherus, V. F. 1907–1908. Leskeaceae. In: A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien* 1(3): 977–1020.
- . 1924–1925. Musci (Laubmoose). In: A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien*, ed. 2. Vols. 10, 11.
- Bruch, P., W. P. Schimper, and W. T. von Gümbel. 1836–1855. *Bryologia europaea seu genera muscorum Europaeorum monographice illustrata*. Stuttgart: E. Schweizerbart. [Note: Schimper alone was responsible for the pleurocarps.]
- Buck, W. R. 1980a. A generic revision of the Entodontaceae. J. Hattori Bot. Lab. 48: 71–159.

- . 1980b. Animadversions on *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum*. *Bryologist* 83: 451–465.
- . 1987. Taxonomic and nomenclatural rearrangement in the Hookeriales with notes on West Indian taxa. *Brittonia* 39: 210–224.
- Buck, W. R., and H. Crum. 1978. A re-interpretation of the Fabroniaceae with notes on selected genera. *J. Hattori Bot. Lab.* 44: 347–369.
- Buck, W. R., and R. R. Ireland. 1985. A reclassification of the Plagiotheciaceae. *Nova Hedwigia* 41: 89–125.
- Buck, W. R., and D. H. Vitt. 1986. Suggestions for a new familial classification of pleurocarpous mosses. *Taxon* 35: 21–60.
- Crosby, M. R., and R. E. Magill. 1981. A dictionary of mosses. Third printing. *Monogr. Syst. Bot. Missouri Bot. Gard.* 3: i–vii, 1–43.
- Crum, H. 1984. Notes on tropical American mosses. *Bryologist* 87: 203–216.
- Crum, H., and L. E. Anderson. 1967. The status of *Hylocomium splendens* var. *tenuis*. *Bryologist* 70: 98–101.
- . 1981. *Mosses of eastern North America*. New York: Columbia University Press.
- Fleischer, M. 1904–1923. *Die Musci der Flora von Buitenzorg*. Leiden: E. J. Brill.
- Gangulee, H.C. 1978. *Thuidium*. In *Mosses of eastern India and adjacent regions* 7: 1618–1649. Publ. by author, Calcutta.
- Gier, L. J. 1980 [1981]. A preliminary study of the Thuidiaceae (Musci) of Latin America. *J. Bryol.* 11: 253–309.
- Grout, A. J. 1928–1940. *Moss flora of North America north of Mexico*. Published by the author, New York & Newfane, VT.
- Hampe, E. 1867. Bryologische Mittheilungen aus dem Herbarium von E. Hampe. *Flora* 50: 65–80.
- . 1869. Musci frondosi a cl. H. Krause in Ecuador, Prov. Loja collecti. *Bot. Zeitung (Berlin)* 27: 433–437, 449–458.
- . 1872. Musci frondosi in insulis Ceylon et Borneo a Dr. Od. Beccari lecti. *Nuovo Giorn. Bot. Ital.* 4: 273–291.
- Hedwig, J. 1801. *Species muscorum frondosorum descriptae at tabulis aeneis LXXVII coloratis illustratae*. Leipzig: Barth.
- Mitten, W. 1868. A list of the Musci collected by the Rev. Thomas Powell in the Samoa or Navigator's Islands. *J. Linn. Soc., Bot.* 10: 166–195, pls. 5, 6.
- . 1869. Musci austro-americi, sive enumeratio muscorum omnium austro-americanorum mihi hucusque cognitorum, eorum praecipue in terris Amazonicis Andinisque Ricardo Spruceo lectorum. *J. Linn. Soc., Bot.* 12: 1–659.
- Noguchi, A. 1972. Musci Japonici IX. The Leskeaceae. *J. Hattori Bot. Lab.* 36: 499–529.
- Norris, D. H., and T. Koponen. 1985. Bryophyte flora of the Huon Peninsula, Papua New Guinea. VII. Trachypodaceae, Thuidiaceae and Meteoriaceae (Musci). *Acta Bot. Fennica* 131: 1–51.
- Robinson, H. 1968. Notes on bryophytes from the Himalayas and Assam. *Bryologist* 71: 82–97.
- . 1974. Additions to the genus *Taxiphyllum* (Hypnaceae, Musci). *Phytologia* 28: 64–66.
- Rohrer, J. R. 1985a. A phenetic and phylogenetic analysis of the Hylocomiaceae and Rhytidiaceae. *J. Hattori Bot. Lab.* 59: 185–240.
- . 1985b. A generic revision of the Hylocomiaceae. *J. Hattori Bot. Lab.* 59: 241–278.
- Schimper, W. P. 1855 [1856]. *Corollarium bryologiae europaeae, conspectum diagnosticum familiarum, generum et specierum, adnotationes novas atque emendationes complectens*. Stuttgart: E. Schweizerbart.
- . 1860. *Synopsis muscorum europaeorum praemissa introductione de elementis bryologicis tractante*. Stuttgart: E. Schweizerbart.
- . 1876. *Synopsis muscorum europaeorum*, ed. 2. Stuttgart: E. Schweizerbart.
- Scott, G. A. M., and I. G. Stone. 1976. *The mosses of southern Australia*. London: Academic Press.
- Sharp, A. J. 1933. Three new mosses from Tennessee. *Bryologist* 36: 20–23.
- Smith, A. J. E. 1978. *The moss flora of Britain and Ireland*. Cambridge: Cambridge University Press.
- Touw, A. 1976. A taxonomic revision of *Thuidium*, *Pelekium*, and *Rauarella* (Musci: Thuidiaceae) in Africa south of the Sahara. *Lindbergia* 3: 135–195.
- Touw, A., and L. Falter-van den Haak. 1989. A revision of the Australasian Thuidiaceae (Musci), with notes on species from adjacent regions. *J. Hattori Bot. Lab.* 67: 1–157.
- Watanabe, R. 1972. A revision of the family Thuidiaceae in Japan and adjacent areas. *J. Hattori Bot. Lab.* 36: 171–320.
- Wilson, P., and D. H. Norris. 1989. *Pseudoleskeella* in North America and Europe. *Bryologist* 92: 387–396.