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ACTA BOTANICA FENNICA

138

JAAKKO HYVÖNEN

A synopsis of genus *Pogonatum* (Polytrichaceae, Musci)

HELSINKIN YLIOPISTON KIRJASTO

30-11-1989

LUONNONTIETEIDEN KIRJASTO

HELSINKI 1989

ANNALES BOTANICI FENNICI ACTA BOTANICA FENNICA

Published by the Finnish Botanical Publishing Board, Helsinki

ANNALES BOTANICI FENNICI and ACTA BOTANICA FENNICA are international journals publishing botanical research articles (ANNALES, quarterly) or monographs (ACTA). The journals are open to Finnish and foreign botanists.

Publisher – The Finnish Botanical Publishing Board, an organ formed by the *Finnish Academy of Sciences and Letters, Societas Scientiarum Fennica, Societas pro Fauna et Flora Fennica* and *Societas Biologica Fennica Vanamo*.

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Distributor – The Academic Bookstore, P.O. Box 128, SF-00101 Helsinki, Finland. **Subscriptions** — Should be paid through the Distributor. The annual subscription for ANNALES is FIM 200 (or the equivalent) for 1990, for ACTA it depends on the number and size of the issues. **Exchange** – All correspondence concerning exchange should be sent to the Exchange Centre for Scientific Literature, Rauhankatu 15B, SF-00170 Helsinki, Finland. **Back issues** – Still available (from 1978 onwards) from the Distributor at reduced prices.

Manuscripts – Instructions for authors are included in the first issue of each volume of Annales.

Annales is indexed by the following data bases: Arct. Bibl., Biol. Abst., CABS (Current Awareness Biol. Sci.), Chem. Abstr., Curr. Cont. Ab & ES, Excerpt. Med., Field Crop Abstr., Forest. Abstr., Forest Prod. Abstr., Geo. Abstr., Geo. Ref., Hort. Abstr., Ind. Sci. Rev., Ocean. Abstr., Plant Breed. Abstr., Pollut. Abstr., Ref. Zh., Rev. Plant Path., Sci. Cit. Ind., Sel. Water Res. Abstr., Soils & Fert.

Acta is indexed in: Biol. Abstr., Chem. Abstr., Geo. Abstr., Geo.Ref., Ref. Zh., Soils & Fert., VITIS.

Suomen kasvitieteen julkaisu-toimikunnan perustajaseurojen jäsenet voivat tilata sarjat jatkoilauksena toimittajalta. Annalesin jäsen-tilaushinta 1990 on 120 mk. Tilaukset tehdään maksamalla tilaushinta julkaisu-toimikunnan postisiirtotilille 178494-3. Actan vuositilaushinta määräytyy vuosikerran sivumäärän mukaan ja laskutetaan vuoden lopussa. Vuosikertoja 1978–1982 on saatavissa alennettuun hintaan noutamalla toimittajalta tai ostamalla Tiedekirjasta, Kirkkokatu 14, 00170 Helsinki (p. 90-635 177)

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A synopsis of genus *Pogonatum* (Polytrichaceae, Musci)

JAAKKO HYVÖNEN

Hyvönen, J. 1989: A synopsis of genus *Pogonatum* (Polytrichaceae, Musci). — Acta Bot. Fennica 138:1–87. Helsinki. ISSN 0001-5369 ISBN 951-9469-32-X

The genus *Pogonatum* P. Beauv. is characterized by a mammillose exothecium, 32 compound peristome teeth and by the absence of stomata. As so delimited the genus comprises 52 species including those species formerly assigned to *Neopogonatum* Xu & Xiong, *Pseudatrichum* Reim., *Plagioracelopus* Smith Merrill and *Racelopus* Dozy & Molk. The relationship of *Pogonatum* to other genera of the Polytrichaceae is evaluated and a cladogram of the genus is presented. Several monophyletic groups within the genus are recognized. The genus is divided into four subgenera. Subg. *Alienum* Hyvönen includes only *Pogonatum volvatum* (C. Müll.) Par. Subg. *Dendroidea* (Schimp.) Hyvönen, *comb. nov.* consists of three species formerly assigned to the sections *Cephalotrichum* (C. Müll.) Besch. and *Dendroidea*. Subg. *Catharinella* (C. Müll.) Hyvönen, *comb. nov.* contains 31 species including the nine species formerly accommodated in sect. *Racelopus* Touw. These species form a monophyletic group but distinction at sectional level is not supported by the cladistic analysis. Subg. *Pogonatum* comprises 17 species. The taxonomy of all species is revised including 395 specific and infraspecific combinations in the genera *Neopogonatum*, *Plagioracelopus*, *Pogonatum*, *Pseudatrichum* and *Racelopus*. 130 new synonyms are presented along with the selection of 13 new lectotypes. *Pogonatum norrisii* Hyvönen is described as new to science, and short diagnoses of other species are given with notes on phylogeny and ecology. Distribution of all species is illustrated by maps and diagnostic characters by line drawings. Citations of relevant illustrations are given. A key for the genus is presented. Discussion of morphology and anatomy is restricted to those characters used to infer the phylogeny of the genus.

Key words: Bryophytes, cladistics, Musci, nomenclature, *Pogonatum*, Polytrichaceae, systematics, taxonomy

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I. INTRODUCTION

The present study of the genus *Pogonatum* P. Beauv. is not intended to be exhaustive and monographic. It is a preliminary study which will offer a taxonomically sound framework for further, more detailed studies of the largest and most diverse genus in the Polytrichaceae. My study has been disciplined by a rigorous uniformity of approach to each of the taxa represented.

The supplemented "Index muscorum"-files of the Missouri Botanical Garden (MO) list over 400 names within the genus *Pogonatum*, and I have attempted to study each of these names, except those transferred to other genera by previous authors. The results of previous revisions are generally accepted

except that I found all three species of *Neopogonatum* Xu & Xiong to be assignable to the highly variable *Pogonatum cirratum* (Sw.) Brid. The species assigned by Smith Merrill (1987) to the genera *Plagioracelopus* Smith Merrill, *Pseudatrichum* Reim. and *Racelopus* Dozy & Molk. are all incorporated in *Pogonatum*.

Some names, especially those with incomplete protologues, remain dubious because type specimens have not been located. This is particularly true of specimens in herbaria destroyed during World War II, including the collections studied by C. Müller (Halle), H. Reimers (Berlin) and Y. Horikawa (Hiroshima).

II. HISTORICAL OUTLINE

The genus *Pogonatum*, originally with 15 species, was separated from the conglomerate genus *Polytrichum* Hedw. by Palisot de Beauvois (1804). The genus was gradually enlarged by several authors, especially Müller (1848), Dozy & Molkenboer (1854–1870) and Mitten (1859, 1869). Early studies of the genus were frequently hampered by inadequate material and by lack of field studies. For these reasons the older species concepts were excessively narrow, and too many taxa were described. As early as 1847 Hampe emphasized the need for critical revision of the "exotic" species because he recognized that the number of species was much inflated. Brotherus (1925) in his treatment of the moss flora of the world, gives 158 species for the genus, and Wijk et al. (1967) list 182 species in their index (Smith 1971).

During the first half of the 20th century there were very few revisional studies either of the genus *Pogonatum* or of the Polytrichaceae in general. Dixon (1915, 1916, 1922, 1935) and Bartram (1939, 1949) studied SE Asian and American taxa in their floras of the mosses of several geographic areas, but they did not critically revise the work of the earlier authors. Gangulee (1969) extensively listed Indian species, but quite uncritically accepted almost all of the species described by earlier authors.

A foundation for modern studies of the family Polytrichaceae was laid by Smith (1971). He has continued studies on the family with many contributions (Smith 1972, 1974a, b, 1975a, b, 1976, Smith Merrill 1987). Recent revisional studies of *Pogonatum* are few (e.g. Frye & Duckering 1946, Touw 1986) and unfortunately partly remained unpublished (Cadée-Coenen 1965, Huffelen & Vries 1980). However, several regional studies of the family also include pertinent taxonomic results on *Pogonatum* (e.g. Osada 1965, Schiavone 1978). Recently Menzel (1986a, b, 1987) has thoroughly studied the genus in Latin America, and I have studied SE Asian species of the Polytrichaceae (Hyvönen 1986, 1989, Hyvönen & Lai 1989). Chinese taxa have been lately studied by Xu & Xiong (1982, 1984). The contributions by Long (1985) and De Sloover (1986) are the most comprehensive works to date on Arctic and African taxa of the family.

Subdivision of the genus has remained fairly stable with the large section *Pogonatum*, under a variety of names, incorporating most of the species. The section *Cephalotrichum*

(Müller 1848) was originally described by Bruch et al. (1844) as a new genus. The name is, however, illegitimate as it was already occupied by a genus of fungi. Sect. *Dendroidea* was described by Schimper (1860) to incorporate *P. urnigerum* (Hedw.) P. Beauv. along with *P. alpinum* (Hedw.) Roehl. (= *Polytrichastrum alpinum* (Hedw.) G.L. Sm.). Bruch et al. (1844), studying *Pogonatum nanum* (Hedw.) P. Beauv., noted that the columella is very short and without wings and the inner wall of the spore sac is fused to the columella. On these bases, they proposed section *Nana* to segregate that species. However, as stated by Smith (1971), it has not been ascertained whether the characteristic features of *P. nanum* are not found in any other species. Subsequent authors have variously treated the section, but Brotherus (1909, 1925) retained the section to include a group of very small species. Basing his classification primarily on habit, Mitten (1869) recognised only two sections of the genus *Pogonatum*. His section *Eupogonatum* incorporates the species of sect. *Cephalotrichum* along with species of similar habit and capsule. However, Mitten's classification groups together under *Eupogonatum* plants of radically different leaf structure. The section *Anasmogonium* was proposed by Mitten (1869), and followed by Brotherus (1909, 1925). That section includes species with an intensely mammillose exothecium, and with a soft general habit, mostly with contorted or curved leaves.

Smith (1971) followed Brotherus (1925) except that he incorporated section *Nana* under the section *Pogonatum*. Smith's (1971) other modifications of Brotherus (1925) are changes of the names (sect. *Anasmogonium* = sect. *Pogonatum*, sect. *Urnigera* Schimp. = sect. *Dendroidea*) following the rules of nomenclature. Section *Catharinella* (C. Müll.) Besch. was used by Smith (1972) as an additional group, while he evaluated the distribution of the family. A further addition was made by Touw (1986) when he reassigned the species of *Racelopus* Dozy & Molk., *Racelopodopsis* Thér. and *Pseudoracelopus* Broth. to the genus *Pogonatum* as sect. *Racelopus* (Dozy & Molk.) Touw. This was not accepted by Smith Merrill (1987), who assigned *Pogonatum marginatum* Mitt. and *P. rutteri* (Thér. & Dix.) Dix. to the new genus *Plagioracelopus*. He left the other species treated by Touw (1986) to *Racelopus*. He did not, however, make the formal new combinations.

III. MATERIAL AND METHODS

I studied ca. 3 650 specimens mainly from H, L, M, MO, NY and TNS with important additions from several other herbaria (see "Acknowledgements" for the complete list). All studied specimens when cited, are indicated with an exclamation mark "!" after the acronym of the herbarium, where the specimen is currently located. Type specimens lacking this mark are based only on published reports by earlier authors. A query before the acronym means that I am not certain if the specimen which I studied is that cited in the original protologue. Some specimens which I have not seen are also cited with a query before the acronym because I am uncertain of the present location of that specimen. Information of type specimens is primarily based on the data given on their attached labels. When pertinent additional data is given in the protologue, or the label is illeg-

ible, preference is given to the text of the protologue. Where data from apparent duplicates of the same collection deviate from each other, the data given on more duplicates, or the one with more accurate data, is given preference. A query indicates that given location is only assumed and not given by the label data. Some of the specimens studied are listed only when the number of type specimens cited is very small. These specimens are only representative and a detailed list of all specimens studied is available upon request. I ordinarily studied more than 20 specimens of each taxon except in the species of the *Racelopus* group — the number of specimens of these tiny plants available for the study is restricted and consequently less than 10 specimens were studied. Such species as *Pogonatum pergranulatum* Chen, *P. subfuscatum* Broth. and *P. minus* Xu &

Xiong are known only from the type material and accordingly only one or two specimens were studied of each species. However, some of the species (e.g. *P. perichaetiale* (Mont.) Jaeg., *P. cirratum* (Sw.) Brid., *P. neesii* (C. Müll.) Dozy) were, on the other hand, studied extensively, with the material consisting of over 100 specimens. Exsiccatae are not separated from other specimens and are not indicated in any special way. Some type specimens lack the information of the herbaria and in these cases synonymizations by earlier authors are accepted or a new synonymization is based only on the protologue. In the latter case a query in boldface “?” precedes the particular name. These synonymizations are ordinarily not discussed further in the text, but the identity of the plants has been so self-evident that synonymization is warranted.

All citations of literature have been verified according to the original sources with the following exceptions: Stafleu & Cowan (1979, 1983) was the source for citation of Mag. Encycl. 9. Ann. 5:289–330 by Palisot de Beauvois (1804) and *Muscologia britannica*, i–xxxv + 152 pp. Taylor, London by Hooker & Taylor (1818); Wijk et al. (1967) for the citations of Adans. ex Wallr., Fl. Crypt. Germ. 1. 1831; Cardot in Grand., Hist. Madag. 1915; Farn., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser. 2(2). 1892; Göpp. & Menge, Ber. Verh. K. Preuss. Ak. Wiss. Berlin 1853; Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1913(1). 1914; C. Müller, J. Mus. Godeffroy 3(6). 1874; Palisot de Beauvois, Mém. Soc. Linn. Paris 1. 1822; Röhm., Arch. Bot. 3:211. 1805; Thériot, Mem. Soc. Cub. Hist. Nat. “Felipe Poey” 15. 1941; and Röhl., Deutschl. Fl. Krypt. ed. 2(3). 1813; Smith (1971) for the citation of Bals.-Criv. & De Not., Prodr. Bryol. Mediolan. 1833 and Mont. in d’Orbigny, Dict. 8. 1847, and an unpublished list of names of mosses by Crosby and Magill (MO) for Chen, Sci. Exped. Qomolongma Reg. 1962.

A list of illustrations is given under each species. This is not comprehensive. I have not listed those figures which fail to illustrate the important diagnostic features of the species; thus many older figures of high standard are ignored.

The records of distribution are mainly based on specimens which I have studied. Those records based solely upon literature, are accompanied by a bibliographic citation. The geographical units are mainly political, supplemented with the larger units presented in Wijk et al (1962). The scheme of vegetation zones applied follows those of Hämet-Ahti et al. (1974) and Tuhkanen (1984).

Fig. 1 of *Pogonatum urnigerum* illustrates the most important parts of the plants as used in the text below. Terminology within the genus is fairly stable and most of the terms are self-evident. Certain points, however, need additional clarification and remarks. The leaf of almost all Polytrichaceae consists of a distal blade with ventral lamellae, well differentiated from the proximal, more or less widened sheath. Many authors have used the term “lamina” for the proximal part of the leaves. This is, however, not accepted here, because, as pointed out by Osada (1965), in the Polytrichaceae the sheath is probably homologous with the lamina of other mosses. However, it is appropriate to use the terms “lamina” and “laminal cells” for species with extremely reduced blade. The blade is usually serrate at the margins. Serration is normally formed of multicellular teeth, whose sharp apical cells have incrassate and strongly pigmented walls (Fig. 11B). Some species of *Pogonatum*, as well as most species of *Polytrichum* have a margin with single-celled teeth which are differentiated from adjacent marginal cells and seem embedded in the margin. The term “dentate” is reserved for this latter type of serration. The costa is the central part of leaf with conducting tissue and

steroid bands and it is, in most species, of very distinct structure. Marginal parts without ventral lamellae of most of the leaves are generally termed as “leaf-margins” or simply “margins”. These parts are usually easily distinguished from other parts, but in such species as *P. nudiusculum* Mitt. and *P. proliferum* (Griff.) Mitt., the distinction between blade and margin is arbitrary and in these cases the margins are defined as 3–5 marginal cell-rows of the blade. The apical cells of the ventral lamellae are in certain cases simply termed as “apical cells” or “apicals” where there is no chance of misunderstanding. The term is sometimes used for the apical cells of the marginal teeth but also in these cases the accurate meaning of the word is designated by the context.

In the key to the species as well as in the discussions, I have included descriptions of plant sizes — quite a variable character, for which I have generalized to the more common expression. The terms utilized (tiny, small, medium-sized and robust) should be understandable within the context of the family. They should, however, be defined. Tiny plants, such as *Pogonatum spinulosum* Mitt. (Fig. 13G), have only a few leaves on an inconspicuous stem. The setae and the capsules are the most conspicuous parts of these plants and, therefore, they are easily overlooked in the field when sterile. Small plants, such as *P. neglectum* (Hampe) Jaeg. (Fig. 4C), have a recognizable stem with several leaves but the setae and capsules remain the more conspicuous portion of the plant. Medium-sized and robust plants are larger with the stems of the robust plants exceeding 10 cm in length. The term slender is reserved for plants with distant and small leaves on a disproportionately long stem (*P. subfuscatum* Broth. and *P. rufisetum* Mitt.).

All specimens were soaked in ethanol (94%) and weak (ca. 0.5%) solution of KOH before microscopic study. Specimens soaked for a few minutes in both liquids will have their natural form. However, the time required for soaking varies to a great extent and species such as *Pogonatum pergranulatum* and *P. rufisetum* and some old specimens may disintegrate with excessive soaking.

To infer phylogeny is central to most schools of biosystematic study. For this purpose I have used cladistic analysis or, more precisely, manual Hennigian argumentation (Wiley 1981, Mishler & Churchill 1984). The basic concepts were presented almost 40 years ago by the German entomologist, Willi Hennig. The methods of this approach are so well known as to demand no elaborate explanations, but a condensed presentation of the method with definitions of its terminology is appropriate.

Botanical application of Hennigian cladistics was initiated by Koponen (1968) in his study of generic relationships of Mniaceae. Since then only a few bryologists have applied the methods. Koponen continued the study of Mniaceae (1973, 1980) and related groups (1982, 1988). Bremer (1981) and Churchill (1981) used cladistics to infer the phylogeny of the Grimmiaceae, and Mishler & Churchill (1984) with this method evaluated the relationships of major bryophyte lineages and those of other land plants. A further application of the method on a small scale is the study of the genus *Hymenodon* Hook.f. & Wils. (Rhizogoniaceae) by Karttunen & Bäck (1988).

Cladistics have repeatedly been criticized in the journal *Taxon* after publication of the introductory article by Bremer & Wanntrop (1978). Evaluation of “pros” and “cons” presented in the debate is out of place here, but it should be mentioned

that a large part of the criticism seems to have resulted from misunderstanding of the basic concepts of cladistics (Wanntrop 1983) or by inappropriate application of the methods in certain studies. However, I agree with Buck (1986) and Neff (1986), who stress the primary importance of character analysis as the basis for all phylogenetic studies.

The contribution of cladistics to taxonomy and systematics lies in its requirement that formally notified taxa should be demonstrably monophyletic (restricted to, and including all of the descendants of a common ancestor). Cladistic practise excludes paraphyletic groups — groups sharing a common ancestor but with that ancestry not exclusive. The basic idea of cladistics is that only shared, derived characters (termed synapomorphies) should be used to infer phylogenetic relationship. Thus, phylogenies based on overall (phenetic) similarity, including both primitive (termed plesiomorphies) and derived characters, are invalid. Consequently, the general problem in cladistic analysis is to identify apomorphies relevant at the hierarchical level under study. The character state considered to be a synapomorphy at one hierarchical level cannot be used in the separation of groups at a lower hierarchical level. For example, because I postulate that possession of ventral lamellae is a synapomorphy distinguishing the Polytrichaceae, the very same character cannot be used to segregate the genera of the family from each other.

It is apparent that rigorous study is necessary to determine the polarity of character states (to decide which of two characters may be postulated to be plesiomorphic and which is apomorphic). I have used the outgroup comparison method of Maddison et al. (1984). An outgroup is a putatively related

taxon other than, but at the same hierarchical level as the one being studied. In a pair of character states of the studied taxon, the one that is present also in the outgroup is assumed to be more primitive (plesiomorphic). It is obvious that efficient use of the outgroup comparison method requires a preliminary hypothesis of phylogeny at a higher hierarchical level. Fortunately, Maddison et al. (1984) described methods to obtain optimal results even when phylogenetic resolution of outgroups is poor. These methods are followed in this study. Convergent evolution is a special problem to cladistic analysis because it may produce similarities which must be considered analogous rather than homologous because they are derived from different ancestry by separate evolutionary routes. As discussed by Mishler & Churchill (1984) structural, developmental and positional features may be used to distinguish between homologous (synapomorphic) features and merely analogous features. Each hypothesis must, however, be tested against the general pattern obtained from the entire suite of characters and character states within the taxon. Consequently, cladistic analysis enables the testing of each inference of homology.

Cladistic studies will normally suggest several alternative evolutionary relationships between taxa because all assumed apomorphies are not congruent. In these cases, the most parsimonious solution is accepted. A parsimonious solution is one which includes the minimum number of homoplasies (similarities due to convergent evolution). Any presumption of a homoplasy should be carefully examined, with a search for alternate models of the phylogenetic scheme, both ingroup and outgroup.

IV. SPECIES CONCEPT

The Linnaean hierarchy is universally accepted as the basic framework in which to present taxonomic classification. Systematic biological classifications should, however, also reflect our interpretations of the genealogical relationship of the taxa. The species has long been accepted as the basic unit of systematics but precise definition of the word remains dubious and controversial. Biologists have, for decades, followed the biological species concept as put forward by Mayr (1970) and others. But it has become apparent that the concept is not universally appropriate. The biological species concept stresses reproductive isolation as the major factor maintaining independent lineages. The strict application of the concept on plants has, however, been problematic because of the complexity of the reproductive biology (Mishler & Donoghue 1982). In many bryophytes separate populations of a single species have long been isolated from each other, and yet they are indistinguishable morphologically (Schuster in Szweykowski 1984). For example, such species as *Pogonatum urnigerum* show striking uniformity over a broad geographic range on several continents. It seems that some bryophyte species maintain integrity

despite breeding isolation. Consequently, I prefer a phylogenetic, cladistic species concept like that of Mishler & Brandon (1987) to the classical biological one. The latter authors emphasize that all species concepts inherently include both grouping and ranking criteria. Much confusion has, in the past, resulted from failing to clearly define these two aspects (Mishler & Brandon 1987). In the previous chapter the rigorous requirement was outlined that all taxa should be monophyletic, i.e. held together by synapomorphies. Monophyletic groups are defined to include all and only descendants born in the same event. Thus for example, populations born independently by repeated hybridization of two taxa are not a monophyletic group (Mishler & Brandon 1987). The hierarchical ranking given to a group is so pragmatic that even in the bryophytes no one scheme of ranking can be considered universally acceptable. Species are the least inclusive monophyletic groups worthy of formal taxonomical recognition (Mishler 1988). In conclusion, it should be noted that, although formal taxonomic recognition is ordinarily given only to species, recognition of genetic variants, ecotypes etc. is not rejected. Some of these

might even be monophyletic but are too minor to be formally recognized (Mishler 1988).

It is acceptable taxonomic procedure to recognize a metasppecies, a species not defined by apomorphies (Donoghue 1985, Mishler 1988). It should be pointed out that further, more profound study of a metasppecies may reveal apomorphies, showing it to be monophyletic, or it may prove to be paraphyletic when some of the included lineages are revealed to share synapomorphies with other, related species. Consequently, formerly recognized metasppecies is abandoned as unworthy of taxonomic recognition. These entities with uncertain monophyly or not confirmed paraphyly should, however, be clearly distinguished from known monophyletic species (Donoghue 1985). The latter author proposed a nomenclatural convention that they should be distinguished by an asterisk (*), and I follow this convention. As pointed out by Mishler (1985), rigorous application of these cladistic methods would certainly mean a substantial lumping within certain bryophyte groups. I agree with Zander (1985) that many studies using traditional methods of alpha taxonomy are actually trying to solve problems at the population level. Nevertheless, this has probably been done far less in studies of the Polytrichaceae than with some other groups.

While classification should be natural (phylogenetic) redundancies and novelties should be mini-

mized without compromising information content (Wiley 1981). It is pragmatically necessary that species as the basic units used by non-taxonomists be sufficiently accurate that identification is possible without specialization and without the study of numerous specimens. However, this is an ideal that rarely, if ever, is consistently achieved even in a small group of organisms.

I have ordinarily avoided the recognition of mere geographical or ecological variants not defined by apomorphies. In these cases, identification to a sub-specific taxon would usually be based on locality data, and not on morphological features of the specimen. However, to meet the practical necessity for identification, I have twice recognized subspecies, and these result from the reduction of status of traditionally accepted species. Preservation of certain, traditionally accepted taxa as subspecies is done in order to give maximal information and to avoid premature taxonomic conclusions which might only further complicate the situation. I await evidence on whether these subspecific taxa are truly monophyletic — evidence which may require changes in the hierarchical level. In this paper the word subspecies is used as a purely technical taxonomical unit without further connotations. I use this category without a claim for validity of such unit in groups other than *Pogonatum*.

V. KEY TO THE SPECIES OF POGONATUM

Sterile specimens may be difficult to place in the proper genus in the Polytrichaceae. Some species of *Pogonatum* are more likely to be mistaken as species of other genera than to be mixed with other species of *Pogonatum*. A key to the entire family is, however, beyond the scope of this paper. An artificial key for specimens with sporophytes is given by Smith (1971), and regional keys are provided in such works as Osada (1966), Schiavone (1978), Long (1985), De

Sloover (1986), Hyvönen (1986, 1989), Schultze-Motel & Menzel (1987) and Hyvönen & Lai (1989). In the following key, characters of gametophytes are given preference and this applies even to those species assigned to sect. *Racelopus* by Touw (1986), species easily distinguished by their scabrous setae. The key is rather cumbersome, partly because of my intention of dealing with infraspecific variability.

- | | | | |
|--|-------------------------------|---|-----------------------------------|
| 1. Leaf-margins entire or with few small, indistinct teeth | 2 | 4. All laminal cells narrow and elongated | 35. <i>P. piliferum</i> p. 42 |
| 1. Leaf-margins at least apically serrate or dentate ... | 13 | 5. Plants tiny, protonema persistent | 6 |
| 2. Leaves without lamellae | 3 | 5. Plants small or large, protonema not persistent ... | 9 |
| 2. Leaves with abundant ventral lamellae | 5 | 6. Blade reduced | 6. <i>P. pensilvanicum</i> p. 18 |
| 3. Upper laminal cells with incrassate walls, vestiges of ventral lamellae sometimes present | 30. <i>P. misimense</i> p. 40 | 6. Blade well developed | 7 |
| 3. All cells with thin walls | 4 | 7. Apical cells of lamellae with very small lumen and extremely incrassate walls | 38. <i>P. brachyphyllum</i> p. 45 |
| 4. Upper laminal cells broadly rectangular to isodiametric | 33. <i>P. petelotii</i> p. 41 | 7. Apical cells with thin or firm walls | 8 |
| | | 8. Sheaths of leaves with indistinct shoulders (southern Africa) | 39. <i>P. capense</i> p. 47 |

8. Sheaths of leaves with distinct shoulders (western Eurasia) 37. *P. nanum* p. 44
9. Apical cells of lamellae coarsely papillose 2. *P. urnigerum* p. 9
9. Apical cells of lamellae essentially smooth 10
10. Leaf apices gradually narrowed to sharp apex 4. *P. perichaetiale* p. 13
10. Apices gradually narrowed or rounded 11
11. Blade narrow, apical cells of lamellae irregularly crenate as seen in side view 48. *P. minus* p. 56
11. Blade wide, as wide as sheath or only slightly narrower, apical cells regularly crenate as seen in side view .. 12
12. Sheaths of leaves with indistinct shoulders (southern Africa) 39. *P. capense* p. 47
12. Sheaths of leaves with distinct shoulders (western Eurasia) 37. *P. nanum* p. 44
13. Leaves essentially without ventral lamellae or with the lamellae restricted to central part of leaves 14
13. Leaves with abundant lamellae 25
14. Plants tiny, with inconspicuous stem, protonema persistent 15
14. Plants small to large, with well developed stem, protonema fugacious 18
15. Few ventral lamellae present in apical part of leaves .. 29. *P. neo-caledonicum* p. 40
15. Leaves totally without lamellae 16
16. Cells in upper part of leaves with conspicuous cuticular papillae 40. *P. spinulosum* p. 47
16. Leaf-cells essentially smooth 17
17. Lower leaves broadly ovate to circular, leaves without stereid bands 34. *P. camusii* p. 41
17. Lower leaves triangular, leaves with stereid bands 32. *P. iwatsukii* p. 41
18. Leaf-margins bi- to multistratose, leaves totally devoid of ventral lamellae 27. *P. marginatum* p. 39
18. Leaf-margins unistratose, ventral lamellae present or absent 19
19. Leaves totally devoid of lamellae 20
19. Leaves with at least some ventral lamellae 21
20. Plants anisophyllous, stems over 2 1/2 cm long, leaves gradually narrowed to acute apex 28. *P. rutteri* p. 40
20. Plants isophyllous, stems less than 2 1/2 cm long, leaves abruptly narrowed to obtuse or widely acute apex 31. *P. philippinense* p. 40
21. Leaf-margins with small or obtuse teeth 22
21. Leaf-margins with distinct sharp teeth 23
22. Dorsal stereid band of leaves very wide, plants small to medium-sized with proportionally short stem ... 51. *P. congolense* p. 58
22. Dorsal stereid band of leaves narrow, plants small and slender 23. *P. subfuscatum* p. 36
23. Leaves with only 15 or less (rarely more) ventral lamellae 24. *P. proliferum* p. 37
23. Ventral lamellae more than 20 per leaf 24
24. Dorsal cells of blade ca. 10–20 μm \varnothing , dorsal teeth on blade common 17. *P. nudiusculum* p. 29
24. Dorsal cells of blade ca. 14–40 μm \varnothing , dorsal teeth on blade absent 25. *P. semipellucidum* p. 38
25. Apical cells of lamellae coarsely papillose 26
25. Apical cells smooth or finely papillose 28
26. Apical cells of lamellae regularly geminate, lamellae mostly 2–3 cells high 15. *P. japonicum* p. 27
26. Apical cells of lamellae solitary, lamellae mostly over 4 cells high 27
27. Apical cells of lamellae more or less convex (Fig. 1B) 2. *P. urnigerum* p. 9
27. Apical cells of lamellae flat in cross-section (Fig. 2E) ... 3. *P. dentatum* p. 11
28. Apical cells of lamellae with all cell-walls extremely incrassate 4. *P. perichaetiale* p. 13
28. Apical cells of lamellae with thin walls or with only the outer wall incrassate 29
29. Lamellae essentially straight as seen in side view ... 30
29. Lamellae more or less crenate as seen in side view 38
30. Cells of lamellae without geminations 31
30. Cells of lamellae with some geminations 36
31. Leaves tightly appressed to stem when dry 1. *P. volvatum* p. 9
31. Leaves contorted or loosely incurved when dry 32
32. Dorsal teeth numerous on costa, marginal teeth fairly small, plants generally small, rarely medium-sized 33
32. Dorsal teeth few on costa, marginal teeth sharp and distinct, plants robust, rarely medium-sized 35
33. Blade of leaves gradually narrowed to sharp apex (Fig. 14C) 41. *P. norrisii* p. 48
33. Apices of leaves broadly acute (Fig. 12A) 34
34. Leaves with widened sheath, capsules mostly terete, protonema persistent, at least some apical cells of lamellae finely papillose 36. *P. aloides* p. 42
34. Sheath not much wider than blade, capsule plicate, protonema fugacious, apical cells of lamellae smooth 52. *P. subulatum* p. 58
35. Dorsal stereid band of costa with extremely incrassate cell-walls, plants robust, margins mostly unistratose, dorsal cells of blade transversely ovate (Africa) 19. *P. convolutum* p. 33
35. Both dorsal and ventral stereid bands with extremely incrassate cell-walls, plants small to robust, margins mostly bistratose, dorsal cells of blade with small, round lumens (Australasia) 18. *P. cirratum* p. 30
36. Dorsal cells of blade with firm but not incrassate walls (Fig. 8D), lamellae often with subapical geminations 16. *P. fastigiatum* p. 29
36. Dorsal cells of blade with transversely ovate or round lumen, lamellae without subapical geminations 37
37. Dorsal stereid band with extremely incrassate cell-walls, plants robust, dorsal cells of blade transversely ovate (Africa) 19. *P. convolutum* p. 33
37. Both dorsal and ventral stereid band with extremely incrassate cell-walls, plants small to robust, dorsal cells of blade with small, round lumens (Australasia) 18. *P. cirratum* p. 30
38. At least some apical cells of lamellae geminate 39
38. Apical cells not geminate 52
39. Apical cells irregularly crenate as seen in side view 40
39. Apical cells regularly crenate 45
40. Leaves with very wide and strong dorsal stereid band (Fig. 7G), blade wide 13. *P. otaruense* p. 25
40. Dorsal stereid band and blade narrowed (Fig. 10B) 41
41. Margins serrate with sharp distinct teeth 21. *P. pergranulatum* p. 36
41. Marginal teeth small and rounded (Fig. 17A) ... 42
42. Dorsal teeth on costa numerous (Africa) 45. *P. gracilifolium* p. 53
42. Dorsal teeth on costa few (SE Asia, Australia and Oceania) 43
43. Gemination of apical cells of lamellae common, apicals

- not retuse 46. *P. tahitense* p. 53
43. Leaves very narrow, apical geminations rare 44
44. Some apicals retuse 47. *P. tubulosum* p. 55
44. No retuse apicals present, blade reduced
..... 48. *P. minus* p. 56
45. Some of the apical cells of lamellae retuse
..... 12. *P. nipponicum* p. 25
45. Apical cells of lamellae never retuse 46
46. Plants with small and reduced blade 47
46. Blade wide and well developed 48
47. Protonema persistent, plants tiny with only few leaves,
blade extremely reduced with less than 15 lamellae, apical
cells of lamellae not consistently geminate
..... 6. *P. pensilvanicum* p. 18
47. Protonema fugacious, plants small, blade distinct with
more than 20 lamellae, apical cells of lamellae mostly
geminate 7. *P. neglectum* p. 19
48. Apical cells of lamellae with thin walls, not very
high 49
48. Apical cells with incrassate outer wall, much higher
than long 50
49. Plants robust, practically all apical cells geminate
..... 9. *P. procerum* p. 21
49. Plants medium-sized, only few apical cells geminate ..
..... 5. *P. tortile* p. 16
50. Apical cells of the lamellae peculiarly bottle-shaped
(Fig. 6H) (Asia) 11. *P. microstomum* p. 24
50. Apical cells of the lamellae high (Fig. 6D) (Ameri-
ca) 51
51. Leaves tightly appressed when dry (Fig. 6A), sheaths of
leaves with distinct shoulders, mostly entire, blade nor-
mally with clear basal constriction, apical cells always
with incrassate outer wall 10. *P. comosum* p. 22
51. Leaves loosely curved when dry (Fig. 5D), sheaths of
leaves narrow and without shoulders, mostly serrate by
margins, blade without or with only an inconspicuous
basal constriction, outer wall of apical cells of lamellae
firm or slightly incrassate 8. *P. campylocarpum* p. 19
52. Apical cells of lamellae irregularly crenate as seen in
side view, plants small with wide and firm leaves
..... 14. *P. microphyllum* p. 25
52. Apical cells regularly crenate, plants small to medi-
um-sized, leaves firm, incurved or contorted 53
53. Apical cells of lamellae retuse or distally widened in cross-
section 54
53. Apical cells never retuse 57
54. Apical cells of lamellae in cross-section much wider
than lower cells 43. *P. inflexum* p. 52
54. Apical cells of lamellae not much wider than lower
cells 55
55. Most apical cells convex with only few retuse cells, upper
margin of lamellae regularly and shallowly crenate or es-
sentially straight 36. *P. aloides* p. 42
55. At least some apical cells distinctly retuse, upper margin
of lamellae deeply crenate 56
56. Leaves very narrow, dorsal teeth on costa very few,
apical cells only partly retuse, marginal teeth very
small 47. *P. tubulosum* p. 55
56. Dorsal teeth on costa normally numerous, most of the
apical cells retuse, marginal teeth distinct
..... 42. *P. neesii* p. 50
57. Marginal teeth large and sharp, sheath-margins serrate or
entire 58
57. Marginal teeth fairly small, sheath-margins entire.... 59
58. Leaves delicate and distinctly contorted when dry,
lamellae low, sheath margins dentate, sheath without
shoulders 20. *P. contortum* p. 34
58. Leaves firm and appressed when dry, lamellae fairly
high, apical cells high with incrassate outer wall,
sheath with distinct shoulders
..... 10. *P. comosum* p. 22
59. Dorsal teeth on costa numerous 60
59. Dorsal teeth on costa few 61
60. Leaves with widened sheath, capsules mostly terete,
protonema persistent, at least some apical cells of
lamellae finely papillose..... 36. *P. aloides* p. 42
60. Sheath not much wider than blade, capsule plicate,
protonema fugacious, apical cells of lamellae
smooth 52. *P. subulatum* p. 58
61. Dorsal cells of blade subquadrate with thin walls
..... 44. *P. patulum* p. 53
61. Dorsal cells of blade transversely ovate, with incrassate
transverse walls 62
62. Marginal teeth indistinct to essentially absent, pro-
tonema persistent 63
62. Marginal teeth distinct, protonema not persistent 64
63. Sheaths of leaves with indistinct shoulders
..... 39. *P. capense* p. 47
63. Sheaths of leaves with distinct shoulders
..... 37. *P. nanum* p. 44
64. Plants slender, leaves distant and small, very narrow,
stereid bands and central cells with extremely incre-
sate walls 22. *P. rufisetum* p. 36
64. Plants medium-sized with more or less crowded
leaves, central cells with firm to thin walls, cell-walls
of stereid bands firm and if extremely incrassate this
is restricted to the cells of the dorsal band ... 65
65. Sheath of leaves widened (Central and South America)
..... 5. *P. tortile* p. 16
65. Sheath of leaves essentially not wider than blade (Austra-
lasia and Africa) 66
66. Dorsal stereid band with extremely incrassate cell-walls
(Australasia) 26. *P. subtortile* p. 39
66. Dorsal stereid band with firm but not extremely in-
crassate cell-walls (Africa) 67
67. Leaves incurved when dry, unistratose margins narrow
..... 49. *P. belangeri* p. 56
67. Leaves contorted when dry, unistratose margins wide
..... 50. *P. usambaricum* p. 58

VI. GENUS POGONATUM P. Beauv.

Mag. Encycl. 9. Ann. 5:329. — Type: *Pogonatum aloides* (Hedw.) P. Beauv. (*Polytrichum aloides* Hedw.), lectotype vide Smith (1971).

The discussion on subdivision of the genus is given in the chapter on Phylogeny and generic relationships.

Subgenus ALIENUM Hyvönen, *subg. nov.*

Plantae simplices; dense folioae; foliis siccis canaliculatis, erectis, marginibus dentatis; lamellae 4–5 cellulas altae, a latere visis integris. Capsula cylindrica, oblonga, cellulis exothecii mammillatis; peristomii dentes 32, compositi; calyptra villosa.

Type: *Pogonatum volvatum* (C. Müll.) Par. (*Polytrichum volvatum* C. Müll.), holotype.

1. *Pogonatum volvatum* (C. Müll.) Par. (Figs. 1F–H, 23 – map)

Ind. Bryol. 990. 1898. — *Polytrichum volvatum* C. Müll., Bull. Herb. Boissier 5:177. 1897. — Type: Guatemala, Cantel Sa. Catharina, X.1876 Bernoulli & Cario 121 (GOET!, iso-type).

Pogonatum alienum G.L. Sm., Bryologist 78:480. 1975 (1976), *syn. nov.* — *P. inclinans* Mitt. ex G.L. Sm., Bryologist 78:480. 1975 (1976), nom. nud. in synonym. — Type: Guatemala, Godman & Salvin (NY!, holotype).

Smith (1975b) described *Pogonatum alienum* apparently without having seen the type specimen of *P. volvatum*. This latter species, described by Carl Müller and based on a specimen collected in Guatemala, proved to be conspecific with *P. alienum*. Although Bartram (1949) suspected *P. volvatum* to be conspecific with *P. procerum* (Lindb.) Schimp. in Jaeg., I find the two species to be readily distinguished from each other. *P. volvatum* more closely resembles *Polytrichastrum* G.L. Sm. than other species of *Pogonatum*. Its leaves are unicellular dentate and not serrate with multicellular teeth — the latter feature is typical for almost all other species of *Pogonatum*. In habit it might easily be mistaken as *P. comosum* (C. Müll.) Mitt. as both species have crowded, firm leaves and long, terete capsules. The high and notched, normally geminate apical cells of the lamellae and serrate leaf-margins of the latter are, however, easily seen diagnostic characters. In *P. volvatum* the apical cells of the lamellae are very slightly smaller than other cells, and the lamellae have an essentially straight upper margin as seen in side view (Fig. 1F).

According to Smith (1975b), *P. volvatum* has been collected on bare roadsides and similar open habitats at 2 100–3 000 m.

Illustrations — Smith 1975b (as *Pogonatum alienum*): 481 (figs. 1–14).

Distribution — Am 2: Guatemala, Mexico.

Specimens examined (representative) — Am 2: GUATEMALA. Quiche: 5 km E of Los Cinquentos, highway between Chimaltenango and Quetzaltenango, 2 500 m, 25.1.1974 Richards, L.O. Williams & T.P. Williams 2938 (CANM!, paratype of *P. alienum*). — MEXICO: Sacre Monte, Amecameca, 8 500 ft., 11.IX.1908 Pringle 15262 (MO!).

Subgenus DENDROIDEA (Schimp.) Hyvönen, *comb. nov.*

Pogonatum sect. *Dendroidea* Schimp., Coroll. Bryol. Eur. 90. 1856. — *Pogonatum* C. *Urnigera* B.S.G., Bryol. Eur. 4:251. 1844. — *Pogonatum* sect. *Urnigera* (B.S.G.) Schimp., Syn. 440. 1860. — *Pogonatum* [subg.?] C. *Urnigera* (Schimp.) Limpr., Laubm. Deutschl. 2:610. 1893. — Type: *Pogonatum urnigerum* (Hedw.) P. Beauv. (*Polytrichum urnigerum* Hedw.), lectotype, vide Smith (1971).

Cephalotrichum B.S.G., Bryol. Eur. 4:248. 1844, hom. illeg. — *Polytrichum* sect. *Cephalotrichum* C. Müll., Syn. Musc. Frond. 1:205. 1848. — *Pogonatum* sect. *Eupogonatum* Mitt., J. Linn. Soc., Bot. 12:612. 1869, nom. inval. — *Pogonatum* sect. *Cephalotrichum* (C. Müll.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:206. 1872. — *Pogonatum* subg. (?) *Cephalotrichum* (C. Müll.) G. Roth, Eur. Laubm. 2:257. 1904. — Type: *Pogonatum oligodus* (C. Müll.) Mitt. (*Polytrichum oligodus* Kunze ex C. Müll.), lectotype, vide Smith (1971).

Trichopilum Schimp. ex C. Müll., Nuovo Giorn. Bot. Ital. n. s. 4:166. 1897. — Type: *Trichopilum polycarpum* Schimp. ex C. Müll. (*Pogonatum polycarpum* (C. Müll.) Par.), holotype.

2. *Pogonatum urnigerum* (Hedw.) P. Beauv. (Figs. 1A–E, 23 – map.)

Prodr. Aetheogam. 85. 1805. — *Polytrichum urnigerum* L. ex Hedw., Spec. Musc. 100. 22:5–7. 1801. — Type: Europe?

Polytrichum pulverulentum Reynier ex Hedw., Spec. Musc. 91. 1801. — *Pogonatum pulverulentum* (Hedw.) P. Beauv., Prodr. Aetheogam. 84. 1805. — *P. urnigerum* var. *pulverulentum* (Hedw.) Brid., Bryol. Univ. 2:126. 1827. — Type: Switzerland. Vaud: Helvetia prope Lausannam in silvaticis et glareosis ad fossarum viarumque cavarum margines solitarium. — Synonymized by Bridel (1805), cf. Wijk et al. (1967).

Polytrichum urnigerum var. *humile* Wahlenb. in Brid., Mant. Musc. 199. 1819. — *Pogonatum urnigerum* var. *humile* (Wahlenb.) Brid., Bryol. Univ. 2:126. 1827. — Type: Sweden?, Wahlenberg?. — Synonymized by Bruch et al. (1844).

Pogonatum urnigerum var. *crassum* B.S.G., Bryol. Eur. 4:252. 1844, *syn. nov.* — Type: Germany?, auf dem Hohneck, 1837 Schimper (BM!, holotype).

Pogonatum himalayanicum Mitt., J. Linn. Soc., Bot. Suppl. 1:151. 1859. — Type: India, in Himalaya boreali-occident., Royle (NY!, lectot. nov.); Thomson 1192 (L!, syntype). — Synonymized by Osada (1965).

?*Pogonatum urnigerum* var. *humile* Kickx, Fl. Crypt. Flandres 1:115. 1867, hom. illeg. — Type: France, Brébisson, Mousses de la Normandie fasc. 2:43 (specim. sinistr.).

Polytrichum urnigerum var. *tetragonum* Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9:136. 1868, *syn. nov.* — *Pogonatum urnigerum* var. *tetragonum* (Lindb.) Par., Ind. Bryol. 990. 1898. — Type: Finland. Ostrobotnia australis: Karijoki (Bötom), 1860 Malmgren (H-SOL!, holotype).

Polytrichum wallisii C. Müll., Linnaea 37:171. 1872. — *Pogonatum wallisii* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 260. 1875 (Adumbratio 1:722). — Type: Philippines, Luzon, Wallis 1870. Herb. C. Müll. (H-BR!), lectotype, vide Hyvönen 1986; JE!, NY, isolectotypes). — Synonymized by Smith (1971).

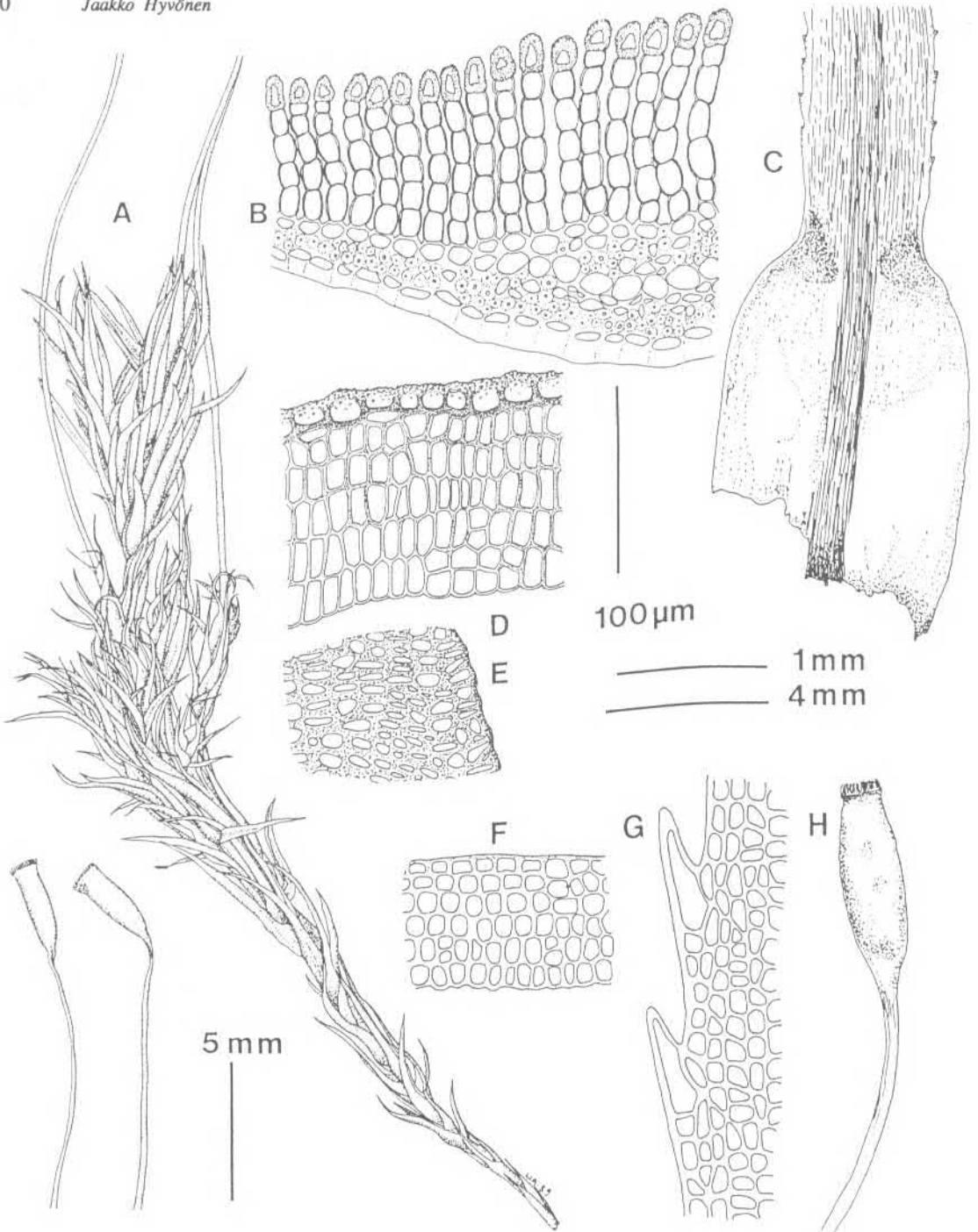


Fig. 1A–H. — A–E: *Pogonatum urnigerum*. A. Habit (Rusinska 29.V.1979, H), B. Leaf cross-section, C. Sheath and basal part of blade with hinge-tissue, D. Lamella in side view and E. Cells of hinge-tissue (Mundua 125, H). — F–H: *P. volvatum*. F. Lamella in side view, G. Margin of blade and H. Capsule (Williams et al. 41506, MO). — Use the 100 µm scale for B and D–G, 1 mm scale for C, 4 mm scale for H, and 5 mm scale for A. Habit figures of all species are drawn from dry specimens if not stated otherwise.

Pogonatum urnigerum var. *isangense* Besch., Ann. Sci. Nat. Bot. sér. 7, 15:70. 1892, *syn. nov.* — Type: China. Yunnan: Tsang-chan, 4 000 m, 29.VIII.1889 *Delavay 4046* (PCI, isotype).

Polytrichum microdendron C. Müll., Nuov. Giorn. Bot. Ital. n. s. 3:93. 1896. — *Pogonatum microdendron* (C. Müll.) Par., Ind. Bryol. 983. 1898. — Type: China. Shaanxi: N Shaanxi, in monte Thae-pei-san, VIII.1896 *Giraldi* (C. Müller 2197) (H-BR!, isotype). — Synonymized by Brotherus (1909).

Polytrichum polythamnium C. Müll., Nuov. Giorn. Bot. Ital. n. s. 3:93. 1896. — *Pogonatum polythamnium* (C. Müll.) Par., Ind. Bryol. 986. 1898. — Type: China. Shaanxi: N Shaanxi, in monte Kuan-tou-san, VII.1894 *Giraldi* (C. Müller 906) (FI!, H-BR!, M!, isotypes). — Synonymized by Brotherus (1909).

Polytrichum thelicarpum C. Müll., Nuov. Giorn. Bot. Ital. n. s. 3:94. 1896. — *Pogonatum thelicarpum* (C. Müll.) Par., Ind. Bryol. 988. 1898. — Type: China. Shaanxi: N Shaanxi, ad latera montis Thae-pei-san, VIII.1894 *Giraldi* (C. Müller 905) (FI!, syntype); in loco dicto Zu-lu, VIII.1894 *Giraldi* (C. Müller 1048) (FI!, M!, syntypes). — Synonymized by Salmon (1900).

?*Pogonatum urnigerum* var. *falcatum* Heufl. ex Torre & Sarnth., Fl. Tirol 5:423. 1904, *syn. nov.* — Type: Austria. Tirol: Innsbruck, Glungezer.

Pogonatum urnigerum var. *subintegrifolium* H. Arn. & C. Jens., Moose Sarekgebietes 137. 1907. — *Pogonatum urnigerum* var. *subintegrifolium* (H. Arn. & C. Jens.) Möller, Ark. Bot. 16(3): 69. 1919. — Type: Sweden. Lule Lappmark: Sarek, Rapadalen, Pellorippe, 29.VII.1902 *Jensen & Arnell*; Pärtefjäll, 16.VII.1902 *Jensen & Arnell* (BM, C!, syntypes). — Synonymized by Long (1985).

Pogonatum afrournerum Biz., Acta Bot. Acad. Sci. Hung. 18:18. 6:1–3, 1'–3'. 1973. — Type: Cameroun, Cameroun occidental, sur les arbres d'une forêt dense au bord du lac Barombi Mbo, *Balázs 73*. — Synonymized by De Sloover (1986).

Pogonatum urnigerum is the most widespread species of the genus. It is found in cool areas of most of northern Eurasia and North America and it occurs in scattered high mountain localities in Africa, south-east Asia and Papua New Guinea.

It is not surprising that a plant with so wide a range is highly variable and the variants have been described under a variety of names. *Pogonatum urnigerum* is especially variable in size, pattern of branching and in dentation of leaf margin. Additionally, the form of apical cells of the lamellae also show some variation. I have, however, not found any correlated suite of character variability which would justify the segregation of subspecific taxa.

The papillose apical cells of the lamellae of *Pogonatum urnigerum* allow comparison with only two other species: *P. dentatum* (Brid.) Brid. and *P. japonicum* Sull. & Lesq. Differentiation of these three species is presented in conjunction with the discussion of the latter two. *P. urnigerum* may also be confused with *Polytrichastrum alpinum*, another plant with papillose apical cells of the lamellae. *P. alpinum*, however, has elongate papillae on highly incrassate distal walls of apical cells of the lamellae,

and this contrasts with the round papillae of *Pogonatum urnigerum*. The distal walls of the apical cells in the latter species are only slightly more incrassate than other walls.

Many Himalayan specimens of *Pogonatum urnigerum* are fairly robust, and specimens from Africa and New Guinea may even approach 20 cm in height. The type material of *P. himalayanum* contains sterile stems of *P. microstomum* (Schwaegr.) Brid., along with fertile stems of another *Pogonatum*. This latter plant conforms closely to Mitten's description of *P. himalayanum* and, except for its robust size, it does not differ from *P. urnigerum*. I therefore follow Osada (1965) who reduced *P. himalayanum* to synonymy under *P. urnigerum*.

While the urn of *Pogonatum urnigerum* is typically terete, some specimens may have plicate capsules. Similar variation in capsule form occurs in some east Asian species, such as *P. cirratum* and *P. neesii*. Specimens with plicate capsules show no other distinctions from *P. urnigerum* and consequently they are not recognized taxonomically.

Pogonatum urnigerum has been collected mostly on open ground as well as from soil-covered rocks and cliffs from sea level to above 4 000 m.

Illustrations — Grout 1937: pl. 59A; Zanten 1964: pl. XXXIII (fig. 5a–d as *Pogonatum wallisii*); Nyholm 1969: 671 (fig. 438); Osada 1965: 180 (fig. 3m–u); Gangulee 1969: 146 (fig. 66); Crum & Anderson 1981: 1265 (fig. 628I–P); Smith A.J.E. 1978: 98 (fig. 38, 13–18); Li 1985: 447 (fig. 193: 12–15); Long 1985: 26 (fig. 7); De Sloover 1986: 269 (figs. 142–163); Hyvönen 1986: 123 (fig. 9); Noguchi 1987: 31 (fig. 11d); Eddy 1988: 38 (fig. 26); Hyvönen 1989: 577 (fig. 4A).

Distribution — Eur: Austria, Czechoslovakia, Denmark, Finland, France, Germany, Great Britain, Hungary, Iceland, Italy, Netherlands, Norway, Poland, Portugal (Azores), Romania, Spain, Sweden, Switzerland, USSR, Yugoslavia; As 1: USSR; As 2: China, Japan, Korea, Mongolia; As 3: Bhutan, India, Nepal, Sikkim, Sri Lanka; As 4: Indonesia, Papua New Guinea, Philippines; Afr 2: Cameroun, Ruanda, Tanzania, Uganda, Zaire; Am 1: Canada, USA.

3. *Pogonatum dentatum* (Brid.) Brid. (Figs. 2A–E, 24 – map)

Bryol. Univ. 2:122. 1827. — *Polytrichum dentatum* Menz. ex Brid., J. Bot. (Schrad.) 1800 (1): 287. 1801. — *Pogonatum capillare* var. *dentatum* (Brid.) G. Roth, Eur. Laubm. 2:259. 1904. — Type: Western North America, *Menzies* (E!, holotype).

Polytrichum capillare Michx., Fl. Boreali-Americana 2:294. 1803. — *Pogonatum yuccaeefolium* P. Beauv., Prodr. Aetheogam. 85. 1805, nom. illeg. superfl. — *P. capillare* (Michx.) Brid., Bryol. Univ. 2:127. 1827. — *P. urnigerum* var. *capillare* (Michx.) Hartm., Handb. Skand. Fl., ed. 3:286. 1838. — *Polytrichum urnigerum* subsp. *capillare* (Michx.) Albrecht, J. Bot. 72:104. 1934. — *Pogonatum urnigerum* subsp. *capillare* (Michx.) Albrecht ex Podp., Consp. Musc. Eur. 62. 1954, nom. inval. in synon. err. pro *Polytrichum*

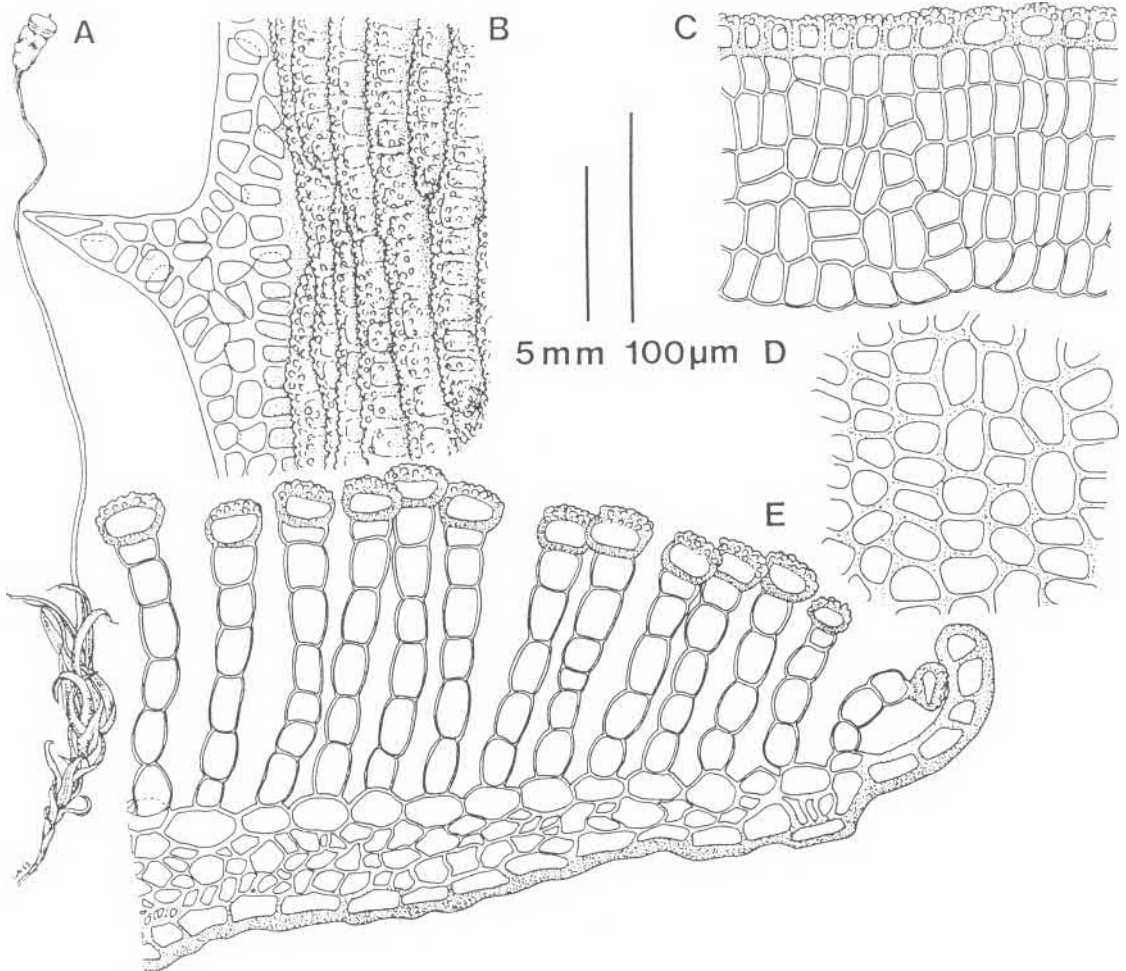


Fig. 2A-E. *Pogonatum dentatum*. A. Habit, B. Leaf-margin as seen above, C. Lamella in side view, D. Dorsal cells of blade and E. Leaf cross-section. — A-C and E (Bridgland 81-018, H), D (Norris 54479, H). Use the 5 mm scale for A, and the 100 µm scale for B-E.

urnigerum ssp. *capillare* (Michx.) Albrecht. — Type: Canada (PC!, holotype). — Synonymized by Crum et al. (1973) and Crum & Anderson (1981).

?*Polytrichum capillare* var. *minus* Wahlenb., Fl. Lapp. 348. 1812. — *Pogonatum capillare* var. *minus* (Wahlenb.) Par., Ind. Bryol. 979. 1898. — *Pogonatum dentatum* var. *minus* (Wahlenb.) Hag., Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1913(1): 32. 1914. — *Polytrichum wahlenbergii* Kindb., Rev. Bryol. 21:37. 1894, nom. nud. — *Pogonatum wahlenbergii* Kindb. ex G. Roth, Eur. Laubm. 2:258. 1904. — Type: Finland. Lappland: ?Kyro. — Synonymized by Long (1985).

Pogonatum intertextum Brid., Bryol. Univ. 2:742. 1827, *syn. nov.* — Type: Canada, New Foundland (in insula Terre Neuve) (B!, holotype; ?G!, isotype).

?*Pogonatum longidens* Ångstr., Bot. Not. 1852: 34. 1852, *syn. nov.* — Type: Finland (Sweden?), ad flumem Tor-nense, *Laestadius*.

?*Polytrichum loricalyx* C. Müll., Bot. Centralbl. 16:92. 1883, *syn. nov.* — *Pogonatum loricalyx* (C. Müll.) Par., Ind. Bryol. 982. 1898. — Type: USSR. Far East: Peninsula Tschutschica, 24.VIII.1881 *Pootén*.

?*Polytrichum loricalyx* var. *brachypodum* C. Müll., Bot. Centralbl. 16:93. 1883, *syn. nov.* — *Pogonatum loricalyx* var. *brachypodum* (C. Müll.) Par., Ind. Bryol. 982. 1898. — Type: USSR. Far East: Peninsula Tschutschica, VIII.1881 *St. Lorenzbai*.

?*Polytrichum micro-capillare* C. Müll., Bot. Centralbl. 16:91. 1883, *syn. nov.* — *Pogonatum micro-capillare* (C. Müll.) Par., Ind. Bryol. 983. 1898. — Type: USSR. Far East: Peninsula Tschutschica, 12.VIII.1881 *Lorenzbai*.

Pogonatum capillare var. *incurvum* Horik. & Saito in Saito, J. Jap. Bot. 31:74. 3. 1956. — Type: Japan. Hokkaido: Kitami, Mt. Rishiri, on soil, ca. 1 570 m, 10.VIII.1952 *Saito* 9529 (Herb. M. Saito, holotype). — Synonymized by Osada (1965).

Pogonatum rubellum Horik. & Saito in Saito, J. Jap. Bot. 31:71. 1. 1956. — Type: Japan. Hokkaido: Kushiro, Mt. Oakan, on sandy soil, ca. 1 200 m, 4.VIII.1951 Saito 5512, 5538 (Herb. M. Saito, syntypes). — Synonymized by Osada (1965).

Pogonatum dentatum, repeatedly mistaken for *P. urnigerum*, is easily distinguished. *P. dentatum* has more distant leaves which are normally more loosely incurved than those of *P. urnigerum*. Marginal teeth are also distinctly patent at least along the lower part of the margin, and they are more clearly multicellular and with a smaller apical cell than in *P. urnigerum*. The clearest diagnostic character is the flat, coarsely papillose apical cells of the lamellae unlike in *P. urnigerum*. Long (1985), in his treatment of the Polytrichaceae of Arctic North America, gives good descriptions of both species and of their differences.

Pogonatum dentatum is almost as widely spread as the closely related *P. urnigerum*. It is confined to cool climates of fairly high latitudes and is almost exclusively restricted to arctic and boreal zones and corresponding vegetation zones of mountain ranges of the northern Hemisphere. Southernmost collections are from mountains of Honshu, Japan and eastern North America. It has been collected on open ground from sea level to 2 700 m.

Illustrations — Grout 1937: pl. 59C; Nyholm 1969 (as *Pogonatum capillare*): 670 (fig. 437); Osada 1965 (as *P. capillare*): 183 (fig. 4); Crum & Anderson 1981: 1265 (fig. 628); Long 1985: 23 (fig. 6); Noguchi 1987 (as *P. capillare*): 31 (fig. 11C).

Distribution — Eur: Finland, Iceland, Norway, Sweden, USSR; As 1: USSR; As 2: China, Japan, Mongolia; Am 1: Canada, USA.

4a. *Pogonatum perichaetiale* (Mont.) Jaeg. subsp. *perichaetiale* (Figs. 3B, C, 24 – map)

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 257. 1875 (Adumbratio 1:719). — *Polytrichum perichaetiale* Mont., Ann. Sci. Nat. Bot. sér. 2(17): 252. 1842. — Type: India. Madras: in montibus Nilghiriensibus, Perrottet 1622 (Crypt. Nilgh. 39) (H-BR!, L!, isotypes).

Pogonatum integerrimum Hampe in Par., Ind. Bryol. 982. 1898, nom. nud. — Original collection: Sikkim, 8 000–11 000 ft., Kurz 2310 (G!, H-BR!). — Synonymized by Ganule (1969).

Pogonatum subperichaetiale Card. & P. Vard., Rev. Bryol. 50:25. 15. 1923, *syn. nov.* — Type: India. Madras: Kodai-kanal, Pambar ravine, on moist ground, 2 400 m, 15.II.1912 Foreau (H-BR!, isotype).

Pogonatum setschwanicum Broth., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 133:583. 1924, *syn. nov.* — Type: China. Sichuan: SW Sichuan, in jugi Linbinkou, 27°46', inter oppidum Yenyüen et castellum Kwapi, regione temperata, in terra abrupta, s. schisto argilloso, ca. 3 150 m Handel-Mazzetti 2844 (H-BR!, holotype).

Pogonatum hirsutum Hampe ex Gang., Mosses E. India 1:149. 1969, nom. nud. in *synon.* — Original collection: India. Darjeeling: Sandakphu-Phalut area, Kurz 2270 (BM!).

Pogonatum perichaetiale with over twenty, closely related taxa has traditionally been distinguished as sect. *Cephalotrichum*. Menzel (1986b) concluded that only one species of this group, *P. oligodus* (C. Müll.) Mitt., is present in South America, and De Sloover (1986) accepted the former species plus the endemic *P. simense* (C. Müll.) Jaeg. for Africa. Magill and Schelpe (1979), however, list the latter species as a synonym under *P. oligodus*. In Asia two species, *P. perichaetiale* and *P. thomsonii* (Mitt.) Jaeg., have traditionally been distinguished. In Asia and Africa two forms can easily be distinguished: *P. thomsonii* and *P. oligodus* with serrate leaf-margins and *P. perichaetiale* and *P. simense* with totally entire margins. In South America all intermediates are found between dentate and the more rare condition of entire leaves. A parallel situation of suppressed development of the marginal teeth has also been found in some forms of *P. urnigerum*. It is not correlated with other characters and I follow Long (1985) in accepting these as mere forms of *P. urnigerum* best left without formal taxonomic recognition.

Sporophytic characters used to distinguish *Pogonatum perichaetiale* and closely related species include the form of sexuality, the number of setae from a perichaetium and the length of the capsule. Asian plants are regularly dioicous, whereas, in Africa and South America, both dioicous and paroicous plants have been found. Brotherus (1925) and De Sloover (1986) describe the African *P. simense* as synoicous. Although it is functionally synoicous, the correct term is paroicous, as antheridia are found in the axils of leaves just beneath the perichaetium. In South America plants with up to 6 setae per perichaetium can be found, whereas, in both Asia and Africa, setae are predominantly solitary. Variation in length of capsule is large. As with other characters, African plants are intermediate between Asian plants with fairly short capsules, and American plants, which can possess urns up to 7 mm long (Menzel 1986b). The differences between plants from different parts of the range are not discrete and do not correlate. Consequently, it would be appropriate to accept only one species, *P. perichaetiale*. The situation is however, further complicated by the variation in sexuality. In *Atrichum* P. Beauv. (Noguchi & Osada 1960) and *Polytrichastrum* (Osada 1966) similarly monoicous plants are known and in these two genera this is accompanied by a diploid chromosome number. The same is true also in the Mniaceae, and studies by Wyatt et al. (1988) indicate that monoicous plants are allopolyploid hybrids between two, closely relat-

ed species. Preliminary genetic studies suggest a similar origin for some monoicous species of the North American Polytrichaceae (Wyatt, pers. comm. 1989) as well. Consequently, it might be possible that monoicous specimens of *Pogonatum oligodus*

with exceptionally long capsules are actually allopolyploids between *P. oligodus* and some other South American species, such as *P. volvatum* or *P. comosum*, with extremely long capsules. While monoicous species of the Mniaceae and the North American

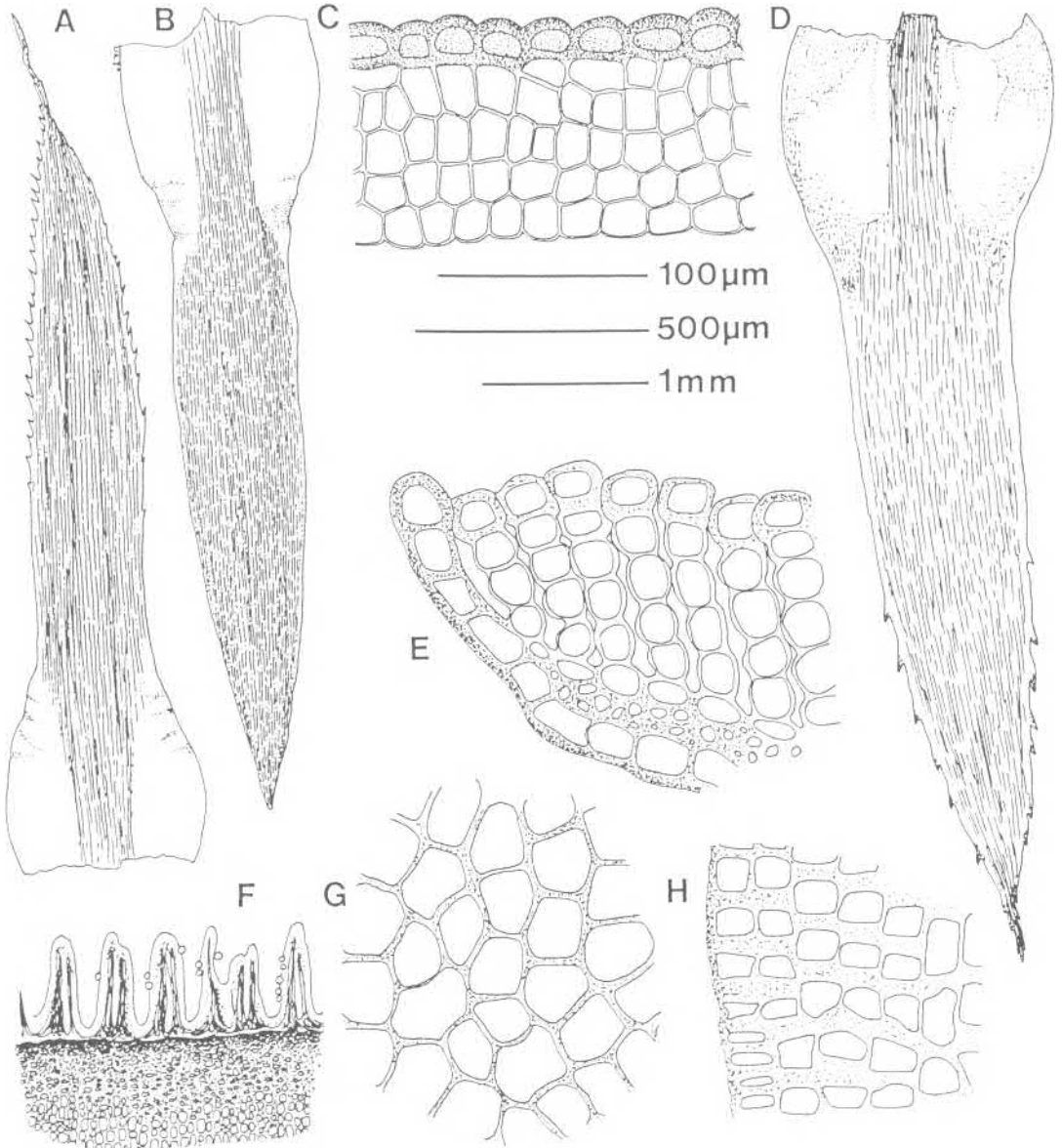


Fig. 3A-H. — A: *Pogonatum perichaetiale* ssp. *thomsonii*. Leaf (Yoda 11620, TNS). — B, C: *P. perichaetiale* ssp. *perichaetiale*. B. Leaf and C. Lamella in side view (Kanai et al. 18.XI.1963, NICH). — D-H: *P. perichaetiale* ssp. *oligodus*. D. Leaf, E. Leaf cross-section, F. Peristome, G. Dorsal cells of blade and H. Upper cells of sheath margin. — D, E, G and H (Lewis 87530, MO), F (Schultes 11318, MO). Use the 100 μm scale for C, E, G and H, 500 μm scale for F, and 1 mm scale for A, B and D.

Polytrichaceae show gametophyte characters which indicate allopolyploidy, no such indications are present in *P. perichaetiale*, accordingly the presence of long capsules in the three South American taxa might be the result of convergent evolution in a similar environment.

At the moment it is thus best to present a more or less traditional treatment accepting one species with three subspecies — *Pogonatum perichaetiale* subsp. *perichaetiale*, *P. perichaetiale* subsp. *thomsonii* (Mitt.) Hyvönen and *P. perichaetiale* subsp. *oligodus* (C. Müll.) Hyvönen in the group. The former two are Asian, while all African and South American specimens are tentatively identified as subsp. *oligodus*. *P. simense* is reduced to synonymy under the latter. The differences between the three species are not constant and therefore they are treated as an unresolved aggregate in my cladistic analysis. I have accepted a pragmatic and unsatisfactory resolution of this problem to avoid premature taxonomical conclusions which might only further complicate the situation.

In cellular details and general habit plants from different continents are surprisingly uniform. They clearly form a monophyletic group as indicated by two synapomorphies: subquadrate apical cells of lamellae with peculiarly incrassate walls and with a peristome of only 16 compound teeth.

Because of the firm and rigid habit, sterile plants of *Pogonatum perichaetiale* might be mistaken for *P. urnigerum*, or even for species of *Polytrichum* or *Polytrichastrum*. Study of the apical cells of the lamellae, however, easily reveals the identity of the plants.

Pogonatum perichaetiale is mostly a plant of high altitudes and has been collected at 600–5 000 m. It grows on soil in open and adverse habitats.

Illustrations — Gangulee 1969: 150 (fig. 68), 151 (fig. 69), 152 (fig. 70); Li 1985: 446 (fig. 192: 14–20).

Distribution — As 2: China; As 3: Bhutan, India, Nepal, Sikkim.

4b. *Pogonatum perichaetiale* subsp. *thomsonii* (Mitt.) Hyvönen, *comb. nov.* (Figs. 3A, 24 – map)

Polytrichum thomsonii Mitt., J. Linn. Soc., Bot. Suppl. 1:155. 1859. — *Pogonatum thomsonii* (Mitt.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 257. 1875 (Adumbratio 1:719). — Type: India, Simla, VII.1849 *Thomson 1231* (NY!, holotype; BM!, isotype).

Polytrichum tortipes Wils. ex Mitt., J. Linn. Soc., Bot. Suppl. 1:155. 1859, *syn. nov.* — *Pogonatum tortipes* (Mitt.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 257. 1875 (Adumbratio 1:719). — Type: Sikkim, Yeyngtong, 12 000 ft., 5.IX.1849 *Hooker 1184*; Kambachen, 12 000 ft., *Hooker 1210* (BM!, NY!, syntypes).

Pogonatum thomsonii var. *tibetanum* Chen, Sci. Exped. Qomolongma Reg. 235. 14. 1962, *syn. nov.* — Type: China, Xizang: N slope of Mt. Jolmolangma (Qomolangma), E Lungpu glacier, 5 450 m, under glaciated rocks, 9.VII.1959 *Wang 80* (PE!, holotype).

Illustrations — Gangulee 1969: 154 (fig. 71), 155 (fig. 72 as *Pogonatum tortipes*); Li 1985: 446 (fig. 192: 14–20).

Distribution — As 2: China; As 3: India, Sikkim.

4c. *Pogonatum perichaetiale* subsp. *oligodus* (C. Müll.) Hyvönen, *comb. nov.* (Figs. 3D–H, 24 – map)

Polytrichum oligodus Kunze ex C. Müll., Linnæa 18:100. 1844, nom. nud.; Syn. Musc. Frond. 1:206. 1848. — *Pogonatum oligodus* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12:613. 1869. — Type: Chile, *Poeppig 271* (BM, lectotype, vide Menzel 1986b; G, H-BR, JE!, isolectotypes).

Polytrichum simense Bruch & Schimp. ex C. Müll., Syn. Musc. Frond. 1:206. 1848. — *Pogonatum simense* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 257. 1875 (Adumbratio 1:719). — Type: Ethiopia, in regione superiore ericarum montis Silke umbrosis ad terram, 15.II.1840 *Schimper 427* (GOET!, H-BR!, H-SOL!, JE!, L!, M!, isotypes). — Synonymized by Montagne in Gay (1850).

Polytrichum schmitzii Lorentz, Moosstud. 156. 1864. — *Pogonatum schmitzii* (Lor.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:207. 1872. — Type: Mexico, *Schmitz* (BM, H-BR!, isotypes). — Synonymized by Menzel (1986b).

Polytrichum cucullatum Hampe, Ann. Sci. Nat. Bot. sér. 3(4): 348. 1865. — *Pogonatum cucullatum* (Hampe) Mitt., J. Linn. Soc., Bot. 12:613. 1869. — Type: Colombia, Bogota, ad Barrancos, IV.1863 *Lindig* (H-BR!, isotype). — Synonymized by Brotherus (1909).

Polytrichum toluicense Hampe, Verh. Zool.-Bot. Ges. Wien 19:508. 1869. — *Pogonatum toluicense* (Hampe) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:207. 1872. — Type: Mexico, Volcano Toluca, 1 830 m, *Heller* (BM, holotype; H-BR!, isotype). — Synonymized by Menzel (1986b).

Pogonatum cuspidatum Besch., Mém. Soc. Sci. Nat. Cherbourg 16:206. 1872. — Type: Mexico, vallee de Mexico, 27.IX.1865 *Bourgeau 1337* (BM, holotype; G!, isotype). — Synonymized by Menzel (1986b).

Polytrichum plurisetum C. Müll., Linnæa 42:265. 1879. — *Pogonatum plurisetum* (C. Müll.) Broth., Nat. Pflanzenfam. 1(3): 692. 1905. — Type: Argentina, Argentina subtropical, Sierra de Tucumán, in albus prope Tafi, 1890 *Lorentz* (H-BR!, JE!, S, isotypes). — Synonymized by Schiavone (1978).

?*Polytrichum plurisetum* var. *brevipes* C. Müll., Linnæa 42:266. 1879, *syn. nov.* — *Pogonatum polycarpum* var. *brevipes* (C. Müll.) Par., Ind. Bryol. 986. 1898. — Type: Argentina, Argentina subtropical, Cuesta de Calderia occidentalis in praerupis, 27.V.1873 *Lorentz*.

Polytrichum carionis C. Müll., Bull. Herb. Boissier 5:177. 1897. — *Pogonatum carionis* (C. Müll.) Par., Ind. Bryol. 979. 1898. — Type: Guatemala, Cantel S. Catharina, X.1876 *Bernoulli & Cario 121b* (H-BR!, isotype). — Synonymized by Menzel (1986b).

Trichopilum polycarpum Schimp. ex C. Müll., Nuovo Giorn. Bot. Ital.n.s. 4:166. 1897. — *Pogonatum polycarpum* (C. Müll.) Par., Ind. Bryol. 986. 1898. — Original collection: Bolivia, prope Paxacollo, *Mandon* (H-SOL!). — Synonymized by Schiavone (1978).

Polytrichum itatiaiae C. Müll., Bull. Herb. Boissier 6:25. 1898. — *Pogonatum itatiaiae* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Brasilia. Minas Geraes: Serro do Itatiaia, 2 000 m, II.1894 *Ule 1764* (H-BR!, isotype). — Synonymized by Menzel (1986b).

Pogonatum macei Thér. in Ren., Prodr. Fl. Bryol. Madag. Suppl. 61. 1909, syn. nov. — Type: Comores. Grande Comore: Volcan du Kortala, 600 m, 27.VIII.1900 *Mace* (Herb. Poli) (PC!, holotype).

Pogonatum chiapense Broth. in Card., Rev. Bryol. 37:5. 1910. — *P. toluense* var. *chiapense* (Broth.) Thér., Smithsonian Misc. Collect. 78, 2:21. 1926. — Type: Mexico. Chiapas: in monte Guey-Tepec, prope San Cristobal, 24.XI.1907 *Münch* (BM, H-BR!, JE!, M!, NY, syntypes); Amecameca, 1908 *Pringle 10698* (BM, G, L!, NY, UPS!, syntypes). — Synonymized by Menzel (1986b).

Pogonatum cylindrotheca Herz., Biblioth. Bot. 87:103. 1916. — Type: Bolivia, am Wegrund bei Lagunillas, ca. 3 200 m, VII.1911 *Herzog 3839* (BM, H, L!, M!, NY, S, isotypes). — Synonymized by Schiavone (1978).

Pogonatum jaffuelii Thér., Revista Chilena Hist. Nat. 33:138. 7:2. 1930. — Type: Bolivia, Kala Uyu, 15 km N La Paz, 4 200–5 000 m, II.1922 *Jaffuel 0261* (PC!, holotype). — Synonymized by Menzel (1986b).

Illustrations — Schiavone 1978 (as *Pogonatum oligodus*): 51 (pl. 6); De Sloover 1986: (as *P. oligodus*) 271 (figs. 164–181); (as *P. simense*) 273 (figs. 182–204).

Distribution — Afr 2: Burundi, Cameroun, Ethiopia, Kenya, Ruanda (De Sloover 1986), Tanzania, Uganda (De Sloover 1986); Afr 3: Comores, Reunion (De Sloover 1986); Afr 4: Lesotho, South Africa; Am 2: Guatemala, Mexico; Am 3: Dominican Republic; Am 4: Bolivia, Colombia, Ecuador, Peru, Venezuela; Am 5: Brasilia; Am 6: Argentina, Chile.

Subgenus CATHARINELLA (C. Müll.) Hyvönen, *comb. nov.*

Polytrichum sect. *Catharinella* C. Müll., Syn. Musc. Frond. 1:213. 1848. — *Pogonatum* sect. *Catharinella* (C. Müll.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:208. 1872. — *Catharinella* (C. Müll.) Kindb., Rev. Bryol. 21:33. 1894. — Type: *Pogonatum convolutum* (Hedw.) P. Beauv. (*Polytrichum convolutum* Hedw.), lectotype, vide Smith (1971).

Racelopus Dozy & Molk., Bryol. Jav. 1:37. 1856. — *Pogonatum* sect. *Racelopus* (Dozy & Molk.) Touw, J. Hattori Bot. Lab. 60:11. 1986. — Type: *Racelopus pilifer* Dozy & Molk. (*Pogonatum piliferum* (Dozy & Molk.) Touw), holotype.

Pogonatum sect. *Anasmogonium* Mitt., J. Linn. Soc., Bot. 12:612. 1869. — Type: *Pogonatum semipellucidum* (Hampe) Mitt. (*Polytrichum semipellucidum* Hampe), lectotype, vide Smith (1971).

Racelopodopsis Thér., Monde Pl. sér. 2(9): 22. 1907. — Type: *Racelopodopsis camusii* Thér. (*Pogonatum camusii* (Thér.) Touw), holotype.

Pseudoracelopus Broth., Öfvers. Förh. Finska Vetensk.-Soc. 52A(7):2. 1910. — Type: *Pseudoracelopus philippinensis* Broth. (*Pogonatum philippinensis* (Broth.) Touw), holotype.

Pseudatrachium Reim., Notizbl. Bot. Gart. Berlin-Dahlem 15:399. 1941. — Type: *Pseudatrachium spinosissimum* Reim., holotype.

Pogonatum sect. *Contortia* Chen & Wan, Gen. Musc. Sin. 2:304. 1978. — Type: *Pogonatum contortum* (Brid.) Lesq. (*Polytrichum contortum* Menz. ex Brid.).

Pogonatum sect. *Fastigiata* Chen & Wan, Gen. Musc. Sin. 2:304. 1978. — Type: *Pogonatum fastigiatum* Mitt.

Pogonatum sect. *Microstoma* Chen & Wan, Gen. Musc. Sin. 2:304. 1978. — Type: *Pogonatum microstomum* (Schwaegr.) Brid. (*Polytrichum microstomum* R. Brown ex Schwaegr.).

Neopogonatum Xu & Xiong, Acta Bot. Yunnanica 6:173. 1984. — Type: *Neopogonatum semiangulatum* Xu & Xiong, holotype.

Plagioracelopus Smith Merrill, Mem. New York Bot. Gard. 45:469. 1987. — Type: *Plagioracelopus marginatum* (Mitt.) Smith Merrill (*Pogonatum marginatum* Mitt.), holotype.

5. *Pogonatum tortile* (Sw.) Brid. (Figs. 4A, B, 26 – map)

Bryol. Univ. 2:108. 1827. — *Polytrichum tortile* Sw., J. Bot. (Schrader) 1800(2): 175. 1801. — Type: Jamaica (PC!, isotype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum domingense Brid., Spec. Musc. 1:75. 1806. — *Pogonatum tortile* var. *domingense* (Brid.) Brid., Bryol. Univ. 2:109. 1827. — Type: Dominican Republic (St. Domingus), 1803 (B!, holotype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum liebmannianum C. Müll., Syn. Musc. Frond. 2:563. 1851, syn. nov. — *Pogonatum liebmannianum* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12:614. 1869. — Type: Mexico. Orizaba: Tapiche de la Concepcion, VI.–VII.1842 *Liebmann 45* (BM, C!, NY, PC, isotypes).

Polytrichum octangulare C. Müll., Syn. Musc. Frond. 2:564. 1851, syn. nov. — *Pogonatum octangulare* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12:617. 1869. — Type: Costa Rica, Aquacate, 1 500 ft., *Oerstedt* (JE!, isotype).

Pogonatum cubense Sull., Proc. Amer. Acad. Arts 5:281. 1861. — Type: Cuba, on dry banks, *Wright 57* (GOET!, JE!, H-SOL!, L!, isotypes). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum albo-vaginatatum Hampe, Bot. Zeitung (Berlin) 28:51. 1870, syn. nov. — *Pogonatum albo-vaginatatum* (Hampe) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:209. 1872. — Type: Mexico, Vera Cruz, *Strebel* (BM!, holotype).

Polytrichum subgracile Hampe, Bot. Zeitung (Berlin) 28:51. 1870, syn. nov. — *Pogonatum subgracile* (Hampe) Besch., Mém. Soc. Sci. Nat. Cherbourg 16:208. 1872. — Type: Mexico, Vera Cruz, *Strebel* (BM!, holotype).

Pogonatum crispulum Besch., Ann. Sci. Nat. Bot. sér. 6, (3): 211. 1876. — Type: Guadeloupe, montagne du Matouba, *Balbis & Lenormand*, Herb. Montagne; *Duchassaing*, Herb. Mus. Par.; Guadeloupe, *L' Herminier 3* (H-SOL!, syntype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Pogonatum laxifolium Besch., Ann. Sci. Nat. Bot. sér. 6, (3): 211. 1876. — Type: Guadeloupe, *Beaupertuis* (H-SOL!, isotype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Pogonatum pleeanum Besch., Ann. Sci. Nat. Bot. sér. 6(3): 212. 1876. — Type: Martinique, *Plée 869* (H-SOL!, isotype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

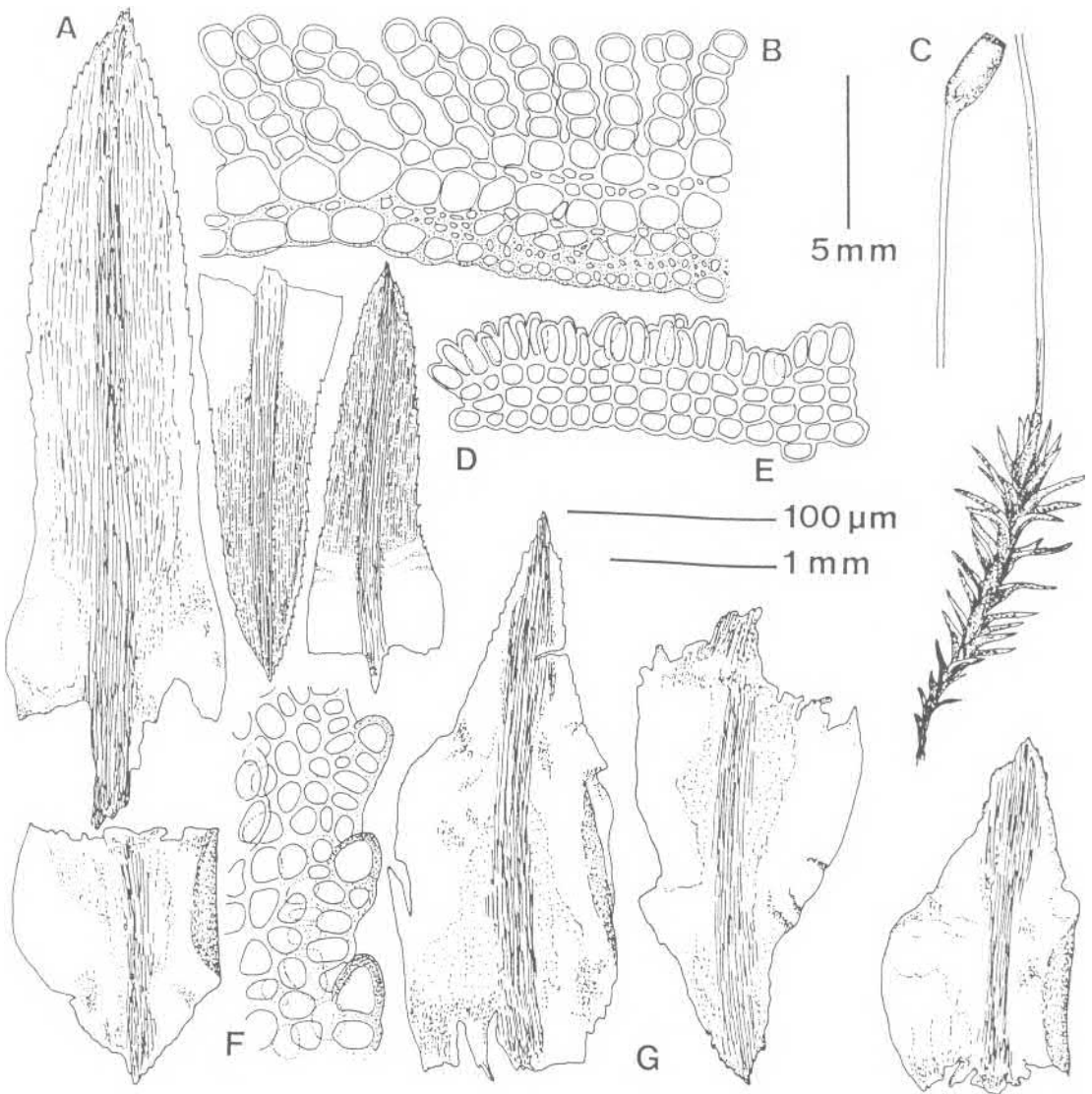


Fig. 4A-G. — A, B: *Pogonatum tortile*. A. Leaf and B. Leaf cross-section (Crosby 6383, MO). — C-E: *P. neglectum*. C. Moist habit, D. Leaves and E. Lamella in side view (Sastre-De Jesús et al. 1328, MO). — F, G: *P. pensilvanicum*. F. Leaf-margin and G. Leaves (Yano & Lopes 4338, H). — Use the 5 mm scale for C, 100 µm scale for B, E and F and 1 mm scale for A, D and G.

Polytrichum tortile subsp. *glaucinum* Besch., Ann. Sci. Nat. sér. 6(3): 210. 1876. — *Pogonatum tortile* var. *glaucinum* (Besch.) Par., Ind. Bryol. Suppl. 278. 1900. — *P. glaucinum* Besch. ex Frye & Duck., Bryologist 49:36. 1946. — Type: Martinique, Hahn 776 (H-SOL!, isotype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Pogonatum tortile subsp. *husnotianum* Besch., Ann. Sci. Nat. Bot. sér. 6(3): 210. 1876. — *P. tortile* var. *husnotianum* (Besch.) Par., Ind. Bryol. Suppl. 279. 1900. — Type: Martinique, rivière Rouge, la Découverte, bords des chemins, Hus-

not 153 (BM!, holotype; L!, M!, isotypes) — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Pogonatum consobrinum Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 171. 1893, *syn. nov.* — Type: Costa Rica, forêts de Juan Viñas, 25.I.1890 Tonduz 5578 (BR!, syntype); forêts de la Palma, versant atlantique, 1 550 m, 18.XII.1888 Pitier 5580. (BR!, syntype).

Polytrichum imbricatum C. Müll., Hedwigia 37:222. 1898. — *Pogonatum imbricatum* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Puerto Rico, prope Adjuntas, in

sylva primaeva, inter Cath. Sintenisi, V.1886 *Sintenis* Herb. Krug et Urban. — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum obscuro-viride C. Müll., Hedwigia 37:223. 1898. — *Pogonatum obscuro-viride* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Jamaica, in montibus copia pluviali minore prope Kingston, 1897 *Hansen*; Haiti, in montibus prope Furcy, VIII.1891 *Picarda* Herb. Berlin 1898. — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum sintenisii C. Müll., Hedwigia 37:222. 1898. — *Pogonatum sintenisii* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Puerto Rico, Guaraguao, V.1886 *Sintenis*; Adjuntas, 25.III.1886 *Sintenis* 74 (MO!, syntype). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Polytrichum sintenisii var. *parvum* C. Müll., Hedwigia 37:222. 1898. — *Pogonatum sintenisii* var. *parvum* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Puerto Rico, Adjuntas, 25.III.1886; Maricao, XII.1884 *Sintenis* (BM!, syntypes). — Synonymized by Frye & Duckering (1946), cf. Frye (1956).

Pogonatum laxirete Williams, Bull. New York Bot. Gard. 6(21): 235. 1909, *syn. nov.* — Type: Bolivia, near Mapiro, 700 m, 13.VI.1902 *Williams* 1925 (NY, holotype; BM, JE!, isotypes).

Pogonatum sinuato-dentatum Card., Rev. Bryol. 37:5. 1910, *syn. nov.* — Type: Mexico. Vera Cruz: Zacuapan, moist banks, XI.1907 *Purpus* 5 (MO!, syntype); near Jalapa, earth banks, 4 000 ft., 7.VII.1908 *Pringle* 10700 (CANM!, L!, M!, MO!, UPS!, syntypes).

Pogonatum tortile has been described under a variety of names despite a rather low level of variability. Plants growing in shady habitats tend to have lower lamellae and more pronounced serration of leaf-margins, but even in these specimens the marginal teeth are typically somewhat rounded. The lamellae always have undifferentiated apical cells of the lamellae, which are distinctly crenate as seen in side-view and in some specimens some of the cells are even geminate. This combination of features is unique to *P. tortile* among South American species.

Two other species of the genus, the SE Asian *Pogonatum subtortile* (C. Müll.) Jaeg. and the Australian *P. subulatum* (Brid.) Brid. fairly closely resemble *P. tortile*. In *P. subulatum* the apical cells of the lamellae are not as regularly crenate — they can even be essentially straight as seen in side view. Marginal teeth are small also in the latter species but they are generally more patent than in *P. tortile*. *P. subulatum* has the costa with more numerous dorsal teeth. The clearest difference between *P. tortile* and *P. subtortile* can be seen in the form of leaves. In the latter they are very gradually widened to the sheath whereas in *P. tortile* the shoulders of the sheath are more distinct. The dentation of the costa is also generally more pronounced in American species while the costa itself is more often stronger and clearly percurrent in the Asian *P. subtortile*.

Pogonatum tortile is a very common weedy plant of trail- and road-sides especially on the Caribbean

islands. It has been collected from near sea level to 2 200 m.

Illustrations — Smith 1975b (as *Pogonatum liebmanianum*): 482 (figs. 15–26).

Distribution — Am 2: Costa Rica, Guatemala, Mexico, Nicaragua, Panama; Am 3: Cuba, Dominican Republic, Guadeloupe, Jamaica, Martinique, Puerto Rico, Trinidad; Am 4: Bolivia, Colombia, Ecuador, Peru (Schultze-Motel & Menzel 1987), Venezuela.

6. *Pogonatum pensilvanicum* (Hedw.) P. Beauv. (Figs. 4F, G, 26 – map)

Mém. Soc. Linn. Paris 1:461. 1822. — *Polytrichum pensilvanicum* Bartram ex Hedw., Spec. Musc. 96. 21:1–6. 1801. — *Pogonatum brevicaule* P. Beauv., Prodr. Aethcegam. 84. 1805, nom. illeg. superfl. — *Pogonatum tenue* Rau & Herv., Cat. N. Amer. Musci 30. 1880, nom. illeg. superfl. — Type: USA, Pennsylvania: circa Lancaster solo simili, *Mühlenberg* (BM!, isotype).

?*Pogonatum brevicaule* var. *torreyanum* Brid., Bryol. Univ. 2:115. 1827. — *P. torreyanum* Brid., Bryol. Univ. 2: 115. 1827, nom. nud. in synonym. — *P. pensilvanicum* var. *torreyanum* (Brid.) Par., Ind. Bryol. 985. 1898. — Type: USA, Massachusetts, *Torrey*. — Synonymized by Crum et al. (1965) and Crum & Anderson (1981).

Polytrichum gardneri C. Müll., Syn. Musc. Frond. 2:560. 1851, *syn. nov.* — *Pogonatum gardneri* (C. Müll.) Mitt., J. Linn. Soc., Bot. 8:156. 1864. — Type: Brazil, Tejuca, clay bank, XI.1836 *Gardner* 15 (E!, GOET!, JE!, L!, isotypes).

Polytrichum glaziovii Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 4: 54. 1872, *syn. nov.* — *Pogonatum glaziovii* (Hampe) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 254. 1875 (Adumbratio 1:716). — Type: Brasilia, *Glaziou* 5156 (BM!, holotype).

Polytrichum perpusillum C. Müll., Hedwigia 36:90. 1897, *syn. nov.* — *Pogonatum perpusillum* (C. Müll.) Par., Ind. Bryol. 985. 1898. — Type: Paraguay, Caraguaza, *Balansa* 3618 (H-BR!, isotype).

Pogonatum subabbreviatum Broth., Denkschr. Kaiserl. Akad. Wiss. Math.-Naturwiss. Kl. 83:350. 1924, *syn. nov.* — Type: Brasilia, Minas Geraes: Serra do Itatiaia, Macieiras, ad margines viarum, 16.I.1925 *Vaughan Baudeira* 91 (H-BR!, holotype).

Pogonatum pensilvanicum is easily distinguished from all other American species of the genus by its pronounced neoteny — stems are reduced, bearing only a few leaves with depauperate blades. The protonema is obvious and persistent. Several neotenic species with persistent protonema have been described from North and South America, but after study of the type specimens and protologues all these are reduced to synonymy under *P. pensilvanicum*. *P. brachyphyllum* (Michx.) P. Beauv. is a North American species with persistent protonema growing in habitats similar to those of *P. pensilvanicum*. *P. brachyphyllum* is, however, distinguished from the latter because its leaves have a wide blade and a rounded apex, and lamellae are high and well developed. *P. pensilvanicum* has been reported from

many parts of both South and North America, and southern plants have traditionally been treated as a distinct species. Certain differences can be observed: perichaetial leaves of northern plants are generally longer, with more abruptly narrowed blades and with many geminate apical cells of the lamellae. The capsules are long and terete. I did not have the chance to study the type specimen of *P. pensilvanicum* var. *torreyanum*, but according to the original description it is distinct only in having a longer blade. This is a variable character and accordingly there is no need to recognize this variation taxonomically. In southern plants the capsules are mostly clearly plicate and the apical cells of the lamellae are irregular and only occasionally geminate. These differences are neither very significant nor constant and, in their anatomical and cellular details, the leaves from both South and North American plants are essentially identical. It is clear that separation of the two at any taxonomic level is superfluous. Mexican plants are intermediate between plants of North and South America in many characters and assigning them to a sub-specific taxon would be arbitrary.

In its neoteny *Pogonatum pensilvanicum* resembles the SE Asian *P. spinulosum*. However, I agree with Smith (1971) that the two are not closely related, but instead they demonstrate convergence due to a similar environment.

Pogonatum pensilvanicum is a weedy plant typically of open, bare soil. It is capable of surviving also in fairly deep shade and has been collected from sea level up to 2 900 m.

Illustrations — Grout 1937: pl. 58B; Crum & Anderson 1981: 1262 (fig. 627A-I).

Distribution — Am 1: Canada, USA; Am 2: Mexico; Am 3: Cuba (Crum & Anderson 1981); Am 4: Bolivia, Peru; Am 5: Brazil, Paraguay.

7. *Pogonatum neglectum* (Hampe) Jaeg. (Figs. 4C-E, 26 – map)

Ber. Thätigk. St. Gallischen. Naturwiss. Ges. 1873–74: 265. 1875 (Adumbratio 1:727). — *Polytrichum neglectum* Hampe, Bot. Zeitung (Berlin) 27:867. 1869. — Type: Colombia, Monte del Moro, 2 200 m, 1863 Lindig (G, H-BR!, L!, M!, US, isotypes).

Menzel (1986a) treats *Pogonatum neglectum* as a depauperate form of *P. campylocarpum* (C. Müll.) Mitt., and he accordingly reduces it to synonymy under the latter species. Although the two species are closely related, I, nevertheless, accept the Colombian plant as a good taxon. *P. neglectum* is distinguished from both *P. campylocarpum* and *P. comosum* by its small size. Its leaves are crowded and tightly appressed on short stems when dry. The blade

is gradually narrowed to the sharp apex. The sheath is not much widened, and it has entire margins. *P. neglectum* may be difficult to distinguish from small specimens of *P. campylocarpum* but the latter species has wider leaf apices and its sheath is at least partly serrate.

Pogonatum neglectum is a small plant of open habitats at 1 600–2 780 m.

Distribution — Am 4: Colombia, Venezuela.

Specimens examined (representative) — Am 4. COLOMBIA. Antioquia: Municipio Guatapé, ca. 15 km N-NE del pueblo, bosque muy húmedo Montano Bajo, ca. 6°18'N, 75°9'W, 1 900 m, 4.–5.VII.1985 Sastre-De Jesús et al. 1328 (H!). — VENEZUELA. Aragua: 4 km SW of Colonia Tovar by air, on road to Capachal 2 km east from road between Colonia Tovar and La Victoria, remnant forest with bamboo understorey, on steep bank, 10°22'N, 67°19'W, 7.IV.1982 Liesner & Medina (MO!).

8. *Pogonatum campylocarpum** (C. Müll.) Mitt. (Figs. 5A–D, 27 – map)

J. Linn. Soc., Bot. 12:618. 1869. — *Polytrichum campylocarpum* C. Müll., Syn. Musc. Frond 1:209. 1848. — Type: Venezuela, Caracas, Galipan, 4 000(5 000?) ft., I.1846 Funck & Schlim. 379 (BM, lectotype, vide Schiavone 1978; GOET!, JE!, L!, NY!, isolectotypes).

Polytrichum flexuosum C. Müll., Linnaea 19:208. 1847, syn. nov. — *Pogonatum flexuosum* (C. Müll.) Broth., Nat. Pflanzenfam. 1(3): 691. 1905, hom. illeg. — Type: Venezuela, Silla de Caracas, ad rupes humidiuscul., Moritz 135 (H-SOL!, JE!, L!, isotypes).

Polytrichum andinum Hampe, Linnaea 32:147. 1863. — *Pogonatum andinum* (Hampe) Mitt., J. Linn. Soc., Bot. 12:615. 1865. — Type: Colombia, Bogota, Chapinero, in umbrosis humidis, 2 700 m, 1859 Lindig 2044 (BM!, holotype). — Synonymized by Schiavone (1978).

Polytrichum subcontortum Hampe, Ann. Sci. Nat. Bot. sér. 5(4): 349. 1865. — *Pogonatum subcontortum* (Hampe) Mitt., J. Linn. Soc., Bot. 12:616. 1869. — Type: Colombia, Bogota, Chapinero, in umbrosis humidis, 2 700 m, 1859 Lindig 2044 (BM!, holotype). — Synonymized by Menzel (1986a).

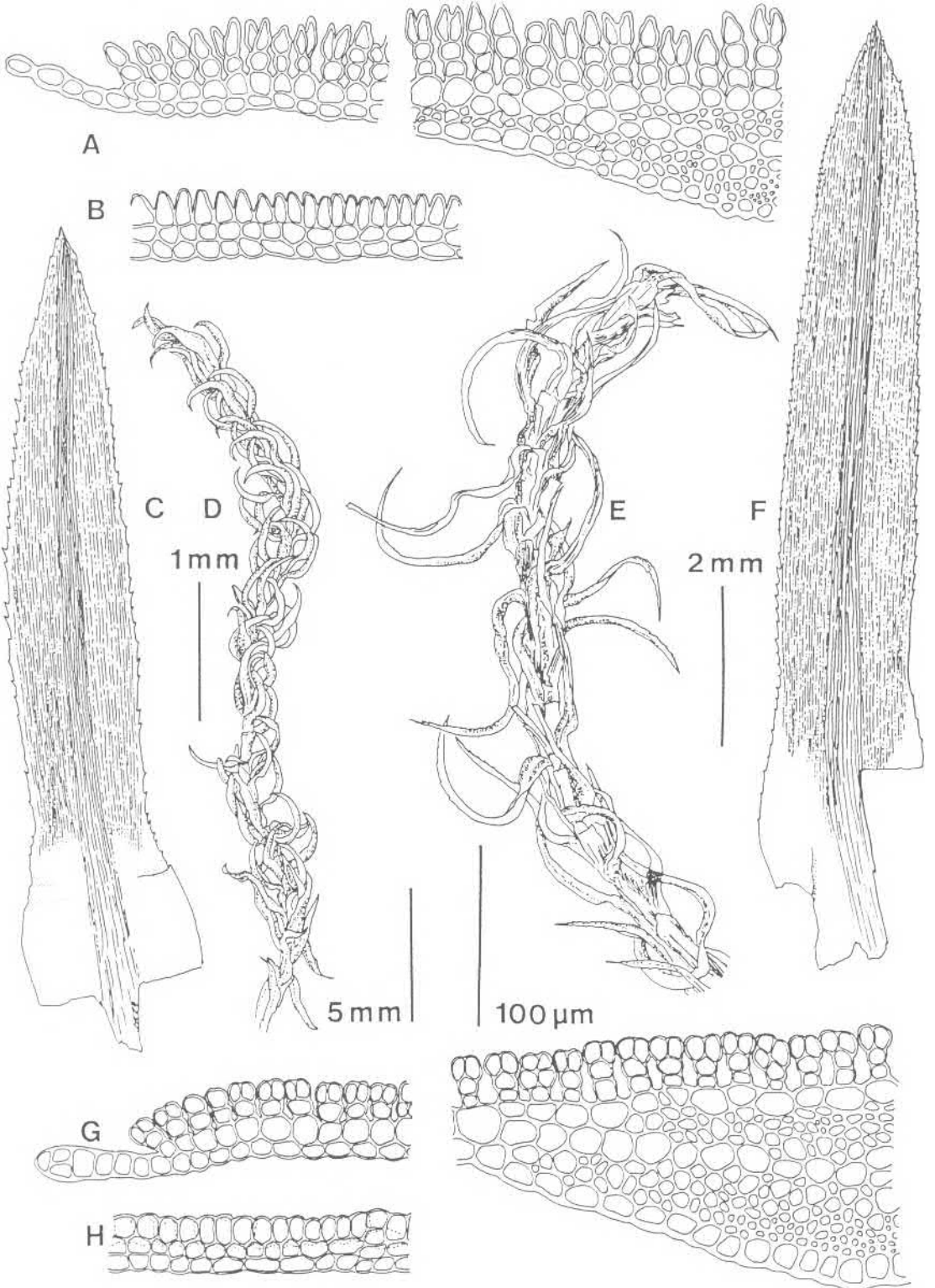
Polytrichum purpurascens Hampe, Linnaea 32:148. 1863, hom. illeg. — *Pogonatum purpurascens* Mitt., J. Linn. Soc., Bot. 12:616. 1869. — Type: Colombia, Manzanas, 2 700 m, VII.1860 Lindig 2114 (H-SOL!, M!, NY, isotypes). — Synonymized by Menzel (1986a).

Polytrichum varians Hampe, Ann. Sci. Nat. Bot. sér. 5(4): 350. 1865. — *Pogonatum varians* (Hampe) Mitt., J. Linn. Soc., Bot. 12:619. 1869. — Type: Colombia, Bogota, ad Barrancos, 2 700 m, IV.1863 Lindig (BM, holotype; H-BR!, M, PC, US, isotypes). — Synonymized by Schiavone (1978).

Pogonatum arcuatum Mitt., J. Linn. Soc., Bot. 12:617. 1869. — Type: Ecuador, Andes Quitensis, in monte Pichincha, 10 000 ft., Weir 207 (BM!, H-BR!, isotypes). — Synonymized by Schiavone (1978).

Pogonatum obscuratum Mitt., J. Linn. Soc., Bot. 12:618. 1869. — Type: Ecuador, Andes Quitensis, in monte Pichincha, 10 000 ft., Spruce 1495 (NY, holotype; BM, H-BR!, isotypes). — Synonymized by Schiavone (1978).

Polytrichum psilopiloides C. Müll., Linnaea 38:576. 1874. — *Pogonatum psilopiloides* (C. Müll.) Jaeg., Ber.



Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 259. 1875 (Adumbratio 1:721). — Type: Colombia. Antioquia: Paramo de Sonson, 10 000–12 000 ft., 1872 Wallis (H-BR!, isotype). — Synonymized by Menzel (1986a).

Polytrichum camptocaulon C. Müll. in Broth., Acta Soc. Sci. Fenn. 19(5): 17. 1891. — *Pogonatum camptocaulon* (C. Müll.) Par., Ind. Bryol. 978. 1898. — Type: Brazil. Minas Geraes: Caraca, in terra arenosa, Wainio (H-BR!, isotype). — Synonymized by Menzel (1986a).

Pogonatum hamatifolium Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 172. 1892. — Type: Costa Rica, Marais à la Palma, 1 550 m, 18.XII.1888 Pittier 5581 (BR!, H-BR!, NY, isotypes). — Synonymized by Menzel (1986a).

Polytrichum germainii C. Müll., Nuov. Giorn. Bot. Ital. n. s. 4:14. 1897. — *Pogonatum germainii* (C. Müll.) Par., Ind. Bryol. 981. 1898. — Type: Bolivia, Cochabamba, prope Choquecamata, VI.1889 Germain 1219 (G!, isotype). — Synonymized by Menzel (1986a).

Pogonatum distantifolium C. Müll. ex Herz., Biblioth. Bot. 87:103. 1916, nom. nud. — Original collection: Brazil. Staat Rio de Janeiro: Nova Friburgo, Ule. — Synonymized by Menzel (1986a).

Pogonatum confertidens Broth. & Thér. in Thér., Recueil Publ. Soc. Havraise Études Diverses 1921(4): 310. 3. 1921. — Type: Costa Rica, Alto del Cascajol, monts de la Palma, 2 500 m, XII.1913 Jimenez (PC!, holotype). — Synonymized by Menzel (1986a).

Pogonatum species with geminate apical cells of the lamellae are typical of South and Central America. As noted by Menzel (1986a) various authors have described over 30 species, many of which are frivolous. Menzel (1986a) reduced the number of these species to only two: *P. campylocarpum* and *P. subflexuosum* (Lor.) Broth. (= *P. comosum*). I am, however, inclined to accept two more valid species, *P. neglectum* and *P. procerum*.

P. campylocarpum is confined to South America and southern parts of Central America. It is distinguished from *P. comosum* of northern Central America by its generally narrower sheath with distinctly serrate margins and plicate, arcuate and fairly short capsules. Apical cells of the lamellae can be notched as in northern plants, but the outer wall of these cells is not always incrassate and finely papillose like those of *P. comosum*. The leaves are also more remote than in the latter species, and the two species are often readily distinguished by their habit. *P. campylocarpum* also has leaves without the basal constriction characteristic of most specimens of *P. comosum* and the Asian *P. microstomum*. However, it should be noted that cladistic analysis left *P. campylocarpum* as a metasppecies without any distinctive autapomorphies, and it would not be surprising, if

further study proves *P. campylocarpum* and *P. comosum* to be conspecific.

Pogonatum campylocarpum is confined to open ground on roadsides and similar habitats. It has been collected at altitudes of 900–4 050 m.

Illustration — Schiavone 1978: 47 (fig. 5).

Distribution — Am 2: Costa Rica, El Salvador, Panama; Am 3: Dominican Republic; Am 4: Bolivia, Colombia, Ecuador, Peru, Venezuela; Am 5: Brazil; Am 6: Argentina.

9. *Pogonatum procerum* (Lindb.) Schimp. in Jaeg. (Figs. 5E–H, 26 – map)

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 265. 1875 (Adumbratio 1:727). — *Polytrichum procerum* Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9:98. 1868. — Type: Mexico, Mirador, Liebmann Herb. Schimper (H-SOL!, holotype).

Pogonatum robustum Mitt., J. Linn. Soc., Bot. 12:616. 1869, *syn. nov.* — *P. wilsonii* Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 263. 1875 (Adumbratio 1:725), nom. illeg. superfl. — Type: Jamaica, Wilson 3808 (NY, holotype; BM!, isotype).

Polytrichum humboldtianum Hampe, Verh. Zool.-Bot. Ges. Wien 21:384. 1871, nom. nud. — *Pogonatum humboldtianum* Hampe ex Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 454. 1880 (Adumbratio 2:718), nom. nud. — Original collection: Guatemala, Las Nubes, VIII.1866 Wendland, 10.I.1857 Wendland 183 (GOET!).

Pogonatum robustum Schimp. in Besch., Mém. Soc. Sci. Nat. Cherbourg 16:210. 1872, hom. illeg. — *P. robustiusculum* Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74:264. 1875 (Adumbratio 1:726). — Type: Mexico, Liebmann (PC!, lectot. nov.).

Pogonatum pittieri Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 169. 1893, *syn. nov.* — Type: Costa Rica, forêts du Barba, 2 600 m, 6.VII.1888 Pittier 5575; bois humides du volcan de Barba, 2 400 m, I.1889 Pittier 5576; forêts du Barba, versant pacifique, 2 500 m, 6.II.1890 Tondus 5577 (BR!, syntypes).

Polytrichum bernoullii C. Müll., Bull. Herb. Boissier 5:178. 1897, *syn. nov.* — *Pogonatum bernoullii* (C. Müll.) Par., Ind. Bryol. 977. 1898. — Type: Guatemala, Cumbre inter Cabulco et Sojabay, IX.1870 Bernoulli & Cario 103 (BM, GOET! isotypes).

Study of the type material of *Pogonatum procerum* reveals it to be conspecific with *P. robustum*. The latter name has traditionally been used for this conspicuous plant, but *P. procerum* is an older name, which unfortunately replaces the more familiar *P. robustum*.

Fig. 5A–H (Left). — A–D: *Pogonatum campylocarpum*. A. Leaf cross-section, B. Lamella in side view, C. Leaf and D. Habit (Liesner & Gonzales 10004, MO). — E–H: *P. procerum*. E. Habit, F. Leaf, G. Leaf cross-section and H. Lamella in side view (Sharp 59163, H). — Use the 1 mm scale for C, 2 mm scale for F, 5 mm scale for D and E, and 100 µm scale for A, B, G and H.

Pogonatum procerum is often confused with large forms of *P. comosum*. However, the two species differ clearly by their lamellae and especially by the form of the apical cells of the lamellae. This latter character has traditionally been much used to distinguish species of the Polytrichaceae, and it still proves to be one of the most reliable and stable characters. In *P. procerum* the lamellae are only 3–4 cells high, very rarely higher (up to 6 cells), and the apical cells are more or less rounded both in cross-section and side view. They are mostly smooth, while those of *P. comosum* are at least partly papillose and higher than wide as seen in side view. Specimens of *P. campylocarpum* with low lamellae and few dorsal teeth may be difficult to identify, but even in these cases the apical cells are typically higher than in *P. procerum*. In the latter species lamellae are also more tightly set on the blade. Differences in form of the capsule (essentially straight and terete in *P. comosum*; arcuate and plicate in *P. procerum*), and habit in the dry condition (leaves of *P. comosum* are more tightly appressed with margins more inrolled) also help in identification. The sheath of the leaves is normally entire in the latter species whereas it is almost always serrate in *P. procerum*.

Menzel (1986a) does not distinguish *Pogonatum procerum*, but instead the robust plants are interpreted as *P. subflexuosum* (= *P. comosum*). This view, as well, is acceptable — the distinction of the two species might be difficult in certain cases. But as discussed above, most specimens are readily identified as either *P. procerum* or *P. comosum* and consequently both species are tentatively accepted here.

Pogonatum procerum has been collected on the soil of trail, road and stream banks at 1 200–3 600 m. Generally it seems to favor fairly moist habitats.

Distribution — Am 2: Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Panama; Am 3: Dominican Republic, Jamaica; Am 4: Peru.

10. *Pogonatum comosum* (C. Müll.) Mitt. (Figs. 6A–E, 27 – map)

J. Linn. Soc., Bot. 12:614. 1869. — *Polytrichum comosum* C. Müll., Syn. Musc. Frond. 2:561. 1851. — Type: Mexico, Pico de Orizaba, Liebmann 46 (8372) (C!), lectotype, vide Smith 1975a).

Polytrichum subflexuosum Lor., Moosstud. 157. 1864, syn. nov. — *Pogonatum subflexuosum* (Lor.) Broth., Nat. Pflanzenfam. 1(3): 691. 1905. — Type: Mexico, 1833 Andrieux (G, lectotype; H-BR!, isolectotype; vide Menzel 1986a).

Pogonatum glaciale Mitt., J. Linn. Soc., Bot. 12:614. 1869, syn. nov. — Type: Mexico, in summo monte San Felipe, Andrieux 19; 21 (BM, G, H-BR!, M!, NY, syntypes).

Pogonatum beschellei Hampe in Besch., Mém. Soc. Sci. Nat. Cherbourg 16:207. 1872. — Type: Mexico, Desierta Vieja, Valle de Mexico, XI.1865 Bourgeau 1336 (NY!, H-SOL!, isotypes). — Synonymized by Smith (1975a).

Pogonatum cylindricum Schimp. in Besch., Mém. Soc. Sci. Nat. Cherbourg 16:211. 1872. — Type: Mexico, Vera Cruz: Orizaba, F. Müller (BM!, lectotype, vide Menzel 1986a). — Synonymized by Brotherus (1909).

Pogonatum ericaefolium Besch., Mém. Soc. Sci. Nat. Cherbourg 16:210. 1872, syn. nov. — *P. orizabanum* Besch., Mém. Soc. Sci. Nat. Cherbourg 16:210. 1872., nom. nud. in synon. — Type: Mexico, Vera Cruz: Orizaba, Bourgeau 3294 (BM, holotype; G, L!, isotypes).

Pogonatum leptocarpum Besch., Mém. Soc. Sci. Nat. Cherbourg 16:209. 1872, syn. nov. — Type: Mexico, Vera Cruz: Cordillera, Pic d'Orizaba, VI–X.1840 Galeotti 6982 (BM, holotype; BR!, G, isotypes).

?*Pogonatum macropogon* Schimp. in Besch., Mém. Soc. Sci. Nat. Cherbourg 16:211. 1872, syn. nov. — Type: Mexico, Vera Cruz, F. Müller Herb. Schimper.

Pogonatum schlumbergeri Schimp. in Besch., Mém. Soc. Sci. Nat. Cherbourg 16:210. 1872, syn. nov. — Type: Mexico, Vera Cruz: Orizaba, F. Müller (BM!, holotype).

Polytrichum sartorii C. Müll., Linnaea 38:621. 1874, syn. nov. — *Pogonatum sartorii* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 258. 1875 (Adumbratio 1:720). — Type: Mexico, Mirador, Sartorius (NY!, isotype).

Pogonatum barbanum Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(1): 170. 1892, syn. nov. — Type: Costa Rica, forêts du Barba, 1889 Pitier 5579 (BR!, G, H-BR!, isotypes).

Polytrichum leptopelma C. Müll., Bull. Herb. Boissier 5:178. 1897, syn. nov. — *Pogonatum leptopelma* (C. Müll.) Par., Ind. Bryol. 982. 1898. — Type: Guatemala, inter Culbulco et Sojabay, IX.1870 Bernoulli & Cario 106 (B, GOET!, isotypes).

Pogonatum lozanoi Card., Rev. Bryol. 37:6. 1910, syn. nov. — *P. ericaefolium* var. *lozanoi* (Card.) Card. in Thér., Smithsonian Misc. Collect. 81(1): 26. 1928. — Type: Mexico, Hidalgo: near Honey-station, 7 000 ft., 11.VI.1908 Pringle 15117 (FH!, isotype).

Pogonatum barnesii Card., Rev. Bryol. 38:38. 1911. — Type: Mexico, Jalisco: Ezatlan, talus humides, 1908 Barnes 280 (NY!, isotype). — Synonymized by Smith (1975a).

Pogonatum ekmanii Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 15:230. 22:4. 1941, syn. nov. — Type: Cuba, Oriente: Sierra Maestre, Pico Turquino, 2 040 m, 18.IV.1915 Ekman 5519 (NY!, syntype); Haiti, Massif de la Hotte, Torbec, Mt. Formon, 2 225 m, 1.I.1927 Ekman 7507 (US, syntype).

Pogonatum hirtellum Kelly, Bryologist 44:94. 1–10. 1941. — Type: Mexico, Michoacan: Hidalgo, on clay of cut along highway to Moralia, 19°50'N, 101°W, 2 000 m, 18.V.1939 T.C. Frye & E.M. Frye 2810 (BR!, CANM!, H!, MO!, NY!, isotypes). — Synonymized by Smith (1975a).

Pogonatum comosum and *P. campylocarpum* may closely resemble each other and as noted above, more extensive study might even prove them to be conspecific. The two species have been distinguished by width of sheath and number of ventral lamellae (Menzel 1986a). I, instead, emphasize other characters such as form of apical cells of the lamellae as described in discussions below and under *P. procerum*.

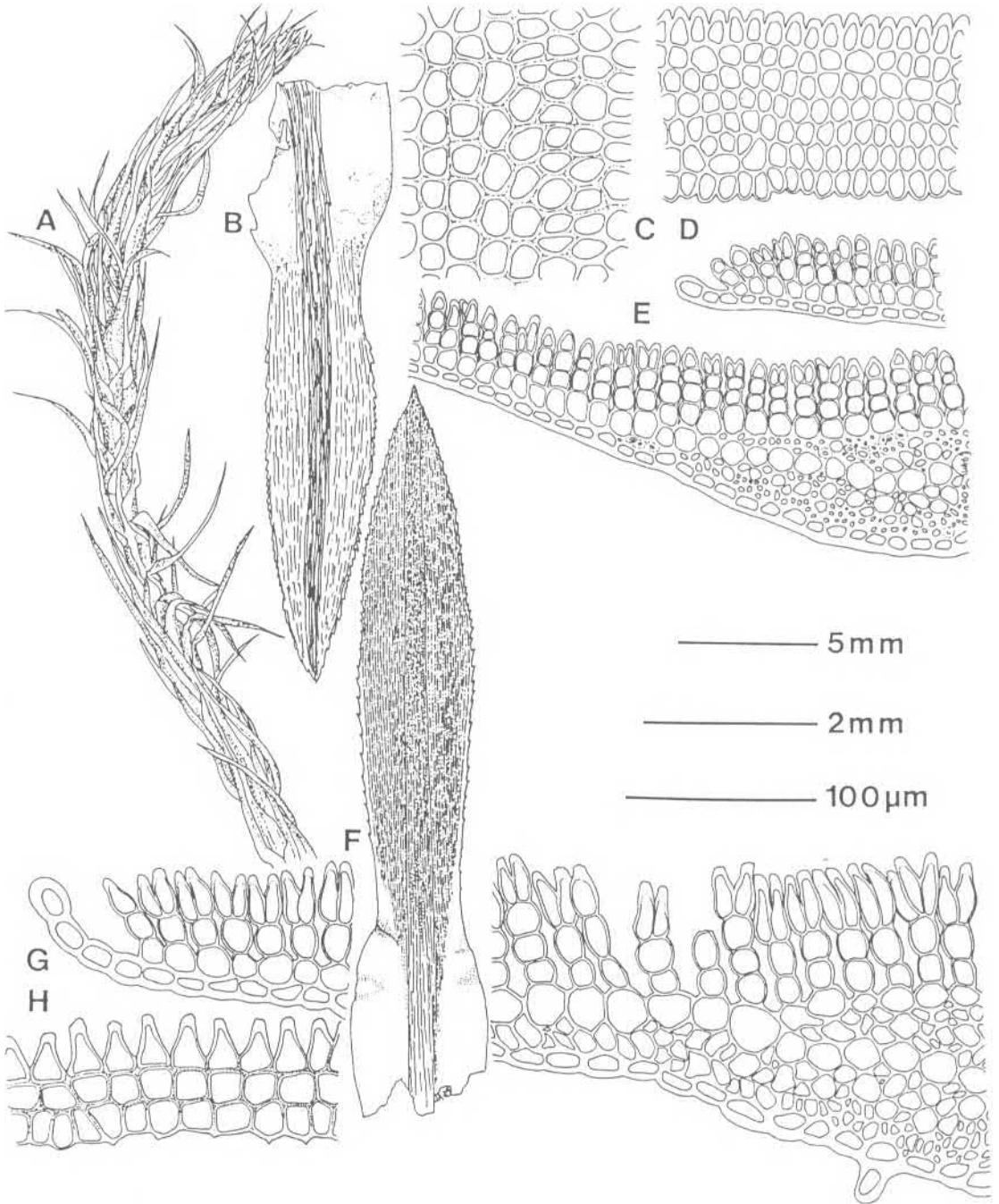


Fig. 6A-H. — A-E: *Pogonatum comosum*. A. Habit, B. Leaf, C. Dorsal cells of blade, D. Lamella in side view and E. Leaf cross-section. A and E (Manuel 663, H) and B-D (Santos 3602, H). — F-H: *P. microstomum*. F. Leaf, G. Leaf cross-section and H. Lamellae in side view (Hara et al. 11.V.1960, NICH). — Use the 5 mm scale for A, 2 mm scale for B and F, and 100 µm scale for C-E, G and H.

P. comosum is a common plant in Central America. In the past it has been described under many different names as indicated by the long list of synonyms given above. The plants show great variation in size, form of apical cells and shape of the leaves. Traditionally more than one species have been distinguished under such names as *P. cylindricum* and *P. glaciale*. In all of them the apical cells of lamellae are typically high and notched. The proportion of geminated apical cells continuously varies from practically absent to predominant. The blade is typically constricted above the sheath. This constriction is often very faint in large plants and the leaves are gradually narrowed to the sharp apex. However, I do not give formal recognition to this variation.

Like the closely related *P. campylocarpum*, *P. comosum* is a plant of open habitats growing on bare soil at 1 350–3 660 m.

Distribution — Am 2: Costa Rica, El Salvador, Guatemala, Honduras, Mexico.

11. *Pogonatum microstomum* (Schwaegr.) Brid. (Figs. 6F–H, 27 – map)

Bryol. Univ. 2:745 1827. — *Polytrichum microstomum* R. Brown ex Schwaegr., Spec. Musc. Suppl. 2(2): 10. 154. 1826. — *Pogonatum minutum* Brid., Bryol. Univ. 2:127. 1827, nom. illeg. superfl. — Type: Nepal, Taylor (FH!, isotype).

Polytrichum clavatum Dozy & Molk. in Miquel, Pl. Jungh. 3:326. 1854, syn. nov. — *Pogonatum clavatum* (Dozy & Molk.) Dozy & Molk., Bryol. Jav. 1:40. 30. 1856; Ned. Kruidk. Arch. 4, 1:75. 1856. — Type: Indonesia. Java: Mt. Kawi, *Junghuhn 696* (L!, holotype; L!, H-BR!, isotypes).

Pogonatum paucidens Besch., Rev. Bryol. 18:89. 1891. — Type: China. Yunnan: bois de Ma eul Chan, 2 800 m, 9.VII.1889 *Delavay* (PC!, isotype). — Synonymized by Salmon (1901).

Pogonatum macrocarpum Broth., Symb. Sin. 4:135. 1929, syn. nov. — Type: China. Yunnan: ab urbe Yünnanfu septentr. versus ad viam parvam directam Huili ducentem, in regione calide temperata ad serram durifruticetorum prope vicum Djiaohsi, substr. arenaceo, 2 400 m, 17.III.1914 *Handel-Mazzetti 685* (H-BR!, holotype).

Pogonatum submicrostomum Broth., Symb. Sin. 4:134. 1929, syn. nov. — Type: China. Sichuan: auf Schiefer im *Rhododendron*-Wald der ktp. St. am Gonshiga SW von Muli, 4 300–4 400 m, 6.VIII.1915 *Handel-Mazzetti 7508*; Yunnan: NW Yunnan, in tergi inter vicos Haba et Dugwantsun ad austro-orient. pagi Dschungdien ("Chungtien"), regione frigide semperata lat. occ. locis humosis, substr. schisto-argilloso, 4 050 m, 22.VI.1915 *Handel-Mazzetti 6870* (H!, syntype).

Pogonatum mirabile Horik., Bot. Mag. (Tokyo) 49:671. 26. 1935. — Type: China. Taiwan: Chiayi, Mt. Morrison, 18.–19.VIII.1932 *Horikawa* (HIRO, holotype, probably destroyed). — Synonymized by Noguchi (1958).

?*Pogonatum subclavatum* Dix., Ann. Bryol. 12:56. 1939, syn. nov. — Type: Indonesia. Sumatra: G. Kemiri, 3 200–3 300 m, 8.III.1937 *Steenis 10257* Herb. Bog. 4018 (?BM).

?*Pogonatum longicollum* Chen & Wan in Chen, Gen. Musc. Sin. 2:304. 1978, syn. nov. — Type: China. Yunnan: Adunzi, Sanjia village, on soil of mountain slope, 3 000 m, 23.IX.1935 *Wang 5329a* (PE!, holotype).

Pogonatum microstomum var. *ciliatum* Xu & Xiong, Acta Bot. Yunnanica 6:183. 8:15–18. 1984, syn. nov. — Type: China. Xizang: Gyirong Xian, on ground in *Abies* forest, 3 200–3 700 m, pH 5.5–6, 4.VII.1975 *Chen Chu-kuen 265* (YUNU, holotype; H!, KUN, isotypes).

Pogonatum microstomum is perhaps the most easily identified and one of the least variable species of the genus. However, it has been described under a variety of names. The species is easily identified even in the field by its apically wide and basally narrow blade. The sheath is abruptly narrowed and the leaf-margins have numerous sharp teeth. Teeth are also abundant on the dorsal side of the costa. The color of the leaves is characteristic, olivaceous to brownish because of the strong incrassation of dorsal walls of the blade cells. In a dry condition the leaves are incurved and appressed. Especially diagnostic are the bottle-shaped and geminate apical cells of the lamellae. These terminal cells are normally smooth, occasionally with slight papillosity.

In some specimens from Sichuan and Yunnan, China (including the type specimen of *Pogonatum paucidens*), numerous teeth are arranged in oblique rows on the dorsal side of the blade resembling some *Atrichum* species. Similar dentation is also present in *P. nudiusculum* Mitt. (Smith Merrill 1987) as well as in some specimens of the African *P. gracilifolium* Besch. and the mostly Eurasian *P. aloides* (Hedw.) P. Beauv. *P. microstomum* may have rhizoids on the dorsal side of the costa and on the sheath margins, a feature unusual in the family but they have also been found in *P. rufisetum* and in some other species such as *P. tortile* and *P. neesii*. Xu and Xiong (1984) described *P. microstomum* var. *ciliatum* based on specimens with short marginal rhizoids. I do not think that these features deserve any formal taxonomic recognition as they are probably ecologically induced and seem to be fairly common in some areas. Rhizoids on basal part of the leaves are present even in type material of *P. microstomum*.

In the field *Pogonatum microstomum* might be mistaken for *P. urnigerum*, which often grows in the same habitats. The shape of the leaves (blade widest basally) and coarsely papillose apical cells of the lamellae are, however, reliable distinctive characters of the latter species.

Pogonatum microstomum has been collected at altitudes from 1 000 to over 4 000 m. It is especially abundant on cool upper slopes in orotemperate and orboreal forests. It grows on soil by trails and roadbanks, and has been collected from soil-covered rocks and cliffs and fallen trunks as well. *P. micro-*

stomum even thrives on shaded forest floor, but it is then confined to sites of fairly recent disturbance where, in the long run, it is unable to compete with dominant pleurocarpous species of the ground layer.

Illustrations — Gangulee 1969: 143 (fig. 65); Li 1985: 446 (fig. 192:7-11).

Distribution — As 2: China; As 3: Burma, Bhutan, India, Nepal, Sikkim, Sri Lanka, Thailand, Vietnam; As 4: Indonesia, Philippines.

12. *Pogonatum nipponicum* Nog. & Osada in Osada (Figs. 7A–F, 26 – map)

J. Hattori Bot. Lab. 28:195. 10. 1965. — Type: Japan. Kiu-shu: Miyazaki, Mt. Shinmoe, 30.III.1930 *Noguchi* 9329 (Herb. Noguchi, holotype).

Pogonatum nipponicum is identified by its very peculiar habit when dry with brownish leaves mostly curved to one side. The blade of the leaves is widest apically with short and very narrow sheath. As noted already by Osada (1965) these features are characteristic of sterile plants. However, by closer study other unique and easily observed characters of the gametophyte can also be found in fertile plants. The apical cells of the lamellae are typically narrow and retuse in cross-section and they are slightly pointed by unequal incrossation of the outer walls. By these characters *P. nipponicum* is distinguished from other sympatric species of the genus such as *P. neesii*, *P. inflexum* (Lindb.) Sande Lac. and *P. otaruense* Besch. The last species resembles *P. nipponicum* by its firm habit and the apical cells of the lamellae with geminations. The form of the apical cells of the lamellae is, however, clearly different in the two. They are irregularly crenate in side view and never retuse as seen in cross-section in *P. otaruense*. The marginal serration of the latter is also less pronounced than that of *P. nipponicum*. The apical cells of the lamellae in *P. inflexum* are widened and never geminate, neither in *P. neesii*. The form of the leaves of the two is also totally different from that of *P. nipponicum*, as the blade is always widest basally and leaves are contorted to various degrees in the dry condition.

Osada (1965) gives *Pogonatum aloides*, *P. otaruense* and *P. neesii* as the closest relatives of *P. nipponicum* and ignores the affinity with the SE Asian *P. microstomum* and its allies. Many undisputed apomorphic characters such as the form of the apical cells of the lamellae and the apically widest blade are shared by the species and indicate a close relationship.

As already exhibited by its compact and firm habit *Pogonatum nipponicum* favors fairly dry and adverse habitats, growing on thin soil on rocks and stone-walls from sea level to ca. 1 200 m. The range of

P. nipponicum is very small and it is confined almost exclusively to the meridional (warm-temperate) vegetation zone of Japan and Korea.

Illustrations — Osada 1965: 197 (fig. 10); Noguchi 1987: 43 (fig. 14C).

Distribution — As 2: Japan, Korea (after Osada 1965).

Specimens examined (representative) — As 2: JAPAN.

Honshu: Aichi, Horai-cho, Mt. Horaizi, *Cryptomeria japonica*–*Aucuba japonica* woodland on NE-slope, 400–550 m, 22.III.1970 *Koponen* 11134 (H!); Komegatani, Mt. Ohuchi, 3.III.1935 *Magohuku* 11 (TNS!); Saitama, Chichibu, road side cliff in valley with deciduous temperate woodland, 740 m, 25.V.1971 *Koponen* 19581; Hokkaido: Kamikawa, Kamikawa-cho, Mt. Daisetsu Nature Park, Sounkyo spa, Momizitani, canyon of small river with *Picea*–*Abies*–*Acer*–*Cercidiphyllum*–*Tilia* wood, ca. 700–800 m (lower oroboreal zone), 9.VIII.1970 *Koponen* 15464 (H!).

13. *Pogonatum otaruense** Besch. (Figs. 7G, H, 27 – map)

Ann. Sci. Nat. Bot. sér. 7, 17:352. 1893. — Type: Japan. Hokkaido: (Yezo), Otaru, 1889 *Faurie* 79 (PC, H-BR!, KYO, isotypes).

Pogonatum otaruense is closely related to the SE Asian *P. microphyllum* (Dozy & Molk.) Dozy & Molk., which it resembles by its firm and stout habit. Its leaves are similarly stiff and incurved when dry. A diagnostic character is the regular gemination of the apical cells of the lamellae in *P. otaruense*. Marginal serration is also more pronounced than in *P. microphyllum*. In size, Japanese plants are generally smaller.

As is its SE Asian relative, *Pogonatum otaruense* is a pioneer plant of volcanic ash and rocks and is a rare plant, confined almost exclusively to the meridional zone at lower elevations (Osada 1965).

Illustrations — Osada 1965: 191 (fig. 7); Noguchi 1987: 33 (fig. 12C).

Distribution — Endemic for Japan.

Specimens examined (representative) — As 2: JAPAN.

Kiu-shu: Miyazaki, Nichinan-shi, Obi, hilly terrain N of Obi castle, 20–50 m, 8.V.1970 *Koponen* 10143; Honshu: Tottori, Mt. Daisen, Amidagawa between Kawadoko and Amidaki, river valley with cool temperate *Fagus*–*Acer*–*Betula* wood, 650–800 m, 20.V.1971 *Koponen* 21901; Hokkaido: Ishikari, between Mt. Tarumae (active volcano) and L. Shikotsu-ko, river valley bored in tuff cliff (moss tunnel), 300–500 m, 10.VI.1971 *Koponen* 21679 (H!).

14. *Pogonatum microphyllum* (Dozy & Molk.) Dozy & Molk. (Figs. 7I–K, 27 – map)

Bryol. Jav. 1:39. 29. 1856, Ned. Kruidk. Arch. 4(1): 75. 1856. — *Polytrichum microphyllum* Dozy & Molk. in Miquel, Pl. Jungh. 3:326. 1854. — Type: Indonesia. Java: in rupibus desertis montis Merapi, *Junghuhn* (L!, holotype).

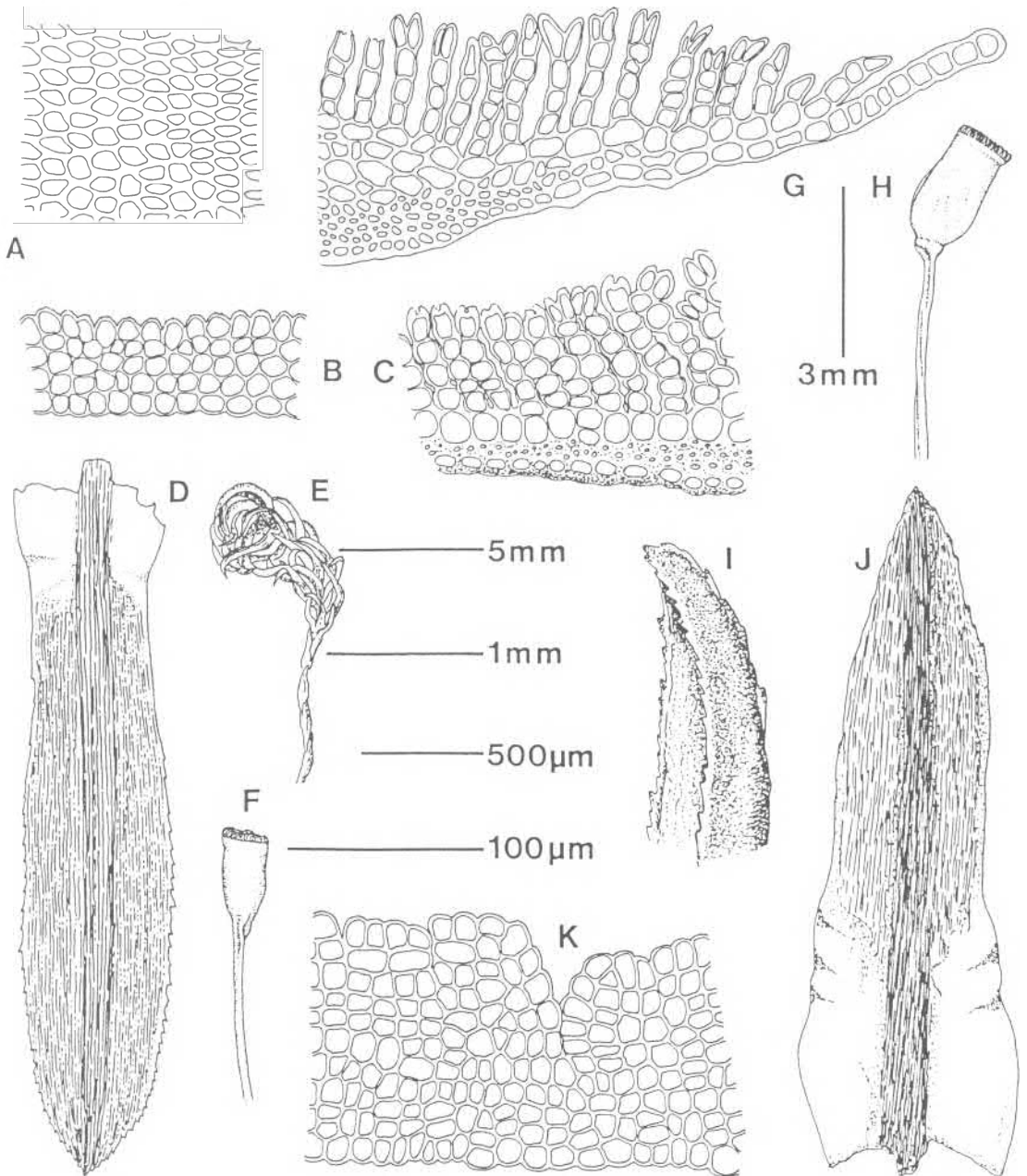


Fig. 7A-K. — A-F: *Pogonatum nipponicum*. A. Dorsal cells of blade, B. Lamellae in side view, C. Leaf cross-section D. Leaf (Watanabe 14092, TNS), E. Habit (Koponen 19581, H) and F. Capsule (Sugino 18.III.1962, TNS). — G, H: *P. otaruense*. G. Leaf cross-section (Koponen 21679, H) and H. Capsule (Koponen 10143, H) — I-K: *P. microphyllum*. I. Cucullate leaf-apex, J. Leaf and K. Lamella in side view (Meijer B4201, L). — Use the 3 mm scale for F and H, 5 mm scale for E, 1 mm scale for D and J, 500 µm scale for I, and 100 µm scale for A-C, G and K.

Polytrichum obtusum C. Müll., *Linnaea* 37:171. 1872. — *Pogonatum obtusum* (C. Müll.) Jaeg., *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* 1873–74: 265 (Adumbratio 1:727). — Type: Philippines, in regione montosa, *Cumming 2215* (BM!, isotype). — Synonymized by Eddy (1988).

Pogonatum microphyllum fo. *elatum* Dozy & Molk., *Bryol. Jav.* 1:39. 1856, *syn. nov.* — *P. microphyllum* var. *elatum* (Dozy & Molk.) Fleisch., *Musci Buitenzorg* 4:1586. 1923. — Type: Indonesia. Java: West-Java, Gedeh auf dem alten Kraterboden Aloen-Aloen, 2 800 m (?L!, holotype).

Pogonatum microphyllum var. *integrifolium* Broth. ex Fleisch., *Musci Buitenzorg* 4:1586. 1923, *syn. nov.* — Type: Indonesia. Java: Merapi, ca. 3 000 m, *Warburg* (FH!, holotype).

?*Pogonatum sexangulare* Mitt. ex Fleisch., *Musci Buitenzorg* 4:1586. 1923, *nom. nud.* — Original collection: Sri Lanka (Ceylon).

Pogonatum microphyllum resembles *P. microstomum* by its firm habit with stiff and crowded leaves which are incurved but not contorted in the dry condition. Accordingly the dorsal stereid band of the leaves is wide, filling almost the whole leaf-width; the ventral band consists of only few cells. The marginal teeth are small and normally restricted to the upper half of the blade. Dorsal serration of the costa is also indistinct. Apically the leaves are clearly cucullate. All these characters make identification easy. Distinction from *P. neesii* is easy, also, as the latter species has retuse and finely papillose apical cells of the lamellae and, leaves with strong marginal serration and without distinctly cucullate apices. The leaves of *P. neesii* are also more contorted in the dry condition.

Lamellae with irregularly crenate apical cells are typical for *Pogonatum gracilifolium*, *P. tahitense* Schimp., *P. tubulosum* Dix. and the Japanese *P. otaruense*. The last is closely related to *P. microphyllum*, whereas the other three species are more closely related to *P. neesii*. In *P. microphyllum* the apical cells are irregular but very rarely geminate and never retuse.

Study of the type specimen of *Pogonatum microphyllum* var. *integrifolium* revealed the plants to be extremely small with entire leaf-margins or only possessing very small apical teeth. However, I do not think this kind of variation deserves formal taxonomic recognition. Marginal serration of *P. microstomum* is in general very weak and the size of plants also varies to a great extent. Similar diminutive forms with entire margins have also been found in other species and these abnormalities are probably induced by some ecological factors.

The majority of specimens of *Pogonatum microphyllum* have been collected on volcanoes. Some specimens have been found even near active craters and apparently *P. microphyllum* is one of the first pioneers on bare volcanic ash. It grows at altitudes of 950–3 250 m in open and dry habitats on rock

and soil. Because of its habitat preference *P. microphyllum* is far less common than, for example, the almost ubiquitous *P. neesii* of the same areas.

Illustration — Hyvönen 1986: 124 (fig. 10).

Distribution — As 4: Indonesia, Papua New Guinea, Philippines; Oc: Fiji.

15. *Pogonatum japonicum* Sull. & Lesq. (Figs. 8A–C, 28 – map)

Proc. Amer. Acad. Arts 4:278. 1859. — Type: Japan, Mts. of Hakodaki, *Wright* (NY!, isotype).

Polytrichum grandifolium Lindb., *Acta Soc. Sci. Fenn.* 10:264. 1872. — *Pogonatum grandifolium* (Lindb.) Jaeg., *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* 1873–74: 253. 1875 (Adumbratio 1:715). — Type: USSR. Far East: Amur Distr., Bureja, VII.1859 *Schmidt* (H-SOL!, holotype). — Synonymized by Iwatsuki (1966).

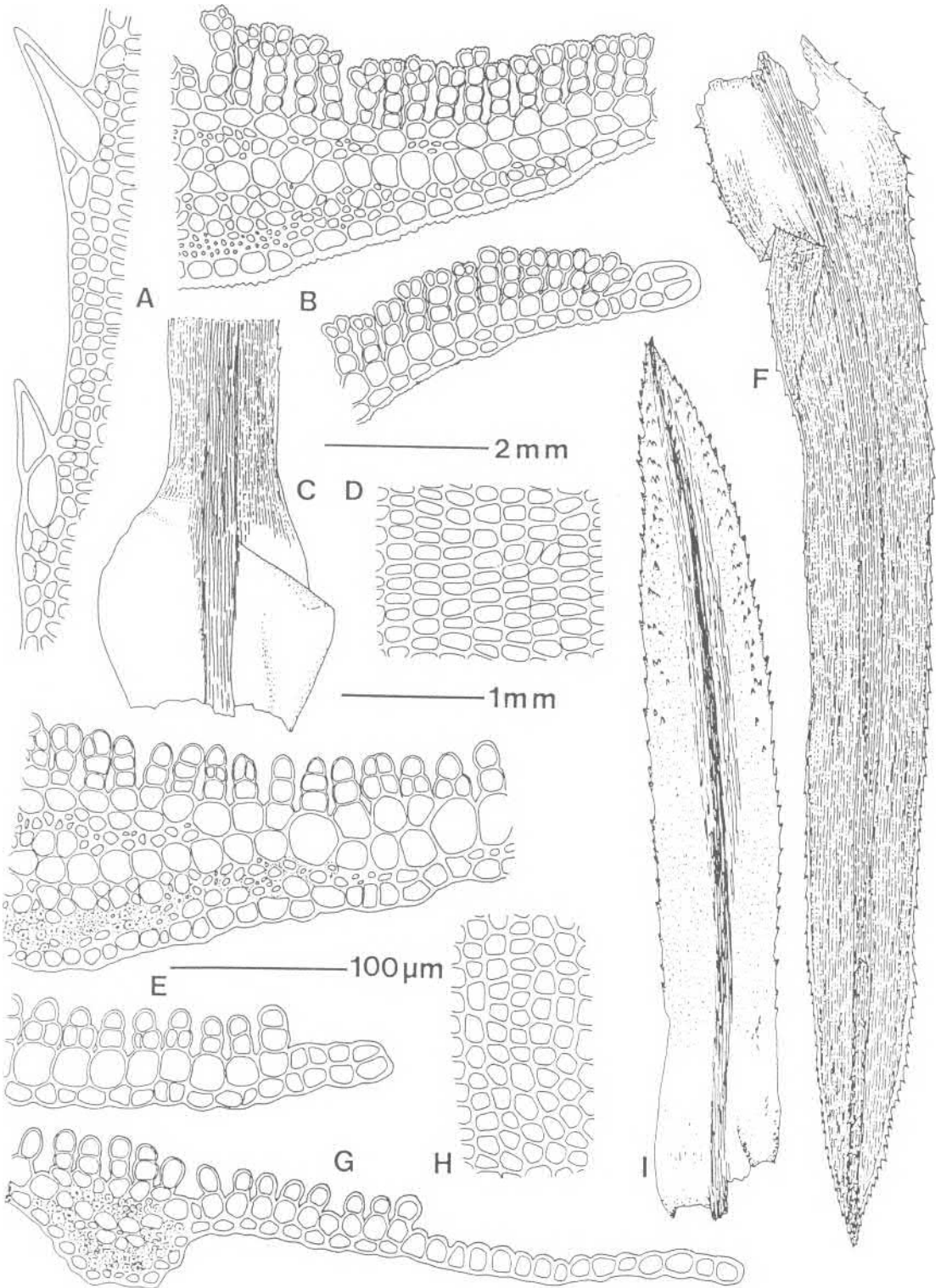
Pogonatum grandifolium var. *tosanum* Card., *Bull. Soc. Bot. Genève sér. 2*, 1:130. 1909. — Type: Japan, Tosa, *Gono; Okamura*. — Synonymized by Osada (1965).

Pogonatum grandifolium var. *ramosum* Ihs., *Classif. Moss. Japan* 100. 1932. — Type: Japan. Shikoku: Ehime, Mt. Isizuti, *Yagi*. — Synonymized by Osada (1965).

In the field *Pogonatum japonicum* might be mistaken as *P. contortum* (Brid.) Lesq. or *P. cirratum*, or as species of the genera *Polytrichastrum* or *Polytrichum*. Closer study reveals the coarsely papillose and mostly geminate apical cells which is readily observed diagnostic character. Gemination of apical cells may be rare in some leaves but coarse papillosity is always seen and is also found on dorsal cells of the blade. In *P. contortum* the leaves are more fragile with a much wider unistratose margin. Apical cells of the lamellae are smooth as in *P. cirratum*. In both species leaf-margins are also typically serrate, while in *P. japonicum* they are dentate (Fig. 8A), reminiscent of the genera *Polytrichastrum* or *Polytrichum*. The margins are unistratose, 3–4 cell-rows wide with a partly bistratose outer row. The dorsal stereid band of the leaves is strong, fairly wide and clearly visible as a lighter area in younger leaves. The ventral stereid band is reduced. In the dry condition the leaves are typically contorted as in *Pogonatum fastigiatum* Mitt. and *P. cirratum*.

Pogonatum japonicum is a plant of cool forests in temperate and boreal zones. In more southern localities it is confined to ecologically corresponding sites in the mountains. According to Osada (1965), it has been collected at the altitudes of 400–2 400 m in Japan. In the northern part of its range the species probably grows even at sea level. The closely related *P. fastigiatum* is an ecological parallel from the Himalayan area.

Illustrations — Osada 1965: 185 (fig. 5); Noguchi 1987: 43 (fig. 14B).



Distribution — As 1: USSR; As 2: China, Japan, Korea.

Specimens examined (representative) — As 2: CHINA. Jilin: Antu, 12 km NW of Mt. Chang Bai, primeval *Abies nephrolepis*-*Larix gmelini*-*Pinus koraiensis* forest, lower oroboreal zone, 41°40'N, 128°00'E, 1 250 m, 24.IX.1981 *Koponen 37125*. — JAPAN. Honshu: Gifu, Mashita-gun, Osaka-cho, Mt. Ontake National forest, valley of small river with cliffy shores NE of Nigorigo spa, lower oroboreal zone, 1 800–1 900 m, 20.VIII.1970 *Koponen 16478* (H!).

16. *Pogonatum fastigiatum* Mitt. (Figs. 8D–F, 28 – map)

J. Linn. Soc., Bot. Suppl. 1:154. 1859. — Type: India. E Bengal: Khasia, Kollong rock 8 000–9 000 ft., *Hooker & Thomson 1240* (NY!, lectot. nov.); Sikkim, Chongtam, 6 000 ft., *Hooker 1182*; E Nepal, Nangkli, 10 000 ft., *Hooker 1183*; Nepal, Yalloon mountains, 12 000 ft., *Hooker 1202* (NY!, syntypes).

Polytrichum nudicaule Wright, J. Bot. 29:106. 1891, *syn. nov.* — *Pogonatum nudicaule* (Wright) Par., Ind. Bryol. 984. 1898. — Type: China. Hubei: Hsingshan, 8.IX.1888 *Henry 6840* (BM!, holotype).

Pogonatum arisanense Okam., J. Coll. Sci. Imp. Univ. Tokyo 38(4): 21. 9. 1916. — Type: China. Taiwan: Chiayi, Ali-shan, 6.IV.1914 *Hayata* (NICH!, holotype). — Synonymized by Kuo & Chiang (1987).

Pogonatum submacrophyllum Broth., Ann. Bryol. 1:27. 1928, *hom. illeg.* — Type: China. Taiwan: Taichung Co., Mt. Noko, 6.VIII.1926 *Suzuki 2662* (H-BR!, holotype).

Pogonatum contortum var. *robustum* Dix., J. Bombay Nat. Hist. Soc. 39:795. 1938, *syn. nov.* — Type: India. Assam: Piri, Aka Hills, in forest, 2 700–3 300 m, X.1933 *Bor* (BM!, holotype).

Pogonatum macrophyllum var. *darjeelingense* Gang., Nova Hedwigia 12:418. 82. 1966 (1967), *syn. nov.* — Type: India, (Sikkim?), Darjeeling, Sinchal, *Wichura 2133* (2733?) (BM!, holotype).

The epithet *fastigiatum* has repeatedly been applied to the large species of *Pogonatum* without or with very reduced lamellae, the correct name being *P. proliferum*. Study of all the type material as well as the description indicates that the name *P. fastigiatum* is correctly assigned to robust plants of higher elevations with well developed but low lamellae and peculiar subapical geminations. Another typical feature is the dentate sheath margins.

By their robust habit *Pogonatum japonicum* and *P. cirratum* have also often been confused with *P. fastigiatum*. *P. japonicum* is a plant of more northern latitudes. It has geminate apical cells of the lamellae with distinct coarse papillae. *P. cirratum* occurs in

the same areas as *P. fastigiatum*, but the dorsal cells of the blade of the former species have distinctly in-crassate transverse walls, leaving the lumen small and essentially round. *P. cirratum* is also found at much lower altitudes than mostly oroboreal *P. fastigiatum*. The apical cells of *P. fastigiatum* are typically narrower and smaller than lower cells of the lamellae as seen in cross section. The same feature is also found in many specimens of *P. cirratum* var. *fuscatum* (Mitt.) Hyvönen and regularly in *Polytrichastrum torquatum* Mitt. ex Osada & G.L. Sm. — a plant of the Himalayan area as well. The last two species, however, never have serrate sheath-margins. Cells of the stereid bands in *Pogonatum fastigiatum*, especially those of the ventral band, have much thinner walls than those of *P. cirratum*.

Ecologically *Pogonatum fastigiatum* is clearly a plant of cool environments, being most abundant in orohemiboreal and oroboreal vegetation zones of high mountains. It has been collected at altitudes of 1 600 to over 3 600 m. Like *P. microstomum*, *P. fastigiatum* also seems to thrive in fairly shaded habitats on the forest floor, where it is restricted to sites of recent disturbance and is unable to compete with dominant species of the ground layer.

In distribution *Pogonatum fastigiatum* is a Himalayan plant and its range reaches from India to Taiwan. The use of the name *P. fastigiatum* has repeatedly been erroneous and consequently the distribution records below are based only on verified specimens.

Illustrations — Okamura 1916: 23 (fig. 9 as *Pogonatum arisanense*).

Distribution — As 2: China; As 3: Bhutan, India, Nepal, Sikkim, Thailand.

17. *Pogonatum nudiusculum* Mitt. (Figs. 8G–I, 28 – map)

J. Linn. Soc., Bot. Suppl. 1:153. 1859. — *Pseudotrichum nudiusculum* (Mitt.) Smith Merrill, Mem. New York Bot. Gard. 45:466. 1987. — Type: India, Khasia, 4 000 ft., *Hooker & Thomson 1249* (BM!, H-BR!, L!, isotypes).

Pogonatum handelii Broth., Symb. Sin. 4:135. 1929, *syn. nov.* — Type: China. Yunnan: Diabasfelsen der tp. St. am Osthang des Dji-schan ne von Dali (Talifu), 3 050–3 350 m, 21.V.1915 *Handel-Mazzetti 6396* (H-BR!, holotype).

?*Pogonatum hetero-prolificum* Horik., Bot. Mag. (Tokyo) 48:461. 4. 1934, *syn. nov.* — Type: China. Taiwan: Ilan, Mt.

Fig. 8A–I (Left). — A–C: *Pogonatum japonicum*. A. Marginal teeth of blade, B. Leaf cross-section and C. Basal part of leaf (*Koponen 15385*, H). — D–F: *P. fastigiatum*. D. Dorsal cells of blade, E. Leaf cross-section and F. Leaf (*Kanai et al. 16.XI.1963*, NICH). — G–I: *P. nudiusculum*. G. Leaf cross-section, H. Dorsal cells of blade and I. Leaf (*Zanten 683941*, H). — Use the 2 mm scale for C and F, 1 mm scale for I, and 100 µm scale for A, B, D, E, G and H.

Taping, 23.VIII.1932 Horikawa (HIRO, holotype, probably destroyed).

?*Pogonatum oligotrichoides* Horik., J. Jap. Bot. 11:416. 2. 1935, *syn. nov.* — Type: China. Taiwan: Nantou, Mt. Morrison (Kodamayama-Tataka), on soil, 18.VIII.1932 Horikawa (HIRO, holotype, probably destroyed).

?*Pogonatum manchuricum* Horik., J. Jap. Bot. 12:24. 10. 1936, *syn. nov.* — Type: China. Manchuria: Kirin, Wei-Hu-Ling, on moist soil, 23.VII.1935 Horikawa (HIRO, holotype, probably destroyed).

Pseudatrichum spinosissimum Reim., Notizbl. Bot. Gart. Berlin-Dahlem 15:401. 1941. — Type: China. Guizhou: Simi-yao, Pa-na, Cheng-feng, on cliff, 22.X.1930 Tsiang 4303 (B, holotype, probably destroyed; PE, isotype). — Synonymized by Smith Merrill (1987).

?*Pogonatum norkeittii* R.S. Chopra, Taxon. Indian Mosses 25. 1975, *nom. inval.* — Original collection: Nepal, on way from Sandakphu to Phalut, growing in loose tufts on moist soil rich in humus, 3 600 m, Chopra 1553 (Herb. Panjab Univ., holotype).

In habit *Pogonatum nudiusculum* resembles *P. cirratum*, *P. proliferum* or large specimens of *P. neesii*. All have their leaves contorted when dry. *P. nudiusculum* and *P. proliferum* differ from both *P. cirratum* and *P. neesii* because they have fewer ventral lamellae, and these are restricted to the central part of the leaves. *P. nudiusculum* has normally less than 20 lamellae and they are 2–3 cells high, while, in *P. proliferum*, they are seldom more than 1 cell high and almost exclusively restricted to the costal area.

The type material of *Pogonatum manchuricum* is most probably destroyed and thus the identity of the plant will remain dubious. However, from the original illustrations and description, I am inclined to assume that it is conspecific with *P. nudiusculum*. I did not study the type of *P. norkeittii* either, and consequently synonymization is provisional. It is also possible that the two species are conspecific with *P. proliferum*, another species with approximately the same distribution but it is larger and more delicate in its habit. The latter species is also a plant of warmer habitats and occurrence at high altitudes in the Himalayas and in northern China is unlikely.

Smith Merrill (1987) assigned *Pogonatum nudiusculum* to the monotypic genus *Pseudatrichum*. He drew attention to the oblique rows of dorsal teeth on the blade — a feature suggesting *Atrichum*. The

cells of the blade are so small that one is reminded of *Lyellia* R. Brown or *Bartramopsis* Kindb. *P. nudiusculum* is also reminiscent of the latter two genera because of the wide bistratose portion of the blade. However, I include *P. nudiusculum* in *Pogonatum* as it has all the three synapomorphic characters shared by, and typical of, all species of the genus. Its position is, however, enigmatic and it has many unique characters. Tentatively it is included in subg. *Catharinella* as the most parsimonious alternative.

Pogonatum nudiusculum is a plant of the oromediterranean and orotemperate zones, being collected at 1 600–3 600 m. It thrives on bare soil in fairly shaded conditions.

Illustrations — Horikawa 1934: 461 (fig. 4 as *Pogonatum heteroproliferum*); Horikawa 1935b: 416 (fig. 2 as *P. oligotrichoides*); Gangulee 1969: 133 (fig. 59); Smith Merrill 1987: 468 (figs. 1–4. as *Pseudatrichum nudiusculum*).

Distribution — As 2: China; As 3: Bhutan, India, Nepal, Sikkim (Gangulee 1969); As 4: Philippines.

Specimens examined (representative) — As 2: CHINA. Taiwan: Pingtung: first water resource to Kwai-ku, partially shaded dry slope, on soil, 1 600–2 190 m, 17.VII.1968 Chuang 1267 (H!). — As 4: PHILIPPINES. Luzon: Mt. Tabayoc, Lake Ingcolos, 2 350 m, 16°42'N, 120°53'E, Jacobs B517 (L!).

18a. *Pogonatum cirratum* (Sw.) Brid. subsp. *cirratum* (Figs. 9A–E, 28 – map)

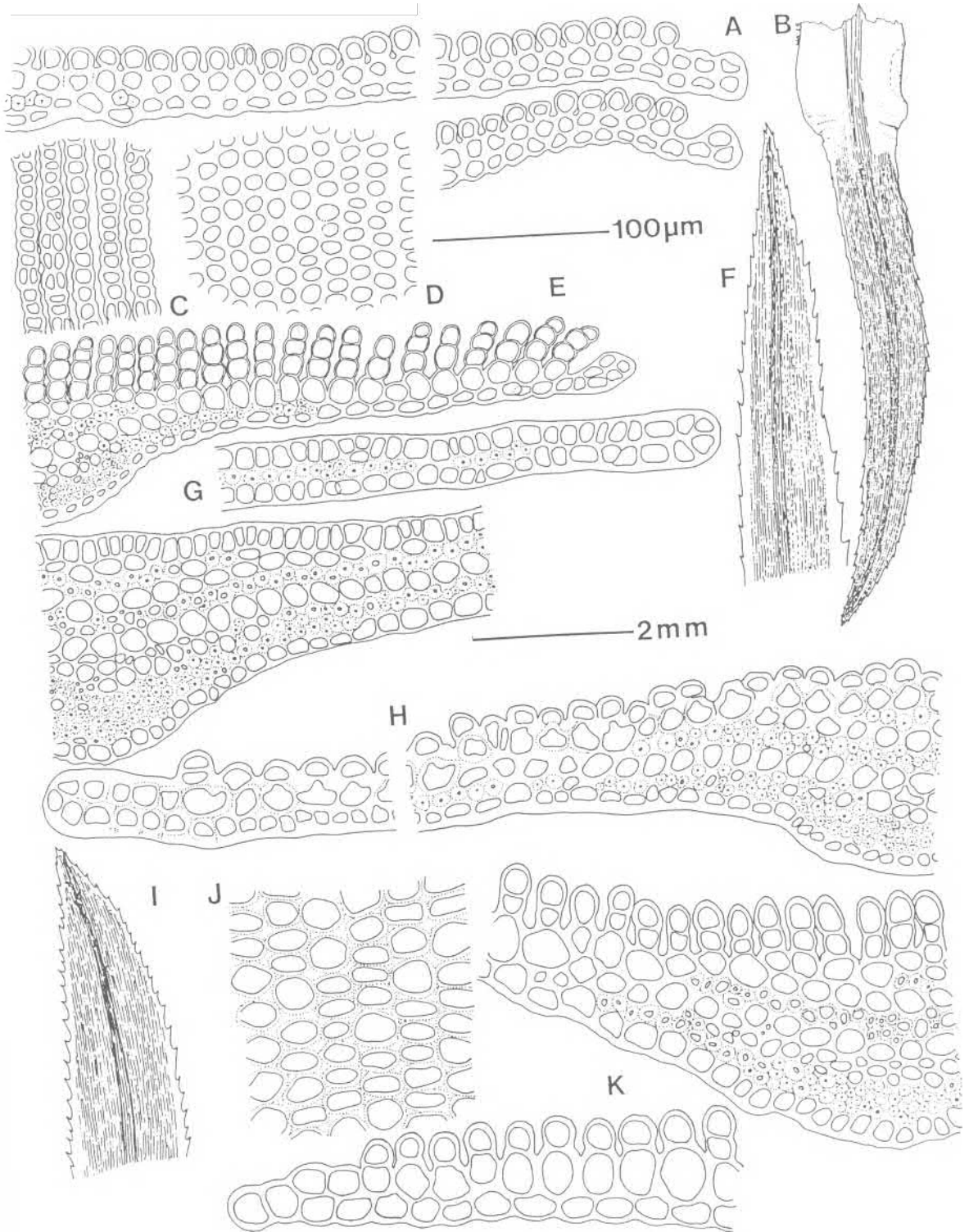
Bryol. Univ. 2:110. 1827. — *Polytrichum cirratum* Sw., J. Bot. (Schrader) 1800(2): 175, 176. 4. 1801. — *Pogonatum convolutum* var. *cirratum* (Sw.) Par., Ind. Bryol. 979. 1898. — Type: Indonesia, Java, Thunberg 25818 (UPS!, lectotype, vide Hyvönen, 1986; S, isolectotype).

Pogonatum serpeninum Par., Ind. Bryol. 987. 1897, *nom. nud.* — Original collection: Papua New Guinea. Central: distr. Moresby, in montosis MoRoka, 1 300 m, VIII.1893 Loria sub. no. 758 (H-BR!, M!). — Synonymized by Hyvönen (1986).

Pogonatum lyellioides Broth. & Par., Rev. Bryol. 29:96. 1902, *syn. nov.* — Type: Laos (Vietnam?), Tonkin, Col de Nuages, Muong Hom et Phong-Pho, 1 800 m, ad rupes, 6.XII.1901 Mercier (H-BR!, isotype).

?*Pogonatum subpellucidum* Dix., Ann. Bryol. 5:50. 1932, *syn. nov.* — Type: Indonesia. Sumatra: in silvis prope cataractas torrentis Petani, infra Brastagi, 1 350 m, 30.IX.1926 Verdoorn 72b (GRO, isotype).

Fig. 9A–K. — A–D: *Pogonatum cirratum* ssp. *cirratum*. A. Leaf cross-section, B. Leaf, C. Lamellae as seen above and D. Dorsal cells of blade. A and C (Thunberg 25818, lectotype UPS), D (Koponen 17650, H) and B (Sukmadiningrat 121, L). — E: *P. cirratum* ssp. *fuscatum*. E. Leaf cross-section (Touw 8841, L). — F–I: *P. cirratum* ssp. *macrophyllum*. F. Leaf apex, G and H. Leaf cross-section, and I. Leaf apex; F and G (Takaki 30.VII.1971, H), H and I (Clemens 3500, H). — J, K: *P. convolutum*. J. Leaf cross-section and K. Dorsal cells of blade (De Sloover 17268, H). — Use the 100 µm scale for A, C–E, G, H, J and K, and 2 mm scale for B, F and I.



?*Pogonatum hetero-contortum* Horik., Bot. Mag. (Tokyo) 49:593. 25. 1935, *syn. nov.* — Type: Japan. Yakushima: between Ishizuka-kokuyurin (ca. 850 m) and Hananoego, 11.VII.1933 Horikawa (HIRO, holotype, probably destroyed).

Neopogonatum semiangulatum Xu & Xiong, Acta Bot. Yunnanica 6(2): 174. 1. 1984, *syn. nov.* — Type: China. Yunnan: SE Yunnan, Xichou Xian, Fadou, Cao-quo-ging, under broad-leaved and conifer forest, 1 550 m, pH 5.5, 13.III.1978 Zhu 78001 (YUNU, holotype; H!, KUN, isotypes).

Neopogonatum yunnanense Xu & Xiong, Acta Bot. Yunnanica 6(2): 176. 2. 1984, *syn. nov.* — Type: China. Yunnan: S Yunnan, Jinping Xian, Fen-shui-lao-ling, under *Pinus* and *Quercus* forest, pH 5.5, 2 300 m, 30.XII.1958 Zhu 5812 (YUNU, holotype; H!, KUN, isotypes).

Pogonatum cirratum is perhaps the most confusing member of the whole genus. It is widespread and common throughout SE Asia and its variability is at least partly due to insular and complex environment within the wide range. The size of the plants, as well as features of the ventral lamellae and of the marginal serration have all been used to distinguish it from closely related species. Study of abundant material from all parts of its range, however, reveals numerous intermediate forms. Different characters do not correlate and consequently many species names are reduced to synonymy under *P. cirratum*. Extreme forms are, however, so dissimilar that distinction as subspecies seems warranted. This is also done to avoid premature taxonomical conclusions which might further complicate the matter. It is, nevertheless, doubtful whether these taxonomic units are truly monophyletic. Are they more closely related to sympatric forms of the same area than to similar plants in other parts of the range? Huffelen and Vries (1980) undertook a biometric study of many specimens and their conclusions are that distinction only at the sub-specific level is warranted.

Typical features distinguishing *Pogonatum cirratum* and its subspecies from other species of the genus are the dorsal cells of blade which have extremely incrassate cell-walls with a small and rounded cell-lumen as seen above (Fig. 9d).

Subsp. *cirratum* is distinguished from subsp. *fuscatum* by its larger size and wider leaves. The lamellae are only 1–2 cells high with partly geminate apical cells. The leaf-margins are uni- to bistratose. The sheath is generally distinctly serrate in plants collected in the western part of the range, but specimens from other parts of the range resemble Indonesian plants except that they lack the basal serration.

Japanese plants are tentatively included in subsp. *cirratum* although they have traditionally been identified as *Pogonatum spurio-cirratum* Broth. The description of the latter species is based on material collected in the Philippines. Japanese material do not match these Philippine plants, which have higher la-

mellae with small apical cells of the lamellae, and the plants are generally smaller than those from Japan.

Pogonatum cirratum subsp. *cirratum* is a plant of soil in fairly moist and shaded sites. It has been collected from near sea level to over 3 000 m.

Illustrations — Horikawa 1935a (as *Pogonatum hetero-contortum*): 594 (fig. 25); Osada 1965 (as *P. spurio-cirratum*): 188 (fig. 6a–j); Xu & Xiong 1984: 175 (fig. 1, as *Neopogonatum semiangulatum*), 176 (fig. 2, as *N. yunnanense*); Noguchi 1987 (as *P. spurio-cirratum*): 43 (fig. 14A); Eddy 1988: 37 (fig. 24); Hyvönen 1989: 577 (fig. 4E).

Distribution — As 2: China, Japan; As 3: Bhutan, Sikkim, Sri Lanka, Thailand; As 4: Indonesia, Papua New Guinea.

18b. *Pogonatum cirratum* subsp. *fuscatum* (Mitt.) Hyvönen, *comb. nov.* (Figs. 9E, 28 – map)

Pogonatum fuscatum Mitt., J. Linn. Soc., Bot. Suppl. 1:154. 1859. — Type: India, Khasia 4 000 ft., Hooker & Thomson 1203 (NY!, lectot. nov., L!, isolecotype); Nepal, Wallich; India, Darjeeling, Hooker 1225; Sikkim, Tongh 9 000–10 000 ft., Hooker 1233; Lachea 9 000 ft., Hooker 1242; India, Khasia 3 000–4 000 ft., Hooker & Thomson 1230 (L!, NY!, syntypes); Kumaon, Sarju valley 3 500 ft., Strachey & Winterbottom (NY!, syntype).

Pogonatum flexicaule Mitt., J. Linn. Soc., Bot. Suppl. 1:152. 1859. — Type: India, Assam, Mack (NY!, holotype). — Synonymized by Smith (1976).

Pogonatum feae C. Müll., Nuovo Giorn. Bot. Ital. 23: 601. 1891, nom. nud. — Original collection: Burma, Dawna Range (catena Dawna), Monte Moolegit, 1 600 m, III.1887 Fea (L!, M!).

Pogonatum celebesicum Card., Rev. Bryol. 28:114. 1901, nom. nud. — Original collection: Indonesia, Sulawesi: Bua Kräng, 5 000–7 000 ft., 1895 Fruhstorfer (L!).

Pogonatum spurio-cirratum Broth., Philipp. J. Sci. C. 5:150. 1910. — Type: Philippines. Lepanto: Mt. Data, on trees, ca. 7 000 ft., XI.1905 Merrill 4908; Luzon: Benguet, Heights in the Oaks, 7 000 ft., Mearns 4557; Pauai, ca. 2 100 m, VI.1909 McGregor 8688; Mt. Tonglon, XII.1908 Ramos 5505; Mt. Pulog, V.1909 Merrill 6396; I.1909 Curran, Merritt & Zschokke 16393; 16412 (H-BR!, JE!, M!, MO!, NY!, syntypes); Laguna, Mt. Banajao, terrestrial, 2 000 m, I.1909 Robinson 6562 (H-BR!, JE!, NY!, syntypes); XI.1907 Curran & Merritt 7992 (H-BR!, NY!, syntypes). — Synonymized by Hyvönen (1989).

Pogonatum kweitschouense Broth., Symb. Sin. 4:133. 1929, *syn. nov.* — Type: China. Guizhou: E Guizhou, prope oppidum Liping in silva mixta, Nandjing-schan, ad terram, substr. marneo, 750 m, 25.VII.1917 Handel-Mazzetti 10983 (H-BR!, holotype).

?*Pogonatum spurio-cirratum* var. *pumilum* Reim., Hedwigia 71:74. 1931, *syn. nov.* — Type: China. Guangdong: Tinfu-shan, 220–400 m, IV.1928 Sin & Whang 86; Guangxi: Yao-shan, 1 200 ft., 1928 Sin & Whang 715 (B, syntypes, probably destroyed).

?*Pogonatum spurio-cirratum* var. *pumilum* fo. *hemisphaericum* Reim., Hedwigia 71:74. 1931, *syn. nov.* — Type: China. Guangxi: Yao-shan, on the dark damp clay, 500 m, 22.XI.1928 Sin 3647; Yao-shan, Lungon, 1 500 ft., 21.IV.1929 Sin 8112 (B, syntypes, probably destroyed).

Neopogonatum tibeticum Xu & Xiong, Acta Bot. Yunnanica 6(2): 177. 3. 1984, *syn. nov.* — Type: China. Xizang: Zayu, under ground in sylvat *Abies* forest, 2 350 m, 18.VII.1974 Wu 1806 (YUNU, holotype; H!, KUN, isotypes).

Subsp. *fuscatum* is as variable as the other two subspecies of *Pogonatum cirratum*. It is the smallest of the three, and the ventral lamellae are up to four cells high. The leaf-margins are typically unistratose, but normally at least the outer row is bistratose like that of the two larger subspecies. The blade of the leaves is mostly rather narrow.

I did not study specimens cited by Reimers (1931) as a new variety and a new form of *Pogonatum spurio-cirratum*, but based on the original description they are without doubt synonymous to subsp. *fuscatum*. This conclusion is supported by my study of ample Chinese material.

Compared with the other two subspecies, subsp. *fuscatum* occupies more adverse and drier habitats. It has been collected from Himalaya to the Philippines at 220–4 000 m.

Illustrations — Gangulee 1969: 110 (fig. 44); Xu & Xiong 1984 (as *Neopogonatum tibeticum*): 178 (fig. 3); Li 1985: 446 (figs. 21–26); Eddy 1988 (as *Pogonatum flexicaule*): 37 (fig. 25); Hyvönen 1989: 577 (fig. 4D).

Distribution — As 2: China; As 3: Bhutan, Burma, India, Laos, Nepal, Sikkim, Thailand, Vietnam; As 4: Indonesia, Malaysia, Philippines.

18c. *Pogonatum cirratum* subsp. *macrophyllum* (Dozy & Molke.) Hyvönen, *comb. nov.* (Figs. 9F–I, 28 – map)

Pogonatum macrophyllum Dozy & Molke., Bryol. Jav. 1:45. 35. 1856, Ned. Kruidk. Arch. 4(1): 75. 1856. — Type: Indonesia. Java: in monte Pangerango, *Junghuhn* (BM!, lectotype *nov.*).

Pogonatum flexuosum Mitt., Trans. Linn. Soc. London 23:56. 6:20. 1860, *syn. nov.* — *P. mittenii* Broth., Nat. Pflanzenfam. 1(3): 691. 1905, *nom. illeg. superfl.* — Type: Niger, *Barter* (original text on one sheet in BM: Kina-Baloo, Borneo, *Low* (NY!, BM!, isotypes).

Pogonatum submacrophyllum Herz., Hedwigia 57:236. 1916. — Type: Indonesia. Seram: Mittel-Ceram, Urwald am Gunung Pinaia, ca. 1 760 m, dichte feuchte Teppiche am Boden bildend, VIII.1911 *Stresemann* 225 (JE!, holotype). — Synonymized by Hyvönen (1989).

Pogonatum macrophyloides Broth., Mitt. Inst. Allg. Bot. Hamburg 7:140. 1928. — Type: Malaysia. Borneo: Sabah, Mt. Kinabalu, Marai Parai Spur, 1.–4.XII.1915 *Clemens* 11125 (H-BR!, lectotype, vide Iwatsuki & Noguchi 1975; BM, JE!, NY, isolectotypes). — Synonymized by Eddy (1988).

Pogonatum euryphyllum Dix., J. Linn. Soc., Bot. 50:138. 4:52. 1935. — Type: Malaysia. Borneo: Sabah, near Kamborangah, 2 200 m, 13.II.1931 *Holtum* 25644 (BM!, holotype). — Synonymized by Hyvönen (1989).

Pogonatum macrophyllum var. *tenuis* Pocs & Tixier, Bot. Közlem. 54:37. 1967, *syn. nov.* — Type: Vietnam, Cime de Phan-si-pan, 2 000–3 000 m, IV.1964 *Trung* (BP, holotype; NY!, isotype).

In the western part of the range subsp. *macrophyllum* is easily distinguished from the two other subspecies of *Pogonatum cirratum*, and distinction even at species level is supportable. However, the close affinity of the taxa is well demonstrated by the study of large New Guinean material. All intermediates are present between typical subsp. *macrophyllum* with partly united and tightly set lamellae and the more fragile subsp. *cirratum*. Assigning specimens to either taxon is in many cases arbitrary and thus distinction at species level seems to me excessive.

Subsp. *macrophyllum* is characterized by its large size with its tightly set and partially united lamellae having many apical geminations. Both other subspecies are smaller plants with higher and more remote lamellae.

Study of type material of *Pogonatum flexuosum* revealed that the text “Niger, *Barter*” was only later attached to cover an original text which indicated that the collection came from Borneo. The specimens are indistinguishable from SE Asian *P. cirratum* subsp. *macrophyllum*. *P. flexuosum* is known only from the type collection (De Sloover 1986), and it seems highly unlikely that such a robust plant could have been ignored even from a poorly collected area such as Western Africa. Consequently, I am inclined to regard the locality data given by Mitten as erroneous, and *P. flexuosum* should be excluded from the African flora and reduced to synonymy under *P. cirratum* subsp. *macrophyllum*. There is, however, a small chance that the text later added on the sheet is correct, but this will be confirmed only if further collections of similar plants are made in western Africa.

The subsp. *macrophyllum* is a plant of closed rainforests but like other species of the genus, it is confined to bare ground near trail-sides and similar habitats. It has been collected at 800–3 120 m.

Illustrations — Iwatsuki & Noguchi 1975 (as *Pogonatum macrophyloides*): 318 (fig. 3); Eddy 1988 (as *P. macrophyloides*): 35 (figs. 22, 23); De Sloover 1986 (as *P. flexuosum*): 285 (figs. 299–317); Hyvönen 1989: 577 (fig. 4F).

Distribution — As 3: Thailand, Vietnam; As 4: Indonesia, Malaysia, Papua New Guinea, Philippines; Oc: Solomon Islands.

19. *Pogonatum convolutum* (Hedw.) P. Beauv. (Figs. 9J, K, 28 – map)

Prodr. Aetheogam. 84. 1805. — *Polytrichum convolutum* Hedw., Spec. Musc. 94. 10:3–5. 1801. — *Pogonatum brachypus* Brid., Bryol. Univ. 2:111. 1827, *nom. nud.* in *synon.* — Type: Reunion (Insula Bourbon), *Commerson* (G!, *lectot. nov.*); Jamaica, *Swartz* (BM!, PC!), *syntypes*; both specimens are *P. tortile*.

Polytrichum rutenbergii C. Müll. ex Geh., Abh. Naturwiss. Vereine Bremen 7:205. 1882, *syn. nov.* — *Pogonatum rutenbergii* (Geh.) Par., Ind. Bryol. 987. 1898. — Type: Madagascar, *Rutenberg* (H-BR!), isotype).

Pogonatum convolutum var. *madagassum* Thér., Recueil Publ. Soc. Havraise Études Diverses 1925: 151. 1926, nom. nud. — Original collection: Madagascar, Moramanga, talus humide, 12.II.1930 *Decary* (PC!).

Pogonatum convolutum is distinguished from all other African species of the genus by its large size and fairly distant leaves. In many characters it greatly resembles the SE Asian *P. cirratum*, but in *P. convolutum*, the ventral stereid band does not possess cells with such extremely incrassate walls like *P. cirratum*. The dorsal stereid band typically has incrassate cell-walls which cause the light costa to be clearly visible even in the dry condition. In Africa *P. convolutum* might be confused with *P. usambaricum* (Broth.) Par. The latter species is normally smaller and it has leaves with wide unistratose margins, whereas the leaf margins in *P. convolutum* are narrow and locally bistratose. The crenation of the apical cells of the lamellae is also more distinctive in *P. usambaricum*, and the marginal teeth are much smaller in that species. *P. convolutum* seems to bear sporophytes rarely as most of the studied specimens were sterile.

The use of the epithet *convolutum* is ambiguous as Hedwig (1801) cited two specimens in original protologue, one from Jamaica and the other from Reunion. Further collections from both areas have proved that it is impossible that the two type specimens are conspecific. Frye and Duckering (1946) revised the American material and proposed the use of *Pogonatum convolutum* for the American plants formerly widely known as *P. tortile*. This was later corrected (Frye 1956) and use of the latter name was proposed. This view was also adopted by De Sloover (1986), who presented *P. convolutum* as a dubious name which should be abandoned. After study of both African and Jamaican type material I am, however, inclined to reserve the epithet for the African plants by selecting the Reunion collection by Commerson as a lectotype.

The species has a very restricted range in the mountains of the islands of Madagascar, Mauritius and Reunion at 200–2 000 m. It grows on trail banks and open ground in fairly moist habitats.

Illustrations — De Sloover 1986: 283 (figs. 276–298).

Distribution — Afr 3: Madagascar, Mauritius, Reunion.

Specimens examined (representative) — Afr 3: MADAGASCAR. Motamanga, Lakato, en forêt, sur le sol, 3.IX.1942 *Decary* 18534. (H!, MO!); Diego Suarez: Montagne d'Ambre, Parc National, 32 km SSW of Diego Suarez, 10 km along trail between Petit Lac and Grand Lac, on tree base, 12°34'S, 49°12'E, 1 200 m, 13.XI.1972 *Crosby* 7153 (MO!). — REUNION. près du sommet de la Grande Montée, forêt des Bois

de Couleur, avec *Cyathea*, sur talus vertical moussu, dans un ravin, ca. 1 550 m, 17.XII.1973 *De Sloover* 17341 (H!, TNS!).

20. *Pogonatum contortum** (Brid.) Lesq. (Figs. 10A, 27 – map)

Mem. Calif. Acad. Sci. 1:27. 1868. — *Polytrichum contortum* Menz. ex Brid., J. Bot. (Schrad.) 1800 (1): 287. 1801. — *Pogonatum laterale* Brid., Bryol. Univ. 2:111. 1827, nom. illeg. superfl. — Type: North America, W coast (in ora occidentali Americae septentrionalis), *Menzies* (FH!), isotype).

Pogonatum atro-virens Mitt., J. Linn. Soc., Bot. 8:49. 1865. — Type: USA. Alaska: Sitka, *Barclay* (NY, holotype; BM!), isotype). — Synonymized by Frye (1910).

Polytrichum contortum var. *pallidum* Lindb., Acta Soc. Sci. Fenn. 10:239. 1872, *syn. nov.* — *Pogonatum contortum* var. *pallidum* (Lindb.) Par., Ind. Bryol. 979. 1898. — Type: USSR. Far East: Sachalin, Due, VIII.1861 *Glehn* (H-SOL!, holotype).

Pogonatum erythrodontium Kindb. in Macoun, Cat. Canad. Pl. 6:150. 1892. — Type: Canada. British Columbia: Vancouver Island, Comox, roadsides, 3.V.1887 *Macoun* 107; USA. Alaska: Prince of Wales Island, 28.IX.1891 *Macoun* (CANM!, syntype). — Synonymized by Cardot (1899).

Pogonatum asperrimum Besch., Ann. Sci. Nat. Bot. sér. 7, 17: 355. 1893. — Type: Japan. Honshu: Aomori, 1886 *Faurie* 184 ep. (PC!, isotype). — Synonymized by Osada (1965).

Pogonatum contortum var. *elatum* Sak., Bot. Mag. (Tokyo) 49:132. 1935. — Type: Japan. Honshu: Yamanashi, Mt. Komagatake, im tiefen Walde, 28.VII.1916 *Sakurai* 53 (MAK, syntype); Tochigi: Nikko, Yumoto, 12.IX.1926 *Sakurai* 91; Kiushu: Bungo, Mt. Kuju, VIII.1934 *Takaki* 3741. — Synonymized by Osada (1965).

The most typical feature of *Pogonatum contortum* is the soft habit caused by the weakness of its stereid bands. It has wide, mostly unistratose leaf-margins and low (2–3 cells high) and remote lamellae. Another typical feature is the extremely incrassate walls of the central cells (Smith 1971), observed also in such species as *P. pergranulatum*, *P. rufisetum* and *P. subfuscatum*. In Asia it is distinguished from *P. cirratum* by its dentate sheath-margins and by its wide, mostly unistratose margins. In Western North America *P. contortum* can hardly be confused with any other species of the Polytrichaceae. All other local species have firmer habit and higher and more crowded ventral lamellae on the leaves. In the dorsal stereid band some cells can possess extremely incrassate walls reminiscent of those of some closely related species. These are interpreted as relicts of a former character state. Species resembling *P. contortum* in their overall habit are *P. tortile*, *P. subortile* and *P. subulatum*. None of their geographic ranges overlap with that of *P. contortum*. Additionally *P. contortum* is distinguished from all these three species by its serrate sheath-margins and by the structure of its central cells.

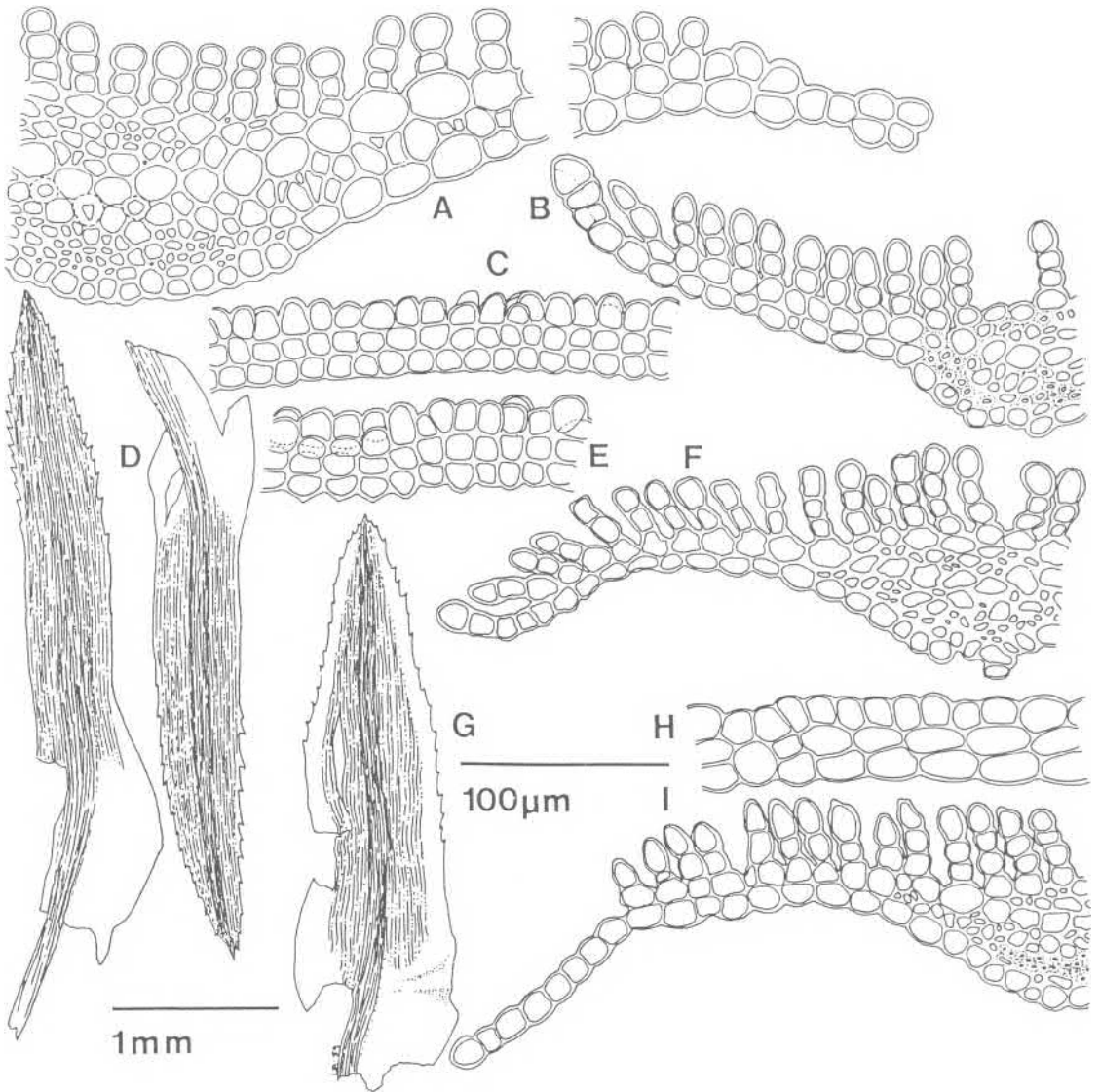


Fig. 10A-I. — A: *Pogonatum contortum*. Leaf cross-section (Koponen 22000, H). — B, C: *P. pergranulatum*. B. Leaf cross-section and C. Lamella in side view (Tai 115, paratype PE). — D-F: *P. rufisetum*. D. Leaves, E. Lamella in side view and F. Leaf cross-section (Hara et al. 9.IV.1967, L). — G-I: *P. subfuscatum*. G. Leaf, H. Lamella in side view and I. Leaf cross-section and (Handel-Mazzetti 8244, holotype H-BR). — Use the 100 µm scale for A-C, E, F, H and I, and 1 mm scale for D and G.

Study of the type specimen of var. *pallidum* revealed it to be exceptionally small but otherwise identical with typical *Pogonatum contortum*. In the Polytrichaceae, and also in the genus *Pogonatum*, size of plants is generally a fairly variable character and consequently this variety is reduced to synonymy.

Pogonatum contortum has a unique distribution for the genus, being confined to both sides of the northern Pacific Ocean. It has been collected from sea level to 2 000 m (Osada 1965), growing in humid temperate and boreal forests. Like other species of the genus, *P. contortum* is usually confined to bare ground.

Illustrations — Grout 1937: pl. 59A; Osada 1965: 188 (fig. 6k–s).

Distribution — As 1: USSR; As 2: China, Japan, Korea; Am 1: Canada, USA.

21. *Pogonatum pergranulatum* Chen (Figs. 10B, C, 29 – map)

Feddes Repert. 58:34. 8. 1955. — Type: China. Sichuan: Omei-schan, Tsi-li-pou, ca. 2 800 m, auf Erde, 25.VIII.1942 Chen 5519 (PE!, holotype).

In its small size and narrow leaves, *Pogonatum pergranulatum* resembles the Himalayan *P. rufisetum*. However, the lamellae are higher (up to 4–5 cells) and they have deeply and irregularly crenate, sometimes geminate apical cells. In closely related species the apical cells are essentially straight as seen in side view. In *P. pergranulatum* the lamellae are remotely set on the blade and not more than 30 per leaf. The leaf-margins are bistratose as in more robust related species. Both stereid bands are weak. The ventral band consists of only a few cells, and even the dorsal band is thin. The central cells have exceedingly incrassate walls like those of *P. rufisetum*.

Pogonatum pergranulatum resembles *P. cirratum* subsp. *fuscatum* in its overall habit. In particular, southern Chinese populations of subsp. *fuscatum* show the same, very small size and narrow leaves. Apical cells of the lamellae in the latter species are, however, essentially straight as seen in side view, and the dorsal cells of the blade typically have the small and rounded lumen.

Similar to *Pogonatum rufisetum*, *P. pergranulatum* is easily dissolved in a KOH-solution, and the specimens should thus be soaked generally less than one minute to avoid excess softening of the leaves.

Pogonatum pergranulatum with *P. minus*, is the rarest species of the genus and they both occur in China. Both taxa are known only from type material, but more specimens should emerge when the areas are explored more thoroughly.

Pogonatum pergranulatum has been collected on forest soil at 2 800 m

Illustration — Chen 1955: 34 (fig. 8).

Distribution — Endemic for Sichuan, China.

Specimens examined — As 2: CHINA. Sichuan: Omei-schan, Chi-li-pou, im Walde auf dem Boden, 7.IX.1939 Tai 115; 118a (PE!, paratypes of *P. pergranulatum*).

22. *Pogonatum rufisetum** Mitt. (Figs. 10D–F, 29 – map)

J. Linn. Soc., Bot. Suppl. 1:153. 1859. — *Polytrichum rufisetum* Wils. ex Mitt., J. Linn. Soc., Bot. Suppl. 1:153.

1859, nom. nud. in synon. — Type: Sikkim, regio temp., *Hooker 1194* (L!, lectot. nov.; H-SOL!, isolectotype); Sikkim, Himalaya orient., *Hooker & Thomson 1235* (H-BR!, syntype).

Pogonatum rufisetum is a surprisingly small plant with disproportionately long stems to be a species of *Pogonatum*. In the dry condition, it may resemble some species of *Oligotrichum* Lam & DC. Leaves of both *P. subtortile* and the Himalayan *P. patulum* (Harv.) Mitt. also have regularly crenate apical cells of the lamellae as seen in side view, but, in both species leaves are much wider and they have more numerous lamellae than those of *P. rufisetum*. Cells of the stereid bands in these two also lack extremely incrassate walls. The leaves of *P. rufisetum* are narrow with less than 35 lamellae on each, and the stereid bands are weak and narrow. The costa is prominent on the dorsal side, and excurrent in a gradually narrowed, sharp apex. *P. pergranulatum* is distinguished by the irregular apical cells of its lamellae. Some specimens of *P. cirratum* subsp. *fuscatum* may also have very narrow leaves, but the apical cells of the lamellae of the latter species are essentially straight as seen in side view. Leaf-margins of the latter species are at least partly bistratose and a ventral stereid band is always present. The dorsal cells of the blade of *P. cirratum* subsp. *fuscatum* typically have a rounded lumen and strongly incrassate walls. The latter species is also generally larger than *P. rufisetum*.

Smith (1971) stated that the incrassate walls of the central cells are unique to *Pogonatum contortum* of the North Pacific area. The same feature is, however, also found in *P. rufisetum* as well as in its close relative, *P. pergranulatum*.

Pogonatum rufisetum is a plant of high altitudes being collected at 2 440–3 550 m, most of specimens being taken from soil above 3 000 m.

Distribution — As 3: Bhutan, India, Sikkim.

Specimens examined (representative) — As 3: BHUTAN. Thimphu: summit of Dochong La, *Tsuga-Rhododendron* forest, on soil, 27°29'N, 89°45'N, 3 100 m, 13.IV.1982 Long 10801 (E!). — INDIA. Darjeeling: Phalut, 3 550 m, 10.V.1960 *Togashi & al.* 200640 (L!, NICH!).

23. *Pogonatum subfuscatum* Broth. (Figs. 10G–I, 29 – map)

Symb. Sin. 4:134. 1929. — Type: China. Yunnan: NW Yunnan, in der tp. und ktp. St. des birm. Mons. im Walde des Tales von Londjre zum Schöndsu-la in der Mekong-Salwin-Kette, 28°6', auf Granit und Glimmerschiefer, 3 200–3 900 m, häufig, c. sp., 22.IX.1915 *Handel-Mazzetti 8244* (H-BR!, holotype).

?*Pogonatum formosanum* Horik., Bot. Mag. (Tokyo) 49:59. 6. 1935, syn. nov. — Type: China. Taiwan: Chiayi,

Ali-shan, on the earth, 17.VIII.1932 Horikawa (HIRO, holotype, probably destroyed).

In its habit *Pogonatum subfuscatum* can be mistaken as a species of *Oligotrichum* or as *P. rufisetum*. The latter species, however, has more tightly set lamellae as seen in cross-section and the cells of the stereid bands have extremely incrassate walls. Species of the genus *Oligotrichum* have the ventral lamellae restricted to the central part of the leaves. When sporophytes are present, distinction is easy as the exothelial cells of *Oligotrichum* are essentially smooth, and stomata are present. The capsule of *P. subfuscatum* is terete, without stomata and typically with clearly mammillose exothelial cells. The ventral lamellae are fewer than 25 and ca. 3–4 cells high with undifferentiated apical cells. The unistratose margins are 5–7 cells wide. The ventral stereid band is absent and even the dorsal band is weak. The central cells have extremely incrassate walls as in *P. contortum*, *P. pergranulatum* and *P. rufisetum*.

In his original description of *Pogonatum formosanum* Horikawa (1935b) noted that the new species was closely related to *P. suzukii* Broth., a species later assigned to the genus *Oligotrichum*. The number of ventral lamellae (ca. 30) in *P. formosanum* is, however, much higher than in specimens of *O. suzukii* (Broth.) Chuang. The mammilosity of the exothecium, mentioned by Horikawa, is a feature not present in *O. suzukii* but instead suggests affinity to the genus *Pogonatum* and particularly to *P. subfuscatum*. Many other species of the genus with their main distribution in the Himalayan area, such as *P. fastigiatum*, *P. microstomum* and *P. nudiusculum*, have similar range with disjunctive occurrence in the mountains of Taiwan. As there is no chance to study the type material the identity of *P. formosanum* remains, however, uncertain.

Pogonatum subfuscatum is so far known only from the type specimen. It was collected on bare ground on rock at 3 200–3 900 m in NW Yunnan. According to the label data, it is common at the site.

Distribution — Endemic to Yunnan, China.

24. *Pogonatum proliferum* (Griff.) Mitt. (Figs. 11A, B, 29 – map)

J. Linn. Soc., Bot. Suppl. 1:152. 1859. — *Polytrichum proliferum* Griff., Calcutta J. Nat. Hist. 2:475. 1842. — Type: India, Mont. Khasian, infra rupes ad Surureem, Griffith (Walls?) ex Herb. Ward (BM, H-SOL1, NY, isotypes).

Pogonatum gymnophyllum Mitt., J. Linn. Soc., Bot. Suppl. 1:153. 1859. — *Polytrichum gymnophyllum* Wils. ex Mitt., J. Linn. Soc., Bot. Suppl. 1:153. 1859, nom. nud. in synon. — Type: India, Khasia, Hooker & Thomson 1208 (NY, lectotype, vide Smith 1976; H-BR!, isolectotype). — Synonymized by Smith (1976).

Pogonatum seminudum Mitt., J. Linn. Bot. Suppl. 1:152. 1859, syn. nov. — *Polytrichum seminudum* Wils. ex Mitt., J. Linn. Soc., Bot. Suppl. 1:153. 1859, nom. nud. in synon. — Type: Sikkim, Tonglo, 7 000–8 000 ft., Hooker 1199 (NY, holotype; BM!, isotype).

Pogonatum warburgii Broth., Nat. Pflanzenfam. 1(3): 690. 1905, nom. nud. — Original collection: Indonesia. Sulawesi: Süd Celebes, Pik von Bonthavn, Warburg (H-BR!, L!). — Synonymized by Bartram (1939).

Pogonatum atrichoides Fleisch., Musci Buitenzorg 4:1592. 1923. — Type: Indonesia. West-Java: am Tjikorai bei Garoet, 1900 Fleischer (FH!, holotype; L!, isotype). — Synonymized by Eddy (1988).

?*Pogonatum takao-montanum* Horik., J. Jap. Bot. 11:505. 7. 1935, syn. nov. — Type: China. Taiwan: Pingtung, Mt. Daijuring, 4.I.1935 Horikawa (HIRO, holotype, probably destroyed).

Pogonatum ugandae P. Vard., Rev. Bryol. Lichénol. 22:13. 6. 1953, syn. nov. — Type: Uganda, Ishaha gorge, on banks, Lind 16 (NY!, isotype).

?*Pogonatum fastigiatum* var. *darjeelingense* Gang., Nova Hedwigia 12:417. 81. 1966 (1967), syn. nov. — India, Darjeeling, Gangulee 5641 (Herb. Gangulee, holotype).

The habit of *Pogonatum proliferum* resembles species of *Atrichum* more than *Pogonatum*. In a dry condition, however, its affinity to the latter genus can be seen immediately. Its leaves are only simply contorted and not tightly crisped as in *Atrichum*. Upon closer examination one sees leaves without specialized marginal cells of *Atrichum*. The form of the capsules is also clearly different in two genera. The urn is much elongated and always terete in *Atrichum*, whereas in *P. proliferum* it is only slightly elongated and typically plicate.

The leaves of *Pogonatum proliferum* are almost totally without lamellae and these are confined to the ventral side of the costa only or to the immediate juxtacostal region. In *P. nudiusculum* the number of ventral lamellae is similarly reduced, but the cells of the blade are much smaller and not collenchymatous as in *P. proliferum*. *P. nudiusculum* is also a smaller plant while the larger *P. proliferum* resembles instead such species as *P. cirratum*. The scarcity of ventral lamellae is in this case an immediately visible diagnostic character. The marginal serration is conspicuous and the number of marginal teeth varies to some extent. In the perichaetial leaves the marginal teeth are more remote than in cauline leaves. Remote marginal teeth are especially typical of African plants, but that is apparently the only difference from Asian specimens and so I hesitate to recognize this variation formally.

Pogonatum proliferum is a plant of moist and shaded habitats. It has been collected at 1 000–2 600 m growing on open soil and soil-covered rocks and trunks.

Illustrations — Horikawa 1935b (as *Pogonatum takao-montanum*): 506 (fig. 7). — Gangulee 1969: 136 (fig. 61),

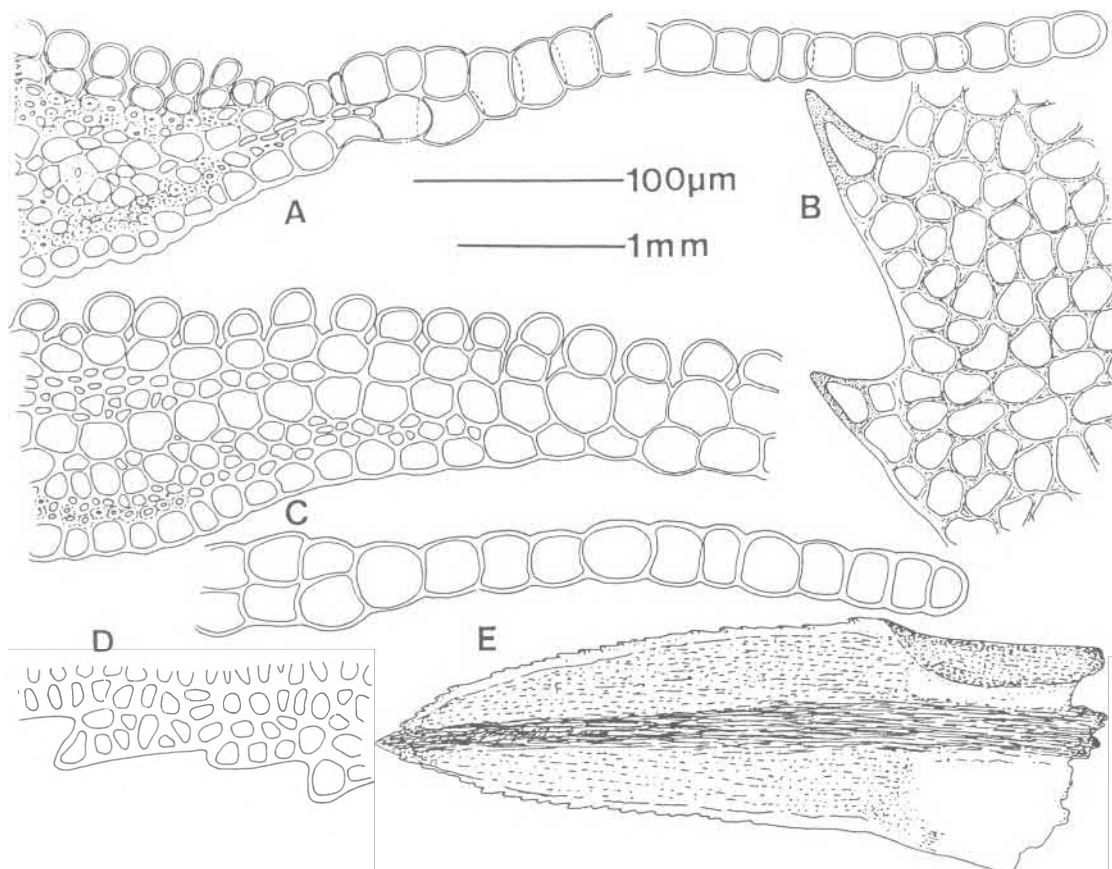


Fig. 11A–E. — A, B: *Pogonatum proliferum*. A. Leaf cross-section and B. Marginal teeth and dorsal cells of blade (Jacobs B 451, L). — C: *P. semipellucidum*. Leaf cross-section (Sastre-De Jesús et al. 1478, H). — D, E: *P. subtortile*. D. Leaf and E. Marginal teeth of blade (Wijk 1294, L). — Use the 100 µm scale for A–D, and 1 mm scale for E.

138 (fig. 62 as *P. fastigiatum*); 140 (fig. 63 as *P. fastigiatum* var. *darjeelingense*); 141 (fig. 64 as *P. gymnophyllum*); De Sloover 1986 (as *P. ugandae*): 293 (figs. 395–415); Eddy 1988: 40 (fig. 28 as *P. gymnophyllum*); Hyvönen 1989: 577 (fig. 4H).

Distribution — Afr 2: Ruanda, Uganda; As 2: China; As 3: Burma, India, Nepal, Sikkim, Thailand; As 4: Indonesia, Philippines.

25. *Pogonatum semipellucidum** (Hampe) Mitt. (Figs. 11C, 29 – map)

J. Linn. Soc., Bot. 12:617. 1869. — *Polytrichum semipellucidum* Hampe, Linnæa 20:80. 1847. — Type: Venezuela, Merida, Moritz 188 (BM, holotype; L!, NY, isotypes).

Pogonatum subbifarium Mitt., J. Linn. Soc., Bot. 12:618. 1869. — Type: Colombia (Nova Granata), in sylvis humidis Osson, Purdie (NY, syntype); Venezuela, Prov. Meri-

da, Funck & Schlim. 994 (H-BR!, syntype). — Synonymized by Robinson (1967).

Pogonatum viride Mitt., J. Linn. Soc., Bot. 12:617. 1869. — Type: Colombia, Andes Bogotenses, inter Bogota et Fusagasuga, 6 500 ft., Weir 137 (NY, holotype; H-BR!, US, isotypes). — Synonymized by Robinson (1967).

Pogonatum flaccidissimum Broth., Bot. Jahrb. Syst. 56 (Beibl. 123): 22. 1920. — Type: Peru, Sandia: Chunchusmayo, Wald, auf Erde, 900 m, 9.VII.1902 Weberbauer 1270 (H-BR!, holotype). — Synonymized by Menzel (1987).

Pogonatum semipellucidum is a robust plant with a pale costa which is clearly seen in the dry condition. However, the dorsal stereid band lacks such incrassate cells as typical of the other closely related species. The leaf sheath is in *P. semipellucidum* better developed than in the closely related *P. proliferum*, and also the blade is proportionally wider than

in the latter species. Lamellae are restricted to the central part of the leaves. This feature, and its large size, are readily observed characters distinguishing it from all other species of the genus in South America. The number of lamellae per leaf varies, but generally they are more numerous than in *P. proliferum*. The large marginal teeth are conspicuous and the margins are deeply serrate.

The type specimen of *Pogonatum flaccidissimum* is an exceptionally small plant with fairly distant leaves and a weak costa. This type of depauperate form has also been observed in such plants as the SE Asian *P. subtortile* and *P. cirratum* subsp. *fuscatum*, and the American *P. tortile*. Such a depauperate condition is probably induced by environmental factors, and thus the forms require no formal taxonomic recognition. All of these specimens were collected in shady and moist habitats, and presumably these exceptionally humid environments have caused similar modifications in all three taxa mentioned above.

Pogonatum semipellucidum is a plant of shaded bare soil by trails and similar disturbed habitats. It has been collected at 900–2 900 m.

Distribution — Am 4: Bolivia, Colombia, Ecuador, Peru, Venezuela.

26. *Pogonatum subtortile* (C. Müll.) Jaeg. (Figs. 11D, E, 29 – map)

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 256. 1875 (Adumbratio 1:718). — *Polytrichum subtortile* C. Müll., Syn. Musc. Frond. 1:216. 1848. — *Pogonatum teysmannianum* var. *tortile* Dozy & Molk., Bryol. Jav. 1:44. 1856. — Type: Indonesia, Java, Zollinger 853 (NY!, lectot. nov., H-BR!, JE!, L!, isoclectotypes).

Polytrichum teysmannianum Dozy & Molk. in Miquel, Pl. Jungh. 3:323. 1854, syn. nov. — *Pogonatum teysmannianum* (Dozy & Molk.) Dozy & Molk., Bryol. Jav. 1:43. 32. 1856, Ned. Kruidk. Arch. 4(1): 75. 1856. — *P. subtortile* var. *teysmannianum* (Dozy & Molk.) Wijk & Marg., Taxon 9:191. 1960. — Type: Indonesia, Java, Junghuhn (L!, holotype).

Pogonatum vitiense Mitt. in Seem., Fl. Vit. 403. 97. 1871, syn. nov. — Type: Fiji (Viti), 1855 Milne (BM!, isotype).

Polytrichum graeffeanum C. Müll., J. Mus. Godeffroy 3(6): 61. 1874, syn. nov. — *Pogonatum graeffeanum* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 254. 1875 (Adumbratio 1:716). — Type: Samoa, Upolu, Graeffe (JE!, H-BR!, L!, isotypes).

Pogonatum teysmannianum var. *mentaweicum* Herz., Hedwigia 66:357. 1926, syn. nov. — *P. subtortile* var. *mentaweicum* (Herz.) Wijk & Marg., Taxon 9:191. 1960. — Type: Indonesia, Sumatra: W Küste, Mentawai Island, auf erdigen Felsen, 1924 Wegner (JE!, holotype).

Pogonatum subcucullatum Dix., J. Bot. 80:34. 1942. — Type: Indonesia, West Irian: Tjenderawasih, Japen Isl., Mt. Eiori, Camp 2, 2 000 ft., IX.1938 Cheesman 120 (BM!, holotype). — Synonymized by Hyvönen (1986).

Pogonatum subtortile is a common plant of tropical SE Asia and adjacent islands of the western Pacific Ocean. It is variable in size and form of leaves. Typical features of all specimens are the undifferentiated, low lamellae, only 2–3(–5) cells high. It has weak stereid bands and unistratose margins. The sheath is not much widened and can even be as narrow as the blade. *P. subtortile* can most easily be mistaken for *P. patulum*. The latter has leaves with a more widened sheath and a longer blade; its leaves are always contorted in the dry condition. The general habit of the plants is firmer than in *P. subtortile*. In most cases, a clear difference can also be seen in the size and form of the dorsal cells of the blade: they are larger, more or less subquadrate with thinner walls in *P. patulum*.

The infraspecific variation within *Pogonatum subtortile* is difficult to interpret. Variation according to the habitat is similar to that observed in, for example, the African *P. belangeri* (C. Müll.) Jaeg. and the American *P. tortile*, with the shade-grown plants having much wider unistratose margins, lower lamellae and more pronounced marginal serration. Dixon (1942) described *P. subcucullatum* from West Irian, based on plants with a rounded apex and with an exceptionally weak costa apically. Further collections of similar plants have also been made in other parts of New Guinea. However, I hesitate to recognize this variation formally because intermediate forms appear occasionally. Also, there are no other distinguishing characters when these plants are compared with others from neighboring countries.

Like other species of the genus, *Pogonatum subtortile* is a plant of bare soil, in open as well as in shady habitats. It has been collected from near sea level to 2 500 m.

Illustrations — Hyvönen 1986: 130 (fig. 13); Eddy 1988: 33 (fig. 21).

Distribution — As 4: Indonesia, Malaysia, Papua New Guinea, Philippines; Oc: Fiji, Samoa, Solomons.

27. *Pogonatum marginatum* Mitt.

J. Proc. Linn. Soc., Bot. Suppl. 1:153. 1859. — *Plagioregelopus marginatus* (Mitt.) Smith Merrill, Mem. New York Bot. Gard. 45:469. 1987. — Type: Sri Lanka (Ceylon), ad Hantani, Gardner 1223 (NY!, holotype).

The discussion on *Pogonatum marginatum* and eight other species below is brief and not furnished with illustrations. They form a monophyletic group, called the *Racelopus* species group in the following discussion. Detailed description and diagnosis of all the taxa, as well as high quality line drawings and distribution maps, were recently given by Touw (1986). The results obtained in his study are closely

followed here and his distributional reports are not modified, and only the total range of the species groups is presented (Fig. 29). However, the sectional status is not retained (for further discussion see the chapter Phylogeny and generic relationships).

As discussed by Touw (1986), all plants in this group are tiny to medium-sized, characterized by scabrous (rarely almost smooth) setae and all, but two, have a persistent protonema. They are confined to shady and humid sites in tropical and subtropical forests and are specialized for rapid growth mostly on clayey, bare soil. Because of their small size the plants, especially when sterile, are easily overlooked in the field and may be much more common than the few collections suggest.

Pogonatum marginatum is easily distinguished from all other species of the genus by a unique combination of characters: it is anisophyllous, has wide leaves with collenchymatous dorsal cells in the blade, it has no ventral lamellae, and the serrated leaf-margins are bi- to multistratose.

Pogonatum marginatum has been collected in scattered localities in SE Asia.

Illustrations — De Sloover 1986: 246 (figs. 1–14); Touw 1986: 13 (fig. 5).

Distribution — As 3: Sri Lanka, Vietnam (Touw, 1986).

Specimens examined (representative) — As 2: SRI LANKA. Tumbagoda road Tamanawatte–Massenne, ca. Balanyoda, Adam's Peak jungle, 200 m, 9.VI.1971 Kortemans 24462; Ratnapura: Sinharaja forest, approach from Weddagala, steep sandy slope under forest, 24.II.1978 Ruinard 24/4; Adam's Peak wilderness, Sudagala forest off Eratna, on rock face, 26.II.1978 Ruinard 26/8 (L!).

28. *Pogonatum rutteri** (Thér. & Dix.) Dix.

J. Bot. 79:76. 1941. — *Atrichum rutteri* Thér. & Dix. in Dix., J. Linn. Soc., Bot. 43:310, 27: fig. 12. 1916. — *Plagiocelopus rutteri* (Thér. & Dix.) Smith Merrill, Mem. New York Bot. Gard. 45:469. 1987. — Type: Malesia. Sabah: Borneo, Rundum, 7.V.1913 Rutter 227 (BM, holotype; H-BR!, isotype).

Pogonatum submarginatum Herz., Hedwigia 66:357. 1926. — Type: Indonesia. Sumatra: Mentawai Islands, auf der erdigen Felsen, Wegner (JE!, isotype). — Synonymized by Touw (1986).

The typical feature of *Pogonatum rutteri* is its sharp and distinct marginal teeth. In contrast to *P. marginatum* the leaves are mostly gradually narrowed to a sharp apex. *P. rutteri* is the only species of the *Racelopus* species group to have large apical cells of the marginal teeth.

Pogonatum rutteri is restricted to tropical SE Asia.

Illustrations — Touw 1986: 15 (fig. 6); Eddy 1988 (as *Pseudoracelopus rutteri*): 44 (fig. 33), 48 (fig. 38).

Distribution — As 4: Indonesia, Malaysia, Philippines.

Specimens examined (representative) — As 4: INDONESIA. Java: W Java, Leuwiliang, above tea-estate Tji Anten, 1 000 m, 21.IX.1952 Meijer B1135; Sumatra: W coast, Lubuk, Sikaping, 470 m, 14.VI.1953 Borssum 1810. — PHILIPPINES. Mindanao: Davao, slopes of Mt. Talomo near Gumate, open logging track in lower montane forest, terrestrial, 4 000 ft., 11.X.1965 Robbins 4022 p.p. (L!).

29. *Pogonatum neo-caledonicum* Besch.

Ann. Sci. Nat. Bot. sér. 5, 18:219. 1873. — Type: New Caledonia, Mont Arago, Balansa 2565 (PC, L, isotypes).

Pogonatum neo-caledonicum is immediately identified and distinguished from the other species of the group by the presence of ventral lamellae on the apical portions of leaves. Similar vestiges are found also on the leaves of *P. misimense* but in the latter species they are much weaker or essentially absent.

Illustrations — Touw 1986: 19 (fig. 8).

Distribution — Endemic to New Caledonia.

Specimens examined — Oc: NEW CALEDONIA. Col Toma, VII.1900 Le Rat; Poindimié: Povila, forêt humide sur crête schisteuse, terrestre, 400 m, 13.VI.1974 McKee 28762; Pente du Mont Koghi, au sol, 400–500 m, McKee 4454 (L!).

30. *Pogonatum misimense** (Bartr.) Touw

J. Hattori Bot. Lab. 60:20. 1986. — *Pseudoracelopus misimensis* Bartr., Blumea 10:150. 1960. — Type: Papua New Guinea. Papua Islands: Misima Islands, Mt. Sisa, Brass 27464 (FH, holotype; BM, GRO, L, isotypes).

Pogonatum misimense might be mistaken for *P. iwatsukii* if no vestiges of ventral lamellae are visible in the apical part of leaves. The inner structure of the leaves in two is, however, different as there is no ventral stereid band in *P. iwatsukii*. The lamina in *P. misimense* is also better developed.

Pogonatum misimense is a plant of the islands of the SE Pacific Ocean and of adjacent New Guinea.

Illustrations — Hyvönen 1986 (as *Pseudoracelopus misimensis*): 138 (fig. 17); Touw 1986: 21 (fig. 9).

Distribution — As 4: Papua New Guinea; Oc: Fiji and Solomon Islands.

Specimens examined (representative) — As 4: PAPUA NEW GUINEA. Morobe: Mindik, ca. 6°28'S, 147°24'E, on vertical clay bank of road, 4 000 ft., Argent N.G.B.F. 28/4/71/23 (H!, LAE!). — Oc: FIJI. Suva, 1898, Armstrong 999. — SOLOMON ISLANDS. San Cristobal: S of Manig-hai, top of ridge, in essentially undisturbed rainforest, moist rather shaded soil of stump throw, 600–720 m, 27.VII.1977 Norris 49102 (H!).

31. *Pogonatum philippinense** (Broth.) Touw

J. Hattori Bot. Lab. 60:16. 1986. — *Pseudoracelopus philippinensis* Broth., Öfvers. Förh. Finska Vetensk.-Soc. 52A(7): 2.

2. 1910. — Type: Philippines. Luzon: Cagayan, III.1909 *Ramos* 7576 (H-BR!, holotype; FH, NY, isotypes).

Pogonatum bornense Thér. & Dix., J. Linn. Soc., Bot. 43:311. 17:13. 1916. — Type: Malasia. Borneo: Sabah, Sandakan, IV.1913 *Binstead* 47 (BM, holotype; GRO, PC, H-BR!, isotypes). — Synonymized by Touw (1986).

Racelopus ponapensis Sak., Bot. Mag. (Tokyo) 57:91. 14. 1943. — Type: Carolines, Ponape, *Kondo* 23 (MAK, holotype). — Synonymized by Touw (1986).

Pogonatum philippinense is, in general appearance, more or less intermediate between the largest plants, *P. marginatum* and *P. rutteri*, and other species of the *Racelopus* species group. The stem is short but well defined and central strand is inconspicuous. The leaves are typically wide and short.

Pogonatum philippinense is confined to the eastern rim of the Pacific Ocean as it has been recorded from Malaysia to the Caroline Islands.

Illustrations — Brotherus 1910 (as *Pseudoracelopus philippinensis*): taf. II (figs. 1–18); Hyvönen 1986 (as *P. philippinensis*): 136 (fig. 16); Touw 1986: 17 (fig. 7); Eddy 1988 (as *P. philippinensis*): 44 (fig. 34).

Distribution — As 4: Indonesia, Malaysia, Papua New Guinea, Philippines; Oc: Caroline and Solomon Islands.

Specimens examined (representative) — As 4: PHILIPPINES. Mindanao: Zamboanga subprov., V.1920 *Brown* 38367 (H!). — PAPUA NEW GUINEA. Morobe: Slate and Gumi creek divide, 17 km W of Bulolo, 30.I.1981 *Streimann* 13905 (CBG, H!). — Oc: SOLOMON ISLANDS. New Georgia group: Kolombangara Island, NW side of island, 0–100 m, 11.VIII.1977 *Norris* 50061 (H!).

32. *Pogonatum iwatsukii** Touw

J. Hattori Bot. Lab. 60:23. 1986. — *Racelopus acaulis* Mitt. in Stapf, Trans. Linn. Soc. London, Bot. ser 2, 4:258. 1894. — Type: Malaysia. Borneo: Sabah, Mt. Kinabalu, *Burbidge* (NY, holotype).

For the distinction of *Pogonatum iwatsukii* from *P. misimense* see the discussion above.

Pogonatum iwatsukii has so far been found only in the northern part of Borneo (Sabah and Sarawak).

Illustrations — Iwatsuki 1969 (as *Pseudoracelopus acaulis* (Mitt.) Iwats.): 286 (fig. 10); Touw 1986: 23 (fig. 10); Eddy 1988 (as *P. acaulis* (Mitt.) Iwats.): 46 (fig. 35); Hyvönen 1989: 575 (fig. 3C).

Distribution — Endemic for Borneo, Malaysia.

Specimens examined (representative) — As 4: MALAYSIA. Borneo: Sabah, E slope of Mt. Kinabalu, in forest between Hot Spring, Poring and Royal Soc. Bungalow, 600 m, on rock, 28.V.1963 *Iwatsuki* 1715 (NICH!); Sarawak, 4th Division, Gunong Mulu National Park, G. Mulu, lower montane forest above camp 2 1/2, on upper side of withered sandstone boulder in small dry pool, full shade, moist, 1 020 m, 4°05'N, 114°55'E, 25.V.1978 *Touw* 20748; Mt. Dulit (Ulu Tinjar), near Long Kapa, on boulder in bed of stream, in shade, scattered, under 300 m, 15.VIII.1932 *Richards* M1287 (L!).

33. *Pogonatum petelotii* (Thér. & Henry) Touw

J. Hattori Bot. Lab. 60:25. 1986. — *Pseudoracelopus petelotii* Thér. & Henry in Henry, Rev. Bryol. n. s. 1:46. 1928. — Type: Vietnam, Tonkin, massif du Pic Ouac, Nam Kep, talus humide d'un ravin, 900 m, *Pételot* 19 ex p. (PC, holotype; L!, isotype).

Pogonatum petelotii is characterized by its essentially entire leaves with a rounded apices. Its leaf-cells are large and thin-walled.

The plant is restricted to continental SE Asia.

Illustrations — Touw 1986: 25 (fig. 11).

Distribution — As 3: Vietnam, Thailand.

Specimens examined — As 3: THAILAND. Nakhon Sawan: along road Doi Musae–Mae Sod, 12 km from Doi Musae, humid evergreen forest along road, on steep loamy bank, 700 m, 16°40'N, 98°55'E, 21.XI.1965 *Touw* 8312 p.p. (L!).

34. *Pogonatum camusii* (Thér.) Touw

J. Hattori Bot. Lab. 60:26. 1986. — *Racelopodopsis camusii* Thér., Monde Pl. sér. 2(9): 22. 1907. — Type: Japan. Ryukyu Islands: Amami-Oshima, Naze, *Ferrié* (PC, holotype).

Pogonatum papillosum Horik., Bot. Mag. (Tokyo) 48: 717. 4. 1934. — Type: Japan. Ryukyu Islands: Iriomote-jima, between Sonai and Shirahama, *Horikawa* 4419; Iriomote-jima, Mt. Hatemura-mori, *Horikawa* 4504. (HIRO, syntypes, probably destroyed). — Synonymized by Touw (1986).

Pogonatum camusii is characterized by small size (stems ca. 5 mm high) and by its extremely reduced leaves. Leaves are ovate to triangular with irregular distal teeth, and they have no ventral lamellae.

Pogonatum camusii is a plant of evergreen rainforests, where it grows on boulders and clayey soil, in shady conditions. It has been collected both on islands and on mainland SE Asia.

Illustrations — Horikawa 1934: 718 (fig. 4 as *Pogonatum papillosum*); Touw 1986: 27 (fig. 12); Hyvönen 1989: 575 (fig. 3D).

Distribution — As 2: China, Japan; As 3: Thailand, Vietnam; As 4: Indonesia, Philippines.

Specimens examined — As 2: CHINA. Taiwan. Taipei Co.: Yangmingshan National Park, Tzutzu road to Mt. Tatan, roadsides and subtropical secondary rainforest with the undergrowth of *Pseudosasa usawai*, alt. ca. 700–800 m, 8.XI.1987 *Hyvönen* 3363 (H!). — JAPAN. Ryukyu Islands: Ishigaki Island, Mt. Omoto, on moist boulder near stream, ca. 280 m, 17.VII.1982 *Yamaguchi* 2998 (HIRO, L!). — As 3: THAILAND. Nakornsrithamarat, granitic massive Khao (Mt.) Luang, evergreen forest along ridge, terrestrial, 1 250–1 450 m, 8°30'N, 99°45'E, 5.II.1966 *Touw* 11663. — As 4: INDONESIA. Flores: W Flores, Manggarai, 12.III.1981 *Schmutz* 4855 (L!). — MALAYSIA. Borneo: Sabah, Kota Belud, Kinabalu Park, Gunong Kinabalu (30–40°SW), near Cascade waterfall, lower montane forest, 10–15 m, on sedimentary rocks, 1 500–1 700 m, 4.IX.1986 *Menzel* 4266 (B, H!). — PHILIPPINES. Mindanao: Davao, Gumate, Mt. Talomo, open logging track in lower montane forest, terrestrial, 4 000 ft., 11.X.1965 *Robbins* 4022 p.p. (L!).

35. *Pogonatum piliferum* (Dozy & Molk.) Touw

J. Hattori Bot. Lab. 60:29. 1986. — *Racelopus pilifer* Dozy & Molk., Bryol. Jav. 1:37. 27. 1856. — Type: Indonesia. Java: Seribu (Seriboe), *Holle 21* (L, holotype).

Racelopus inermis Mitt. in Geh., Flora 69:351. 1886, nom. inval. in synonym. — Original collection: Malaysia. Borneo: Sabah, Mt. Kinabalu, *Burbidge* (BM).

The leafy gametophyte of *Pogonatum piliferum* is more reduced than that of any other species of the group. The apical portion of the leaf, corresponding to the blade of the other Polytrichaceae, is practically absent. The leaves are basally wide and more or less triangular.

Pogonatum piliferum has a wide distribution, ranging from Thailand to the Solomon Islands.

Illustrations — Dozy & Molkenboer 1854–70 (as *Racelopus pilifer*): tab. 27; Hyvönen 1986 (as *R. pilifer*): 135 (fig. 15); Touw 1986: 31 (fig. 13); Eddy 1988 (as *R. pilifer*): 44 (fig. 32).

Distribution — As 3: Thailand; As 4: Indonesia, Malaysia, Papua New Guinea, Philippines; Oc: Solomon Islands.

Specimens examined — As 4: INDONESIA. Borneo: E Kutai, peak of B.papan, terr. Béal, 600–700 m, 17.VII.1952 *Meijer B2391a* (L!). — MALAYSIA. Borneo: Sarawak, 4th division, Gunong Mulu National Park, G. Mulu, 114°55'E, 4°05'N, mixed forest, on rock, 23.V.1978 *Touw 20706* (H!, L!). — PAPUA NEW GUINEA. Morobe: Aseki–Madamna track, 1 km SW of Aseki, 1 350 m, 23.I.1981 *Streimann J2454* (CBG, H!, LAE). — Oc: SOLOMON ISLANDS. New Georgia group: Kolombangara Island, near Mt. Veve, 1 200–1 400 m, 12.VIII.1977 *Norris 49320* (H!).

Subgenus POGONATUM

Polytrichum sect. *Dorcadia* Adans. ex Wallr., Fl. Crypt. Germ. 1:196. 1831, De Not., Syll. Musc. 164. 1838. — *Polytrichum* sect. *Pogonatum* (P. Beauv.) Bals.-Criv. & De Not., Prodr. Bryol. Mediolan. 21. 1833. — *Polytrichum* subg. *Pogonatum* (P. Beauv.) Mont. in d'Orbigny, Dict. 8:400. 1847. — *Polytrichum* sect. *Aloidella* C. Müll., Syn. Musc. Frond. 1:202. 1848. — *Pogonatum* sect. *Aloidella* (C. Müll.) Besch., Ann. Sci. Nat. 6. 10:249. 1880. — *Pogonatum* sect. *Aloidea* Schimp., Coroll. Bryol. Eur. 90. 1855. — *Pogonatum* [subg.?] *B. Aloidea* (Schimp.) Limpr., Laubm. Deutsch. 2:607. 1893. — Type: *Pogonatum aloides* (Hedw.) P. Beauv. (*Polytrichum aloides* Hedw.), lectotype, vide Smith (1971).

Pogonatum A. Nana B.S.G., Bryol. Eur. 4:249. 1844. — *Pogonatum* [subg.?] *A. Nana* (B.S.G.) Limpr., Laubm. Deutschl. 2:605. 1893. — *Pogonatum* sect. *Nana* B.S.G. ex Broth., Nat. Pflanzenfam. 1:686. 1909. — Type: *Pogonatum nanum* (Hedw.) P. Beauv. (*Polytrichum nanum* Hedw.), holotype.

36. *Pogonatum aloides** (Hedw.) P. Beauv. (Figs. 12A–E, 30 – map)

Prodr. Aethogam. 84. 1805. — *Polytrichum aloides* Hedw., Spec. Musc. 96. 1801. — *Pogonatum nanum* Lindb., Not.

Sällsk. Fauna Fl. Fenn. Förh. 9:139. 1868, hom. illeg. — *Pogonatum mnioides* Hag., Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1913(1): 30. 1914, nom. illeg. superfl. — Type: Europe?

Polytrichum rubellum Menz. ex Brid., J. Bot. (Schrader) 1800(1): 287. 1801. — *Pogonatum aloides* var. *rubellum* (Brid.) Brid., Bryol. Univ. 2:121. 1827. — Type: Great Britain (B!, holotype). — Synonymized by Hooker & Taylor (1818).

Polytrichum dicksonii Turn., Musc. Hib. 90. 10:2. 1804. — *Pogonatum aloides* var. *dicksonii* (Turn.) Brid., Bryol. Univ. 2:121. 1827. — *P. mnioides* var. *dicksonii* (Turn.) Hag., Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1913(1): 31. 1914. — Type: Ireland, Derry, *Brown* (BM!, holotype). — Synonymized by Gangulee (1969).

?*Polytrichum minimum* Crome, Samml. Deutsch. Laubm. Nachl. 2:48. 1806, syn. nov. — *Pogonatum aloides* var. *defluens* Brid., Bryol. Univ. 2:121. 1827, nom. illeg. superfl. — *P. aloides* var. *minus* B.S.G., Bryol. Eur. 4:250. 416b. 1844, nom. illeg. superfl. — *P. nanum* var. *minimum* (Crome) Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9:140. 1868. — *P. aloides* var. *minimum* (Crome) Mol., Jahres-Ber. Naturhist. Vereins Passau 10:199. 1875. — Type: Germany, Mecklenburg, nahe vor Gneben, unwert Schwerin, an der Seite eines Grabens, *Crome*, Samml. Deutsch. Laubm. 2:30.

Polytrichum aloides var. *dicarpon* Brid., Mant. Musc. 201. 1819. — *Pogonatum aloides* var. *dicarpon* (Brid.) Brid., Bryol. Univ. 2:121. 1827. — Type: Italy, in Monte Latiali prope Romam, 1806 (B!, holotype; H!, isotype). — Synonymized by Paris (1898).

Pogonatum nanum var. *longisetum* Hampe ex B.S.G., Bryol. Eur. 4:249. 1844, syn. nov. — *P. polytrichoides* var. *longisetum* (B.S.G.) Müll., Ark. Bot. 16(3): 43. 1921. — Type: Germany, Halle, 1814 *Hampe* (BM!, holotype).

?*Polytrichum aloides* var. *magnum* C. Müll., Syn. Musc. Frond. 1:203. 1848, syn. nov. — *Pogonatum aloides* var. *magnum* (C. Müll.) J. Kickx. fil., Fl. Crypt. Flandres 1:116. 1867. — Type: Austria, Tirol: Innsbruck, in limos. sylvestr. Oenipont, *Heufler*.

Polytrichum subaloides C. Müll., Bot. Zeitung (Berlin) 20:12. 1862, syn. nov. — *Pogonatum subaloides* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 249. 1875 (Adumbratio 1:711). — Type: Canary Islands. Teneriffa: Mt. Agua, 4 000 ft., *Trumppff* (M!, isotype).

?*Polytrichum subaloides* var. *minus* C. Müll., Bot. Zeitung (Berlin) 20:12. 1862, syn. nov. — *Pogonatum subaloides* var. *minus* (C. Müll.) Par., Ind. Bryol. 988. 1898. — Type: Madeira, ut Cl. Hampe communicavit, Cl. Heer retulit.

Pogonatum aloides var. *ramosum* Brockm., Arch. Vereins Freunde Naturgesch. Mecklenburg 23:111. 1870. — Type: Germany, Mecklenburg, Reumahten (?), an der Seite eines Grabens, auf Wiese, *Crome* Samml. Deutsch. Laubm. 1:89. (H!, isotype). — Synonymized by Gangulee (1969).

?*Pogonatum aloides* var. *cyathiforme* Pasquale in Giordano, Bullett. Natural. Med. Napoli 1871, syn. nov. — Type: (?NAP).

?*Pogonatum approximans* Schimp. in Besch., Cat. Mouss. Algérie 29. 1882, nom. nud. in synonym. — Original collection: Algeria, Herb. Durrieu de Maisonneuve.

Pogonatum heerii Hampe in Geh., Flora 69:348. 1886, nom. nud. in synonym. — Original collection: Herb. Heer.

?*Pogonatum briosianum* Farn., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser. 2(2): 199. 26:2–13. 1892, syn. nov. — *P. aloides* var. *obtusifolium* Amann, Ber. Schweiz. Bot. Ges. 5:104. 1895, nom. illeg. superfl. — *P. aloides* var. *briosianum* (Farn.) Warnst., Bot. Centralbl. 72:394. 1897. —

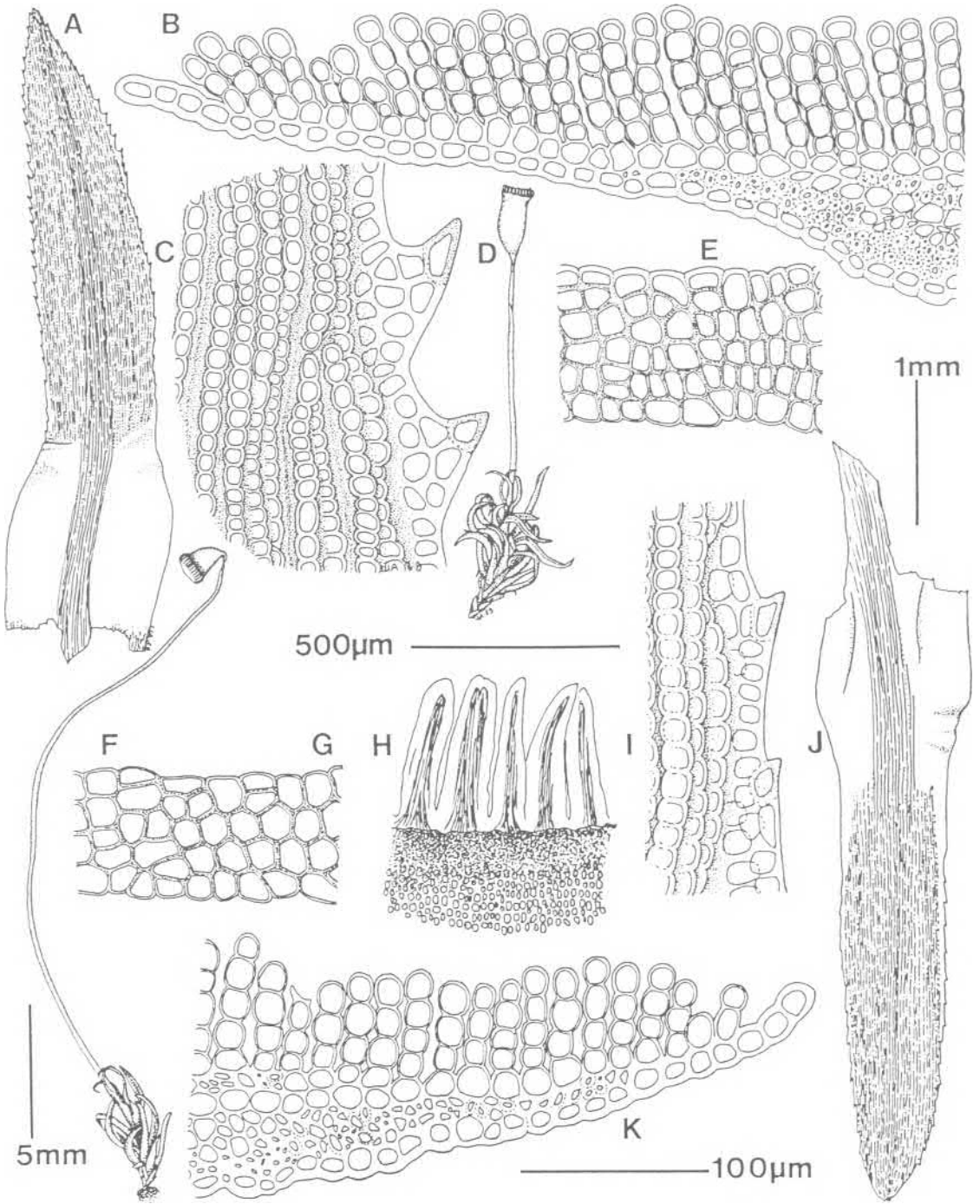


Fig. 12A-K. — A-E: *Pogonatum aloides*. A. Leaf, B. Leaf cross-section, C. Marginal teeth as seen above, D. Habit and E. Lamella in side view (Wojterski 553, H). — F-K: *P. nanum*. F. Habit, G. Lamella in side view, H. Peristome, I. Marginal teeth as seen above, J. Leaf and K. Leaf cross-section (Deyl V.1933, H). — Use the 5 mm scale for D and F, 1 mm scale for A and J, 500 µm scale for H, and 100 µm scale for B, C, E, G, I and K.

Polytrichum aloides subsp. *briosianum* (Farn.) Albrecht, J. Bot. 72:104. 1934. — *Pogonatum aloides* subsp. *briosianum* (Farn.) Albrecht ex Podp., Consp. Musc. Eur. 62. 1954, nom. inval. in synon. err. pro *Polytrichum aloides* subsp. *briosianum* (Farn.) Albrecht. — Type: Italy, Pavia, in substrato calcareo lapidoso, sabuloso, stillicido irrorato, prope San Bonetto valle Stafforae.

Pogonatum aloides var. *polysetum* Kaulf., Abh. Naturhist. Ges. Nürnberg 10:167. 1897, *syn. nov.* — Type: Germany, Franken: Nürnberg, an einem sandigen Strassengraben hinter Lichtenhof, 315 m, 26.III.1897 Kaulfuss (B!, isotype).

?*Pogonatum aloides* var. *elatum* Warnst. in Jaap, Verh. Bot. Vereins Prov. Brandenburg 43:65. 1901, nom. nud.; Krypt. Fl. Brandenburg 2:1093. 1906. — Type: Poland, Ostprignitz: Triglitz, in der Heide, an den Wänden eines Grabens, Jaap.

Pogonatum aloides var. *gombaulti* P. Vard., Rev. Bryol. Lichénol. 21:13. 1952, *syn. nov.* — Type: Libanon, Bikfaya, à terre, 800 m, VII.1933 Gombault 19 (PC!, holotype).

?*Pogonatum aloides* x *nanum* Warnst., Krypt. Fl. Brandenburg 2:1091. 1106. 2. 1906. — Type: Poland, Potsdam, Ostprignitz: Triglitz, in einem Graben der Heide, IV.1895 Jaap 237.

Pogonatum aloides is closely related to another European species of the genus, *P. nanum*. Without sporophytes the two can be indistinguishable because small, depauperate forms of *P. aloides* can have leaves with very stunted serration resembling those of *P. nanum*. Normally the leaves of *P. aloides* have distinct marginal teeth along the entire blade, and plants are also larger. When sporophytes are present, the two species are easily distinguished because *P. nanum* typically has very short capsules and long peristome teeth (320–400 µm), which are often recurved in dry capsules. In *P. aloides*, the length of the teeth is normally about half of that observed in *P. nanum*, but the height of the basal membrane may vary.

In the past, *Pogonatum aloides* has also repeatedly been confused with the Asian *P. neesii*. The two species are very similar in that both have leaves curved in the dry condition, and they have numerous teeth on the dorsal side of the wide costa. *P. neesii* is more variable in size, while *P. aloides* is almost always a plant with fairly short stems. The two species have many good diagnostic characters, which seem to be stable and do not vary to any great extent. In *P. aloides* at least some of the apical cells of the lamellae are finely papillose like those of *P. neesii*. In the latter, however, this papillosity is more pronounced especially in southern populations. In *P. aloides*, the apical cells are mostly rounded in cross-section and only slightly crenate to essentially straight as seen in side view; whereas, in *P. neesii*, they are typically retuse and often even widened, and in side view they are deeply crenate.

In New Zealand distinction from the native *Pogonatum subulatum* can be problematic. For diag-

nostic characters see the discussion under the latter species.

Pogonatum aloides is a plant of open ground at fairly low altitudes (sea level up to 1 500 m). *P. aloides* is mostly restricted to Europe, but it is an introduced weedy plant in New Zealand. Reports of the species from many parts of Asia and continental Africa are probably erroneous. All African and Asian specimens that I have studied proved to be misidentified.

Hybridization between *P. nanum* and *P. aloides* is reported to be common, but the hybrid gametophytes are not easily discerned (Schratz 1928). Thus, it is possible that some of the depauperate varieties described under *P. aloides* are actually hybrids with *P. nanum*. It is not certain whether the hybrid populations are able to produce normal sporophytes. I presume that hybridization takes place repeatedly with the resultant sporophytes probably seldom reproducing successfully. All hybrids are thus not monophyletic and formal recognition becomes superfluous. Accordingly, they are tentatively listed separately under each species after the first partner, as reported in original work.

Illustrations — Nyholm 1969: 668 (fig. 436); Smith, A.J.E 1978: 98 (fig. 38:7–12).

Distribution — Eur: Austria, Belgium, Czechoslovakia, Denmark, Finland, France, Germany, Great Britain, Greece, Hungary, Ireland, Italy, Netherlands, Norway, Poland, Portugal, Romania, USSR, Sweden, Switzerland, Yugoslavia; As 5: Iran, Turkey; Afr 1: Azores, Canary Islands, Madeira; Austr 2: New Zealand.

37. *Pogonatum nanum* (Hedw.) P. Beauv. (Figs. 12F–K, 30 – map)

Prodr. Aetheogam. 84. 1805. — *Polytrichum nanum* Hedw., Spec. Musc. 95. 1801. — *Pogonatum polytrichoides* P. Beauv., Mém. Soc. Linn. Paris 1:461. 1823, nom. illeg. superfl. — *Polytrichum aloides* subsp. *nanum* (Hedw.) Albrecht, J. Bot. 72:104. 1934. — *Pogonatum aloides* subsp. *nanum* (Hedw.) Albrecht ex Podp., Consp. Musc. Eur. 61. 1954, nom. inval. in synon. err. pro *Polytrichum aloides* subsp. *nanum* (Hedw.) Albrecht. — Type: Europe?

Polytrichum pumilum Sw. ex Hedw., Spec. Musc. 97. 21:7–9. 1801. — *Polytrichum subrotundum* Turn., Musc. Hib. 89. 1804, nom. illeg. superfl. — *Pogonatum pumilum* (Hedw.) P. Beauv., Prodr. Aetheogam. 84. 1805. — *P. nanum* var. *subrotundum* Röhl., Ann. Wetterauischen Ges. Gesamte Naturk. 3(2): 231. 1814. — *P. subrotundum* Lindb. in Hartm. Skand. Fl. ed. 9, 2:44. 1864, nom. nud. in synon. — *P. polytrichoides* var. *pumilum* (Hedw.) Brockm., Arch. Vereins Freunde Naturgesch. Mecklenburg 23:111. 1870. — Type: Sweden, Swartz (UPS!, isotype). — Synonymized by Bruch et al. 1844.

?*Polytrichum intermedium* Brid., Spec. Musc. 1:70. 1806, *syn. nov.* — *Pogonatum intermedium* (Brid.) Röhl., Deutschl. Fl. Krypt. ed. 2(3): 60. 1813. — *P. nanum* var. *intermedium*

(Brid.) Röhl., Ann. Wetterauischen Ges. Gesammte Naturk. 3(2): 231. 1814. — *P. pusillum* var. *intermedium* (Brid.) Brid., Bryol. Univ. 2:117. 1827. — *P. polytrichoides* var. *intermedium* Brockm., Arch. Vereins Freunde Naturgesch. Mecklenburg 23:111. 1870. — Type: Switzerland, Lac Leman, Røger; Germany, Mecklenburg (Megapolitano), *Blandow* (B1, syntype).

Polytrichum semi-diaphanum Brid., Mant. Musc. 200. 1819. — *Pogonatum nanum* var. *semi-diaphanum* (Brid.) Brid., Bryol. Univ. 2:119. 1827. — Type: Germany, in rupe Rothstein Thuringiae, 1798 *Bridel*; Italy (Italia), *Bridel* (B1, syntypes). — Synonymized by Bruch et al. 1844.

Pogonatum nanum var. *robustum* Velen., Rozpr. Ceské Akad. Ved, Tr. 2, Vedy Mat. Prir. 7(16): 12. 1898, nom. nud. — Original collection: Czechoslovakia. Bohemia: Bohemia centr., in calluneto inter silvas prope pagum Mnichovice (ca. 25 km ad merid.-occidentem ab urbe Praha versus), IV.1898 *Velenovsky* (PRC!).

?*Pogonatum nanum* × *aloides* Brunnthaler, Österr. Bot. Zeitschr. 47:46. 1897. — Type: Austria. Nieder Österreich: Bezirk Melk, an einer Strassenböschung bei Gansbach, auf Schiefer, ca. 450 m, 8.III.1896 *Baumgartner*.

Pogonatum nanum is almost impossible to distinguish gametophytically from depauperate forms of *P. aloides*. The latter species, however, normally has leaf-margins with larger teeth, and its costa has numerous dorsal teeth. The leaf apices of *P. nanum* are wide and rounded, whereas in *P. aloides* they are acute. With sporophytes the two species are easily distinguished because *P. nanum* has small and spherical capsules with long peristome teeth.

Separate sectional status for *Pogonatum nanum* and some related dwarf species was retained by Brotherus (1909, 1925) on the basis of sporophytic characters. The small roundish capsule and irregular and short columella are, indeed, unique in the genus. However, the columella of at least some capsules has the normal four wings of other species of the genus. The importance of the distortion has probably been overestimated and the taxonomic significance is uncertain (Smith 1971).

Pogonatum nanum is a plant of open habitats which has been collected from sea level to 1 350 m.

Illustrations — Nyholm 1969: 667 (fig. 435A); Smith 1978: 98 (fig. 38:1–6).

Distribution — Eur: Austria, Czechoslovakia, Denmark, Finland, France, Germany, Great Britain, Hungary, Iceland, Italy, Netherlands, Norway, Poland, USSR, Spain, Sweden, Switzerland, Yugoslavia; Afr 1: Canary Islands.

38. *Pogonatum brachyphyllum* (Michx.) P. Beauv. (Figs. 13A–D, 30 – map)

Prodr. Aethogam. 84. 1805. — *Polytrichum brachyphyllum* Michx., Fl. Bor. Am. 2:295. 1803. — Type: USA, in Carolina inferiore (?PC).

?*Pogonatum pusillum* P. Beauv., Prodr. Aethogam. 85. 1805, *syn. nov.* — Type: USA, Carolina, *Boseq.*

Polytrichum vaginans Brid., Spec. Musc. 1:68. 1806. — *Pogonatum vaginans* Brid. ex Par., Ind. Bryol. 978. 1898, nom. inval. in *synon. err. pro Polytrichum vaginans* Brid. — Type: Haiti (Hispaniola), Herb. Desfontaines; USA, Carolina, *Boseq.* — Synonymized by Paris (1898).

Pogonatum brachyphyllum is distinguished from all other American species of the genus by its small size, and by the entire margins and obtuse apices of its leaves. The apical cells of lamellae of *P. brachyphyllum* are unique for the genus because all walls are incrassate and the lumen may be small and rounded. European *P. nanum* may resemble *P. brachyphyllum* but it lacks the extremely incrassate walls of the apical cells. In *P. nanum*, leaves also have at least a few small and rounded teeth on the apical portion of the margins. *P. pensilvanicum*, another species from eastern North America with persistent protonema, is easily distinguished from *P. brachyphyllum* because its leaves have a reduced blade and much fewer ventral lamellae.

Although Bruch et al. (1844) give *Pogonatum pusillum* as a synonym of *P. nanum*, it is most probably a synonym of *P. brachyphyllum*. There are no records of *P. nanum* from the USA but *P. brachyphyllum* is very common and locally abundant in eastern parts of the country. Consequently, *P. pusillum* is tentatively synonymized with the latter species despite my not having seen any type material.

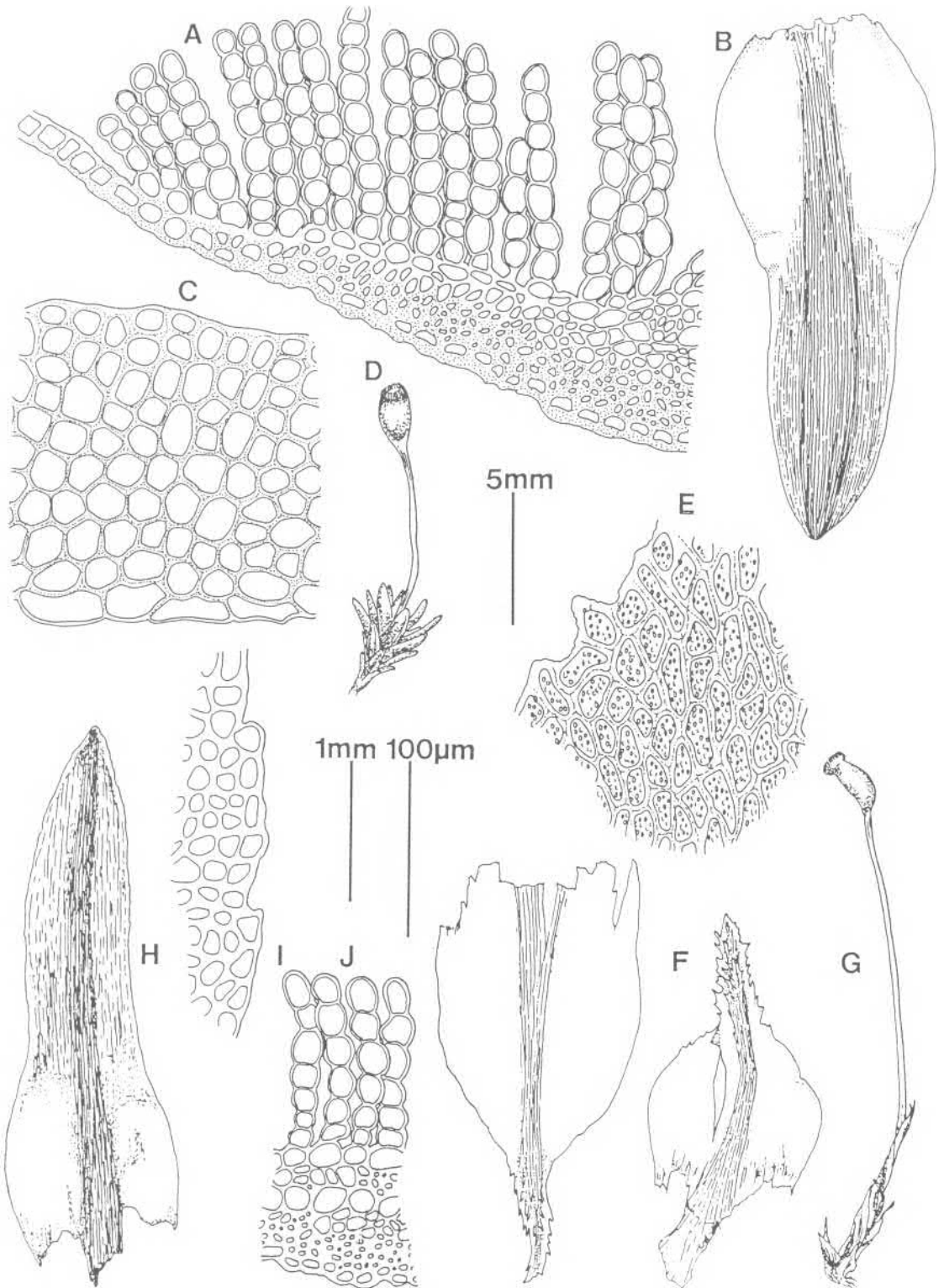
One of the syntypes of *Pogonatum vaginans*, apparently, is an isotype of *P. pusillum* but another syntype was stated to have come from Haiti. I have not seen the latter specimen but it is highly unlikely to be conspecific with *P. brachyphyllum* as there are no further records of this species from the island despite fairly extensive collecting by several bryologists.

Pogonatum brachyphyllum is a plant restricted mostly to southeastern parts of the United States, ranging northward to Connecticut. *P. brachyphyllum* produces persistent protonema on sandy and loamy soil. It is confined to low altitudes — all collections from under 300 m above sea level.

Illustrations — Grout 1937: pl. 58C; Crum & Anderson 1981: 1262 (fig. 627J–N).

Distribution — Endemic to southern and eastern parts of USA.

Specimens examined (representative) — Am 1: USA. Alabama: Lee Co., Auburn, 2.III.1901 *Earle* 22; Arkansas: Clark Co., 10 miles SW of Arkadelphia, on moist shady banks, terrestrial, 27.XII.1941 *Meyer* 108; Georgia: Montgomery Co., 10 miles NW of Uvalde, sandy road bank, 22.III.1960 *Anderson & Crum* 13601; Kansas: Ellsworth Co., Horse Thief canyon area, 12.8 km N of Langly, on prairie hill slope, below sandstone outcrop, 38°42'N, 98°01'W, 14.IV.1979 *Churchill* 10706; North Carolina: Durham Co.,



NE of Durham, 2 miles N of Catsburg, 4.V.1960 Schofield 11266 (H!).

39. *Pogonatum capense* (Hampe) Jaeg. (Figs. 13H–J, 30 – map)

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 249. 1875 (Adumbratio 1:711). — *Polytrichum capense* Hampe, Icon. Musc. 21. 1844. — Type: South Africa, Port Natal, Gueinzius (JE!, lectot. nov.).

?*Pogonatum convolutum* var. *minus* Brid. ex P. Beauv., Prodr. Aetheogam. 84. 1805, nom. nud. — Original collection: South Africa (Cap de Bonne-Esperance).

Polytrichum borgenii Hampe, Bot. Zeitung (Berlin) 28:35. 1870. — *Pogonatum borgenii* (Hampe) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 255. 1875 (Adumbratio 1:717). — Type: South Africa. Natal: Umpumulo, 20.III.1867 *Borgen* (L!, isotype). — Synonymized by De Sloover (1986).

Polytrichum angolense Welw. & Duby, Mém. Soc. Phys. Genève 21:217. 1:2. 1872. — *Pogonatum angolense* (Welw. & Duby) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 251. 1875 (Adumbratio 1:713). — Type: Angola, Huilla, 14–16°S, pascuis humoso-arenosis breviter dumctosis Empalena, 5 200 ft., circiter unico loco reperiit, IV.1860 *Welwitsch* (G!, holotype). — Synonymized by De Sloover (1986).

Polytrichum afro-aloides C. Müll. ex Geh., Abh. Naturwiss. Vereine Bremen 7:204. 1882. — *Pogonatum afro-aloides* (Geh.) Par., Ind. Bryol. 974. 1898. — Type: Madagascar, Wald von Ambatondrazaka, 6.XII.1877 *Rutenberg*. — Synonymized by De Sloover (1986).

Polytrichum obtusatum C. Müll. ex Geh., Abh. Naturwiss. Vereine Bremen 7:204. 1882. — *Pogonatum obtusatum* (Geh.) Par., Ind. Bryol. 984. 1898. — Type: Madagascar, Ambohimara, 9.XI.1877 *Rutenberg*. — Synonymized by Thériot (1924).

Pogonatum tortifolium Rehm. in Dix. & Gepp, Kew Bull. Misc. Inform. 1923: 208. 1923, nom. nud. — Original collection: South Africa. Natal: Umgeni supra Maritzbourg, *Rehmann*: Musci austro-africani 268 (BM!).

Typical *Pogonatum capense* is easily distinguished from all other species of the genus in Africa. The plants are small with stiff leaves and they grow gregariously from persistent protonema. Some small specimens of *P. belangeri* might closely resemble them but this latter species lacks persistent protonema. It should be noted, however, that such a protonema is not always preserved in herbarium specimens. In *P. capense* the ventral stereid band is often very reduced to absent while the dorsal band is wide. This difference between stereid bands is not as pronounced in *P. belangeri*. The unistratose leaf-margins

of the latter are wider and normally more serrate, whereas *P. capense* has margins with very small and rounded teeth, or the margins may simply be only undulate (Fig. 8I). The apex of *P. capense* is rounded and cucullate with the leaf-margins more ascending than in *P. belangeri*. Capsules of the latter are normally longer than those of *P. capense*.

Pogonatum capense is confined to exposed and open habitats at fairly low altitudes (850–2 300 m).

Illustrations — De Sloover 1986: 275 (figs. 205–224).

Distribution — Afr 2: Angola; Afr 3: Madagascar; Afr 4: South Africa, Swaziland.

40. *Pogonatum spinulosum* Mitt. (Figs. 13E–G, 30 – map)

J. Linn. Soc., Bot. 8:156. 1865. — Type: Japan. Kiushu: Nagasaki, on the earth, *Oldham* 426 (NY!, holotype).

Pogonatum pellucens Besch., Ann. Sci. Nat. Bot. sér. 7, 17:351. 1893. — *P. acaule* Schimp. ex Par., Ind. Bryol. Suppl. 277. 1900, nom. illeg. superfl. — Type: Japan. Honshu: Yokoska, *Savaiier* (H-BR!, isotype). — Synonymized by Salmon (1900).

Pogonatum spinulosum var. *serricalyx* Bartr., Ann. Bryol. 8:21. 1936, *syn. nov.* — Type: China. Guizhou: Chian kou, Fang Ching Shan, bark of tree, 2 000 m, 3.X.1931 *Cheo* 646 (FH!, holotype).

Pogonatum spinulosum has pronounced neoteny with the leaf composed almost entirely of sheath. Typically the upper sheath cells and cells of the costa have a clearly papillose cuticula. The protonema is persistent, and the stems emerge gregariously from it. The capsule is normally terete (rarely plicate) and often slightly arcuate. Most specimens include capsules and these are the most conspicuous portions of the plant.

Pogonatum spinulosum is seldom confused with any other species of the genus. The species of the *Racelopus* group have a more or less papillose setae and none of the species of this group has the coarse cuticular papillosity of the laminal cells typical of *P. spinulosum*.

The phylogeny of those *Pogonatum* species with reduced gametophytes is practically impossible to trace. In the American *P. pensilvanicum* we can assume that it evolved from the same ancestral stock as other American species with geminate apical cells of the lamellae. Furthermore, it can be assumed that all species of the *Racelopus* species group are mono-

phyletic, sharing the unique, papillose seta. However, the relationship to other species of the genus is dubious. *P. spinulosum* is tentatively put in the same group with other species possessing a persistent protonema and not included in either of the two groups given above. However, there are no other features to support this decision, and morphological studies with traditional methods would probably not clarify the problem.

Study of the type of *Pogonatum spinulosum* var. *serricalyx* revealed it to fall within the normal circumscription of the species and it is therefore, reduced to synonymy.

Pogonatum spinulosum is a plant of bare ground which has been collected mainly on trail- and road-side from sea level to 3 250 m.

Illustrations — Osada 1965: 176 (fig. 1); Noguchi 1987: 33 (fig. 12B).

Distribution — As 1: USSR; As 2: China, Japan, Korea; As 4: Philippines.

Specimens examined (representative) — As 1: USSR. Far East: in vicinibus urb. Vladivostok prope stationem "Orkeanskaja" ad denudationes in silvis, 2.IX.1954 *Vassiljeva*. — As 2: CHINA. Hubei: W side of Dajiuhe basin, Zhushanyazi pass, Shennongjia forest district, in *Fagus* forest, on soil in shade, 31°30'N, 110°30'E, ca. 1 780 m, 13.IX.1980 *Bartholomew & al.* 1265. — JAPAN. Honshu: Yamanashi-ken, Kitakoma-gun, Sudama-cho, Masutomi spa, deciduous forest, on soil, 27.IX.1978 *Osada*. — KOREA. Munchangdae, Songnisan National Park, 29.VIII.1987 *Lai* 19758 (H!).

41. *Pogonatum norrisii* Hyvönen, *spec. nova* (Figs. 14A–H, 31 – map)

Plantae simplices, caules 20–35 mm, inferne nudi, superne dense foliosi. Folia sicca incurva, vagina hyalina, ovata; lamellis 24–30, 4–7 cellulas altis, a latere visis integris. Seta erecta, ad 21 mm; capsula oblonga; peristomii dentes 32, geminati, rubentes, marginibus hyalinis; calyptra villosa.

Type: Dominican Republic. La Vega: ca. 13 km from Valle Nuevo on the road to San José de Ocoa, on very moist burned and cut pineland near the pyramid, ca. 2 500 m, VIII.1967 *Norris* B7155 (H!, holotype; MO!, isotype).

Eponymy: The name is dedicated to Prof. Daniel H. Norris, who collected the species on one of his field trips. His research has concentrated on the bryoflora of poorly known subtropical and tropical areas.

Plants small to medium-sized, loosely caespitose, yellowish green to oliveaceous. *Stems* unbranched or very rarely branched, erect, up to 20–35 mm high; leaves born on upper 5–25 mm of the stem. *Leaves* crowded, incurved when dry; erect-spreading to slightly squarrose when moist, narrowly linear-lanceolate. *Blade* 2.4–4.7 mm long and 0.4–0.7 mm wide, very gradually narrowed to sharp apex. *Mar-*

gins upcurved, unistratose, 3–5 cell-rows wide, serrate with fairly small, multicellular teeth. *Costa* excurrent, apically reddish brown, with 240–340 µm wide dorsal stereid band, ventral stereid band 90–180 µm wide, cells of stereid bands with firm to incrassate walls, costa apically sharply dentate with numerous dorsal teeth. *Dorsal cells of blade* ovate to subquarate with extremely incrassate transverse walls, cell-lumen 14–18 µm Ø. *Ventral lamellae* 24–36 per leaf, 3–7 cells high, with essentially straight upper margin. *Cells* subquarate to ovate with incrassate to firm walls, lumen 9–22 µm Ø. *Sheath* ovate, gradually narrowed to blade, *cells* subquarate to rectangular with firm walls, lumen 9–14 x 11–46 µm.

Dioicous. Perichaetial leaves similar with cauline leaves, only with gradually longer sheath. Male plants not seen. *Seta* terminal or pseudolateral by subperichaetial innovation; smooth, solitary, 14–23 mm long. *Capsules* erect or slightly inclined, light to dark brown. *Urn* cylindrical, terete, or very faintly plicate, 0.8–1.1 x 3.0–4.1 mm. *Exothelial cells* mammillose, elongated, lumen 14–29 x 23–66 µm, walls firm. *Peristome* with 32 compound teeth. *Teeth* 110–220 µm, basal membrane low, less than 35 µm or essentially absent, teeth with distinct median sinus, each of 64 parts reddish brown, with hyaline margins. *Epiphragm* thin, attached to apices of peristome teeth. *Operculum* rostrate, 0.8 mm long. *Calyptra* hairy, 5–7 mm long (hairs included). Spores ca. 8.5–12 µm Ø, finely papillose.

Pogonatum norrisii has formerly been overlooked or mistaken for *P. tortile*. The two species are, however, easily distinguished by their habit, especially when dry. Leaves of *P. norrisii* are typically incurved or even tightly coiled at the apex when dry, resembling the Asian *P. inflexum*. The leaves are gradually narrowed to a sharp apex and the blade is much narrower than that of *P. tortile*. The marginal teeth are fairly small but sharp and patent, and the dorsal teeth of the costa are conspicuous and numerous. In *P. tortile* the apical cells of the lamellae are regularly crenate in side view, whereas they are essentially straight in *P. norrisii*. The capsule of *P. norrisii* is also much smaller than that of *P. tortile*.

I have not studied type material of many of the species of *Polytrichum* described by Müller from Central America. The protologues of these species are, in many cases, rather imprecise and do not reveal the identity of the plants with certainty. However, none of the descriptions that I have studied conform with *P. norrisii*. Type material of many species described by Müller has probably been destroyed as well, and their identity will thus remain dubious.

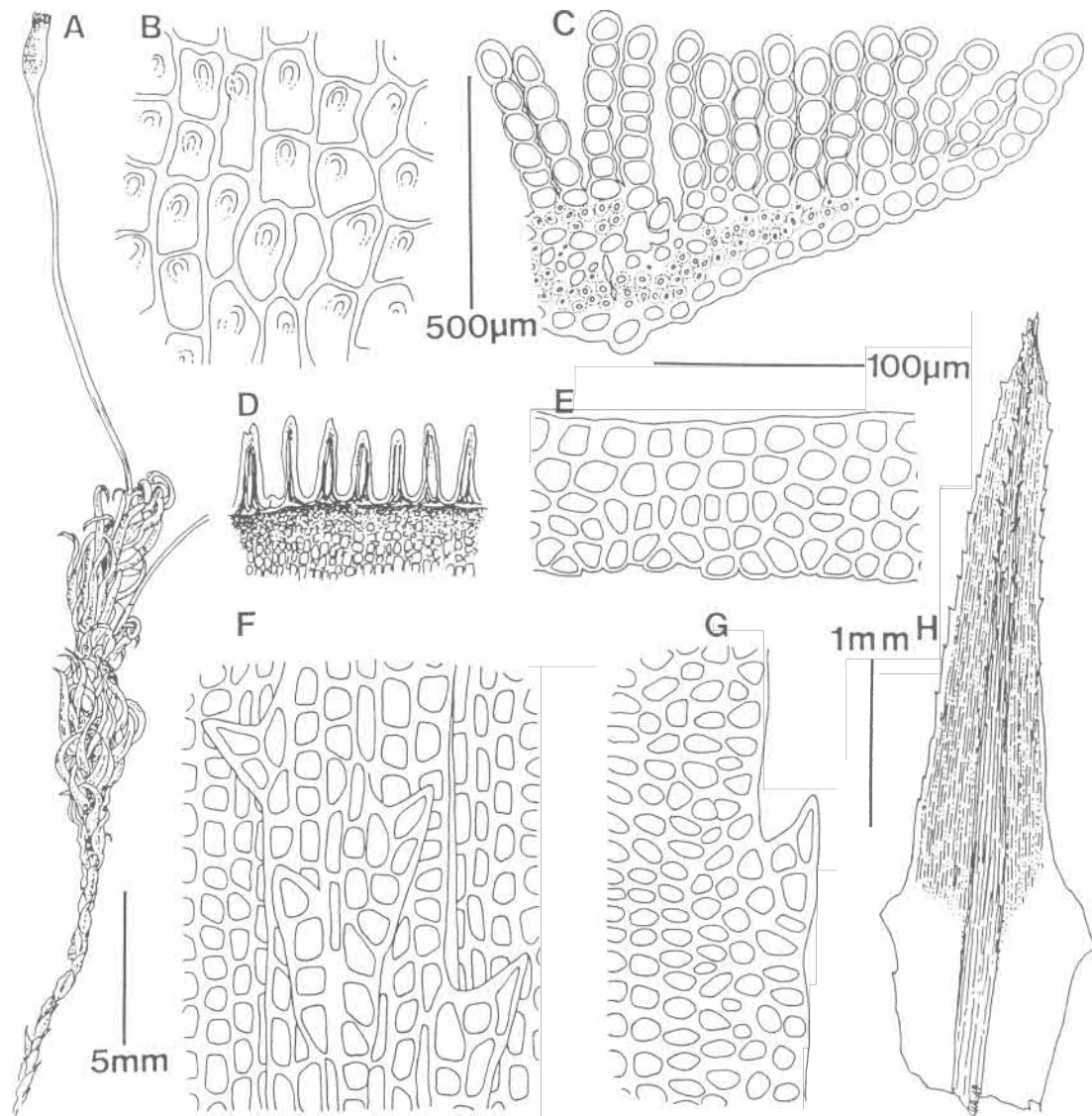


Fig. 14A–H. *Pogonatum norrisii*. A. Habit, B. Exothecial cells, C. Leaf cross-section, D. Peristome, E. Lamella in side view, F. Teeth on dorsal side of costa, G. Marginal teeth and H. Leaf. A, C and E–H (Norris B7155, holotype H), B and D (Steere 19350B, MO). — Use the 500 μm scale for D, 100 μm scale for B, C and E–G, 1 mm scale for H, and 5 mm scale for A.

Pogonatum norrisii is a plant of bare ground growing by trail-sides and similar habitats. It has been collected at 1 350–2 500 m.

Distribution — Am 3: Dominican Republic, Haiti, Jamaica.

Specimens examined (paratypes) — Am 3: DOMINICAN REPUBLIC. La Vega: 10.8 km N of Valle Nuevo, 12.4 km S of Constanza, wet rock face along road, 6 200 ft., 30.IV.1982 Steere 22747 (H!); Ciénaga de la Culata, Constanza, 1 500–1 600 m, 28.XI.1969 Liogier 17059 (NY, TNS!);

Cordillera Central, 5.4 km S of Constanza, broad-leaved forest with *Magnolia pallescens*, 18°50'N, 70°45'W, 6 200–6 300 ft., 24.II.1982 Zandoni & al. 19350B. — HAITI. SE Dept.: in lumber mill town of Mare Rouge, 20 km E of Seguin, *Pinus occidentalis* forest, 18°20'N, 72°02'W, 1900 m, 19.II.1981 Adams & Zandoni 11295; 2–3 km E of Seguin, road to Mare Rouge, humid *Pinus occidentalis* forest, 18°20'N, 72°13'W, 5 800 ft., 19.II.1981 Adams & Zandoni 11289. — JAMAICA. St. Andrew, below Morce's Gap, 1 mile NE of Clydesdale, 18°05'N, 76°40'W, 4 500–4 700 ft., 17.VIII.1966 Crosby 32552 (MO!)

42. *Pogonatum neesii** (C. Müll.) Dozy (Figs. 15A–C, 31 – map)

Bryol. Jav. 1:40. 36. 1856, Ned. Kruidk. Arch. 4(1): 75. 1856. — *Polytrichum neesii* C. Müll., Syn. Musc. Frond. 2:563. 1851. — *Pogonatum aloides* fo. *neesii* (C. Müll.) Gang., Mosses E. India 1:100. 1969. — Type: Indonesia, Java, *Blume* Herb. Al. Braun (B, holotype, probably destroyed).

Polytrichum junghuhnianum Dozy & Molk. in Miquel, Pl. Jungh. 3:324. 1854. — *Pogonatum junghuhnianum* (Dozy & Molk.) Dozy & Molk., Bryol. Jav. 1:41. 31. 1856, Ned. Kruidk. Arch. 4(1): 75. 1856. — Type: Indonesia, Java: in monte Dieng, in terra limosa, ad vias et muros, mense Martio *Junghuhn* (L1, holotype). — Synonymized by Dixon & Potier de la Varde (1927).

Polytrichum junghuhnianum var. *incurvum* Dozy & Molk. in Miquel, Pl. Jungh. 3:325. 1854, syn. nov. — *Pogonatum junghuhnianum* var. *incurvum* (Dozy & Molk.) Dozy & Molk., Bryol. Jav. 1:42. 1856. — Type: Indonesia, Java: Megamendung, ad vias limosas, *Junghuhn* (L1, holotype).

Polytrichum australasicum C. Müll. & Hampe, Linnaea 26:500. 1855, syn. nov. — *Pogonatum australasicum* (C. Müll. & Hampe) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 256. 1875 (Adumbratio 1:718). — Type: Australia, along the wood road over the Blackspur, *F. Müller* (BM!, isotype).

Catharinaea nietneri C. Müll., Linnaea 36:36. 1869, syn. nov. — *Pogonatum nietneri* (C. Müll.) Broth., Nat. Pflanzenfam. 1(3): 687. 1905. — Type: Sri Lanka (Ceylon), *Nietner* (H-BR!, isotype).

Polytrichum albo-marginatum C. Müll., Linnaea 37:172. 1872. — *Pogonatum albo-marginatum* (C. Müll.) Jaeg., Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 266. 1875 (Adumbratio 1:728). — Type: Philippines, *Wallis* (H-BR!, isotype). — Synonymized by Bartram (1939).

Pogonatum circinatum Besch., Ann. Sci. Nat. Bot. sér. 5, 18:220. 1873, syn. nov. — Type: New Caledonia, in terra argillosa montis Arago, 600 m, 27.XI.1869 *Balansa* 2564 (PC!, isotype).

?*Pogonatum aloides* var. *longicolle* Mitt., Trans. Linn. Soc. London, Bot. ser. 2, 3:192. 1891, syn. nov. — Type: Japan. Honshu: Ikao, Ubago et Nikko, *Bisset*.

Pogonatum yunnanense Besch., Rev. Bryol. 18:89. 1891, syn. nov. — Type: China, Yunnan, *Delavay* 1916 (H-BR!, lectot. nov.; isotype in NY! is *P. perichaetiale*).

Pogonatum akitense Besch., Ann. Sci. Nat. Bot. sér. 7, 17:354. 1893, syn. nov. — Type: Japan. Honshu: Akita, X.1885 *Faurie* 1425 (H-BR!, KYO, isotypes).

Pogonatum rhopalophorum Besch., Ann. Sci. Nat. Bot. sér. 7, 17:354. 1893, syn. nov. — Type: Japan. Honshu: Tochigi, Nikko, VII.1888 *Piotrowski* Herb. de Poli (PC, lectotype, vide Noguchi 1960); Japan. Honshu: Yokoska, *Savaiier* (H-BR!, syntype).

Pogonatum junghuhnianum var. *sikkimense* Ren. & Card., Bull. Soc. Roy. Bot. Belgique 34, 2:65. 1896, syn. nov. — Type: India orientalis (Sikkim?), Darjeeling, 1895 *Stevens* (H-BR!, isotype).

Pogonatum leucopogon Ren. & Card., Bull. Soc. Roy. Bot. Belgique 34, 2:64. 1896, syn. nov. — Type: India orientalis (Sikkim?), Darjeeling, 1895 *Stevens* (H-BR!, isotype).

Pogonatum stevensii Ren. & Card., Bull. Soc. Roy. Bot. Belgique 34, 2:65. 1896, syn. nov. — Type: Sikkim?, Darjeeling, 1894 *Stevens* 28 (H-BR!, isotype).

Polytrichum brachypodium C. Müll., Hedwigia 36:342. 1897, syn. nov. — *Pogonatum brachypodium* (C. Müll.) Wats & Whitel., Proc. Linn. Soc. N.S. Wales Suppl. 27:18.

1902. — Type: Australia. New South Wales: Mossvale, Fitzroy Falls, XI.1884 *Whitelegge* Herb. Melbourne 1885 (H-BR!, isotype).

Polytrichum camarae C. Müll., Hedwigia 36:341. 1897, syn. nov. — *Pogonatum baileyi* Broth. in C. Müll., Hedwigia 36:342. 1897, nom. nud. in synon. — *P. camarae* (C. Müll.) Par., Ind. Bryol. 978. 1898. — Type: Australia. New South Wales: Clarence River, XI.1875 *Wilcox* Herb. Melbourne (JE!, syntype); White Cap Mountains, *De la Camera* Herb. Melbourne 1881 (H-BR!, JE!, syntypes).

Polytrichum collieanum C. Müll., Hedwigia 36:342. 1897, syn. nov. — *Pogonatum collieanum* (C. Müll.) Par., Ind. Bryol. Suppl. 277. 1900. — Type: Vanuatu (New Hebrides), Aneityum, *Collie* Herb. Melbourne (H-BR!, isotype).

Polytrichum gippslandiae C. Müll., Hedwigia 36:341. 1897, syn. nov. — *Pogonatum gippslandiae* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Australia. Victoria: Gippsland, Pyers River, 1881 *Tysdale* Herb. Melbourne (H-BR!, isotype).

?*Polytrichum nanocarpum* C. Müll., Hedwigia 36:340. 1897, syn. nov. — *Pogonatum nanocarpum* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: Australia. Victoria: Gippsland, Walhalla, 1884 *Tysdale* Herb. Melbourne.

Pogonatum ochromitrium Par., Ind. Bryol. 984. 1898, nom. nud. — *Polytrichum ochromitrium* C. Müll. ex Par., Ind. Bryol. 984. 1898, nom. nud. in synon. — Original collection: India, NW Himalaya, near Mussoorie, 6 000–7 000 ft., 2.I.1892 *Duthie* 587 (BM!).

Pogonatum benguetiae Par., Ind. Bryol. Suppl. 277:1900, nom. nud. — *Catharinella benguetiae* C. Müll. in Micholitz, M. Philipp. n. 151; C. Müll. ex Par., Ind. Bryol. Suppl. 277: 1900, nom. nud. in synon. — Original collection: Philippines. Luzon: Benguet, 5 000 ft. (H-BR!). — Synonymized by Eddy (1988).

Pogonatum lao-kayense Par. & Broth. in Par., Rev. Bryol. 27:77. 1900, syn. nov. — *P. moutieri* Broth. & Par. in Broth., Nat. Pflanzenfam. 1(3): 687. 1905, nom. nud. — Type: Haut Tonkin, Yen Bay à Lao-Kay, à hauteur du Phou-Lu, 30.III.1900 *Moutier* 3 (H-BR!, PC!, isotypes).

Pogonatum rufinotum Par., Ind. Bryol. Suppl. 278. 1900, nom. nud. — *Catharinella rufinotia* C. Müll. ex Par., Ind. Bryol. Suppl. 278. 1900, nom. nud. in synon. — Original collection: Japan. Kiushu: Kagoshima, Amami-Oshima Island, pr. Naze, 1897 *Ferrié* 2309 (H-BR!).

Pogonatum aloides var. *polysetum* Krieg., Hedwigia 47:203. 1908, hom. illeg., nom. nud. — Original collection: India, NW Himalaya, below Mussoorie, 5 000–6 000 ft., 6.IX.1895 *Duthie* (H-BR!).

Pogonatum pygmaeum Card., Bull. Soc. Bot. Genève, sér. 2, 1:130. 1909, syn. nov. — Type: Japan. Hokkaido: Ochiai, *Faurie* 3023 (H-BR!, KYO, isotypes).

Pogonatum papillosum Card. & Dix., J. Bot. 50:146. 571: 1. 1912, syn. nov. — Type: India, Darjeeling, 1911 *Roper* 59; Himalayas, near Ghoom, 7 000 ft., 1910 *Craig* 9 (H-BR!, syntype).

Pogonatum klossii Dix., J. Linn. Soc., Bot. 45:483. 1922. — Type: Indonesia. West Irian: Paniai, Mt. Carstensz, Camp Vla, 3 050 ft., 16.I.1913 *Boden Kloss* 20 (BM!, holotype). — Synonymized by Hyvönen (1986).

Pogonatum muticum Broth., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 133:583. 1924, syn. nov. — Type: China. Yunnan: Prope urbem Yunnanfu, in regionis calide temperatae rupe abrupta arenacea inter vicus Sidian et Dölo; circa 1 950 m, *Handel-Mazzetti* 233 (H-BR!, holotype).

?*Pogonatum sibiricum* Podp., Spisy Prir. Fak. Masary-

kovy Univ. 116:40. 35. 1929, *syn. nov.* — Type: USSR. Far East: near Vladivostok, II.–III.1920 *Podpera*.

Pogonatum kiusiense Sak., Bot. Mag. (Tokyo) 49:128. 1935, *syn. nov.* — Type: Japan. Kiushu: Kumamoto, VIII.1931 *Sakurai* 3589; 3590 (MAK!, syntypes).

?*Pogonatum shiroumanum* var. *major* Sak., Bot. Mag. (Tokyo) 49: 133. 1935, *syn. nov.* — Type: Japan. Honshu: Tochigi, Nikko, *Sakurai* 51 (MAK, holotype).

?*Pogonatum urasawai* Sak., Bot. Mag. (Tokyo) 52:473. 1938, *syn. nov.* — *P. akitense* var. *urasawai* (Sak.) Osada, J. Hattori Bot. Lab. 28:200. 1965. — *P. neesii* var. *urasawai* (Sak.) Iwats. & Nog., J. Hattori Bot. Lab. 46:236. 1979. — Type: Japan. N Honshu: Iwate prefecture, Mt. Hayachine, 10.X.1937 *Sakurai* 10000 (MAK, holotype).

Pogonatum iliangense Chen & Wan in Chen, Gen. Musc. Sin. 2:302. 1978, *syn. nov.* — Type: China. Yunnan: Yili-

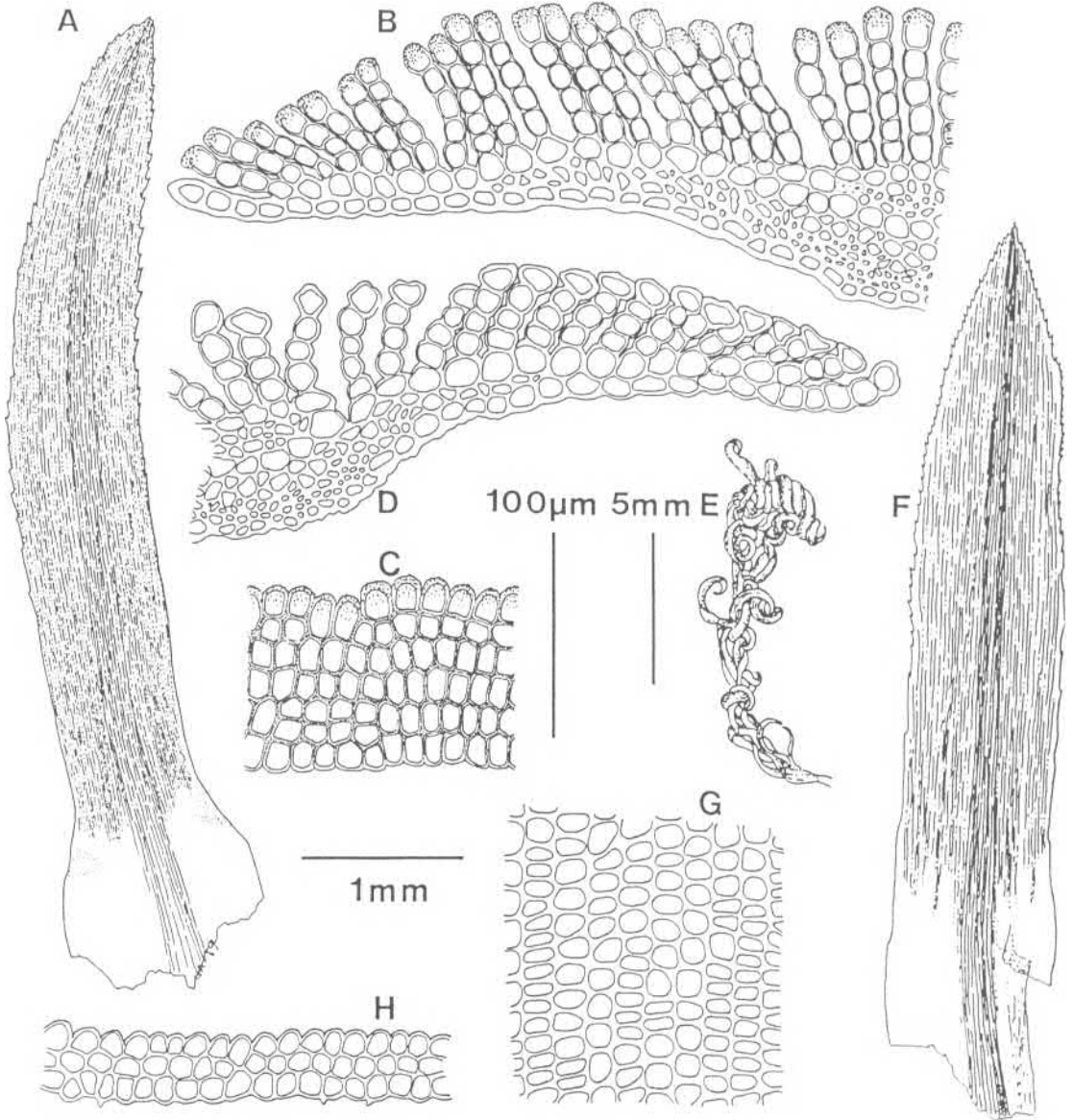


Fig. 15A–H. — A–C: *Pogonatum neesii*. A. Leaf, B. Leaf cross-section and C. Lamella in side view (*Ruinard 11 IV.1978*, L). — D, E: *P. inflexum*. D. Leaf cross-section and E. Habit (*Koponen 19330*, H). — F–H: *P. patulum*. F. Leaf, G. Dorsal cells of blade and H. Lamella in side view and (*Long 10529*, E). — Use the 100 μ m scale for B–D, G and H, 5 mm scale for E, and 1 mm scale for A and F.

ang, Beyangjie village, Yujia temple, on roadside of the back mountain, IV.1958 Xu 2 (PE!, holotype).

Pogonatum neesii is the most common species of the genus in SE Asia. It has a very wide distribution and accordingly has been described under a variety of names. Specimens from all parts of the range have finely papillose apical cells of the lamellae, and these are more or less retuse as seen in cross-section. The pale leaf-margins of dry plants are easily seen even with a hand-lens. This character is, however not invariably present and, in NE Asia, *P. inflexum* also possesses the character. Almost all specimens have numerous teeth on the dorsal side of the costa. The height of the lamellae varies to a great extent with Australian plants having lamellae only 3–4 cells high. However, the observed variation in Australian and Asian populations overlaps to a great extent. Several other characters are variable, but I was unable to find any regular correlation between these variations which would justify distinction even of infra-specific taxa from any part of the wide range. It should, however, be noted here that cladistic analysis left *P. neesii* as a metasppecies without defined apomorphies. More detailed study of the complex thus, might prove it to include more than one species.

The type material of *Pogonatum neesii* is probably destroyed but I studied one specimen from India (Montes Nilgheriensis, Schmid, H-BR!), with a hand-written determination by C. Müller as *P. neesii* mihi. The delimitation of the taxon is based on this authentic identification by C. Müller.

Pogonatum neesii has been found from Australia in the south eastward to the southern parts of the Soviet Far East and westward to near the coast of the Black Sea in Batumi. This disjunction is part of the floristic element with E Asian affinities. Other such relicts are known of several vascular plant genera and some other bryophytes also have such a distribution (Abramova & Abramov 1969). *P. neesii* has, however, often been erroneously identified as *P. inflexum*.

Pogonatum neesii has been collected from sea level up to 3 700 m. It is an aggressive and very successful colonizer of bare ground.

Illustrations — Osada 1965 (as *Pogonatum akitense*): 199 (fig. 11); Gangulee 1969: 104 (fig. 41 as *P. junghuhnianum*), 106 (fig. 42 as *P. akitense*); Chen et al. 1978 (as *P. inflexum*): 303 (fig. 392); Li 1985 (as *P. inflexum*): 446 (fig. 192:1–6); Hyvönen 1986: 128 (fig. 12); Noguchi 1987 (as *P. akitense*): 41 (fig. 13b); Eddy 1988: 31 (fig. 9); Hyvönen 1989: 577 (fig. 4C).

Distribution — Eur: USSR; As 1: USSR; As 2: China, Japan, Korea; As 3: Bhutan, Burma, India, Laos, Nepal, Sikkim, Sri Lanka, Thailand, Vietnam; As 4: Indonesia, Malaysia, Papua New Guinea, Philippines; Austr 1: Australia; Oc: Fiji, New Caledonia, Samoa, Vanuatu.

43. *Pogonatum inflexum* (Lindb.) Sande Lac. (Figs. 15D, E, 31 – map)

Ann. Mus. Bot. Lugduno-Batavum 4:308. 1869. — *Polytrichum inflexum* Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9:100. 1868. — Type: Japan (Japonia), Siebold (S, lectotype, vide Osada & Noguchi 1962; H-SOL!, isolectotype).

Pogonatum yakusimense Thér. in Card. & Thér., Bull. Acad. Int. Geogr. Bot. 18: II.1908. — Type: Japan, Yakushima Island, X.1898 Ferrie (Herb. Noguchi, isotype). — Synonymized by Osada & Noguchi (1962).

?*Pogonatum inflexum* var. *elatum* Reim., Hedwigia 71: 73. 1931, syn. nov. — *P. pelleaenum* Irm. ex Reim., Hedwigia 71:73. 1931, nom. nud. in synon. — Type: China. Jiangxi: Luschan, Kuling, 1 100 m, an Felsen und Berghängen, VII.1915 Bois-Reymond 719 (B, holotype, probably destroyed).

Pogonatum eroso-dentatum Sak., Bot. Mag. (Tokyo) 49: 129. 1935. — Type: Japan. Kiushu: Kagashima, Sakurajima, Mt. Sakurajima, 26.III.1926 Sakurai 1693 (MAK, holotype). — Synonymized by Noguchi (1960).

Pogonatum shiroumanum Sak., Bot. Mag. (Tokyo) 49: 132. 1935. — Type: Japan. Honshu: Nagano, Mt. Shirouma, ca. 8 000 ft., 27.VI.1922 Sakurai 888 (MAK, holotype). — Synonymized by Noguchi (1960).

Pogonatum sordide-viride Sak., Bot. Mag. (Tokyo) 50: 372. 1936. — Type: Japan. Kyushu: Kumamoto, Mt. Naidaijin, 19.III.1935 Sakurai 4504 (MAK, holotype). — Synonymized by Osada (1965).

Pogonatum inflexum is closely related to the widespread *P. neesii*. In Japan the two species can even grow together and distinguishing them in the field is difficult. However, dry plants are easily identified because the leaves of *P. inflexum* are incurved and typically tightly coiled at the apex whereas *P. neesii* has leaves which are contorted with the apices incurved. This feature is elegantly illustrated by Osada and Noguchi (1962). The apical cells of the lamellae of *P. inflexum* are always very wide and flattened, while in *P. neesii* the cells are retuse and fairly narrow. The lamellae tend also to be higher (up to 6–8 cells) in *P. inflexum* whereas in *P. neesii* they can be fairly low (3–4 cells). However, the height varies to a great extent and in itself is not a reliable diagnostic character.

According to Reimers (1931), the type of *Pogonatum inflexum* var. *elatum* was collected growing with typical *P. inflexum*. According to the description, the var. *elatum* differs only in its larger size and capsules which apparently ripen earlier than those of normal *P. inflexum*. As Reimers himself already noted, var. *elatum* is better treated only as a race, and it does not deserve formal taxonomic recognition.

Pogonatum inflexum is restricted to Japan and surrounding areas of NE Asia. Many records from mainland Asia are, however, based on misidentification of either *P. neesii* or *P. fuscatum*. Accordingly, the records from mainland Asia, as cited below, in-

clude only those verified by my study. The latter species is easily distinguished from *P. inflexum* by its narrow apical cells which are essentially straight as seen in side view.

Pogonatum inflexum typically for the genus grows mostly in fairly open habitats and on open ground. It has been collected from sea level to above 2 000 m.

Illustrations — Osada 1965: 195 (fig. 9); Noguchi 1987: 41 (fig. 13A).

Distribution — As 1: USSR; As 2: China, Japan, Korea.

44. *Pogonatum patulum* (Harv.) Mitt. (Figs. 15F–H, 31 – map)

J. Linn. Soc., Bot. Suppl. 1:152. 1859. — *Polytrichum patulum* Harv. in Hook., Icon. Pl. 1: 18, 1. 1836. — Type: Nepal (BM!, holotype).

Pogonatum hexagonum Mitt., J. Linn. Soc., Bot. Suppl. 1:151. 1859, *syn. nov.* — Type: India, Khasia Mountains, 4 000 ft., *Hooker & Thomson 1248* (NY!, lectotype *nov.*); Nepal, *Wallich*; India?, *Noukuen*, 5 000 ft., *Hooker & Thomson 1244*, (NY!, syntypes; the specimen of *Wallich* is *P. neesii* and no. 1244 is *P. microphyllum*).

Pogonatum decolyi Broth. in Brühl, Rec. Bot. Surv. India 13(1): 126. 1931, nom. nud. — Original collection: India. Darjeeling: prope Kurseong, 4 000 ft., 27.XII.1899 *Decoly & Schaul 2361* (H-BR!).

Pogonatum strictifolium Broth. in Brühl, Rec. Bot. Surv. India 13(1): 126. 1931, nom. nud. — Original collection: India, (Sikkim?), Darjeeling, Latpancho, 3 000 ft., 11.IV.1901 *Hartless 2664* (H-BR!).

Pogonatum patulum is distinguished from closely related species by its low lamellae and by its fairly wide blade. *P. neesii* typically has retuse apical cells of the lamellae, and the leaves in the dry condition are incurved rather than contorted as in *P. patulum*. Other closely related species are much smaller plants with narrow blades and this applies also to the Himalayan *P. rufisetum*. *P. cirratum* generally has much taller stems, and the leaves are not as firm as those of *P. patulum*. In Australasia the last species might also be confused with the local *P. subtortile*. The distinction is difficult, but the plants are more stout, the leaves have more than 50 lamellae per leaf and the thin-walled dorsal cells of blade are especially lax in *P. patulum*.

Pogonatum patulum has been collected in SE Asia from the Himalayan area to New Guinea. It grows at fairly low altitudes (200–1 500 m) on soil in shaded, humid habitats.

Distribution — As 3: Bhutan, India, Nepal, Sikkim; As 4: Malaysia, Papua New Guinea.

45. *Pogonatum gracilifolium** Besch. (Figs. 16A–D, 31 – map)

Ann. Sci. Nat. Bot. sér. 6, 10: 249. 1880, *syn. nov.* — Type: Reunion, 1877 *Lépervanche*; Belous, 1875 *l'Isle* (PC!, lecto. *nov.*).

Polytrichum molleri C. Müll., Flora 69:277. 1886, *syn. nov.* — *Pogonatum molleri* (C. Müll.) Par. Ind. Bryol. 983. 1898. — Type: Sao Tome. Prov. Cachoeira: Nova Moka, 800 m, IX.1885 *Moller*; Pico du Thomé, 820 m, *Moller* (H-BR!, JE!, syntypes).

Polytrichum rubenti-viride C. Müll., Flora 69:277. 1886, *syn. nov.* — *Pogonatum rubenti-viride* (C. Müll.) Par., Ind. Bryol. 987. 1898. — Type: Sao Tome, encostas do Pico de S. Thomé, 1 500–2 100 m, *Moller*; Pico du Thomé, 1 400 m, *Moller* (H-BR!, JE!, syntypes).

Pogonatum breviurnaceum Par., Ind. Bryol. ed. 2, Vol. 4:43. 1905, nom. nud. — *Polytrichum breviurnaceum* C. Müll. ex Par., Ind. Bryol. ed. 2, Vol. 4:43. 1905, nom. nud. in synon. — Original collection: Cameroun, in montibus Camerunensibus prope Etome pagum c. 330 m supra mare, in rupibus basalticis adesis (an Felsen von verwittertem Basalte), 22.I.1892 *Dusén 129* (JE!, M!, PC!, UPS!). — Synonymized by De Sloover (1986).

Pogonatum gracilifolium might be confused with other small African species of the genus such as *P. capense* and *P. belangeri*. Good diagnostic characters of *P. gracilifolium* are the irregularity (even with some geminations) of the apical cells of the lamellae (in some plants most of them can be only deeply crenate). It has numerous dorsal teeth on the excurrent costa and the leaves are contorted when dry. The size of plants is fairly variable but they all share the diagnostic characters given above.

Pogonatum gracilifolium is a species of fairly open habitats. It has been collected on soil at 330–3 100 m, and has a scattered distribution in Central and East Africa and adjacent islands.

Illustrations — De Sloover 1986: 287 (figs. 318–357).

Distribution — Afr 2: Cameroun, Ethiopia, Kenya, Malawi, Ruanda, Sao Tome, Tanzania, Uganda, Zaire; Afr 3: Reunion.

46. *Pogonatum tahitense* Schimp. in Besch. (Figs. 16E, F, 31 – map)

Ann. Sci. Nat. Bot. sér. 7, 20:31. 1894. — Type: Tahiti (Taiti), 1847 *Vesco* (BM!, lecto. *nov.*; PC!, isolectotype); environs du fort de Fautaua, vers 500 m, *Nadeaud 52* (BM!, syntype).

Polytrichum baldwinii C. Müll., Flora 82:438. 1896, *syn. nov.* — *Pogonatum baldwinii* (C. Müll.) Par., Ind. Bryol. 977. 1898. — Type: Hawaii. Maui: West Maui, 2 500 ft., 1875 *Baldwin* (NY!, isotype).

Pogonatum tahitense is closely related to both *P. tubulosum* of New Guinea and to the African *P. gracilifolium*. The three closely related species have contorted or incurved leaves when dry; they have

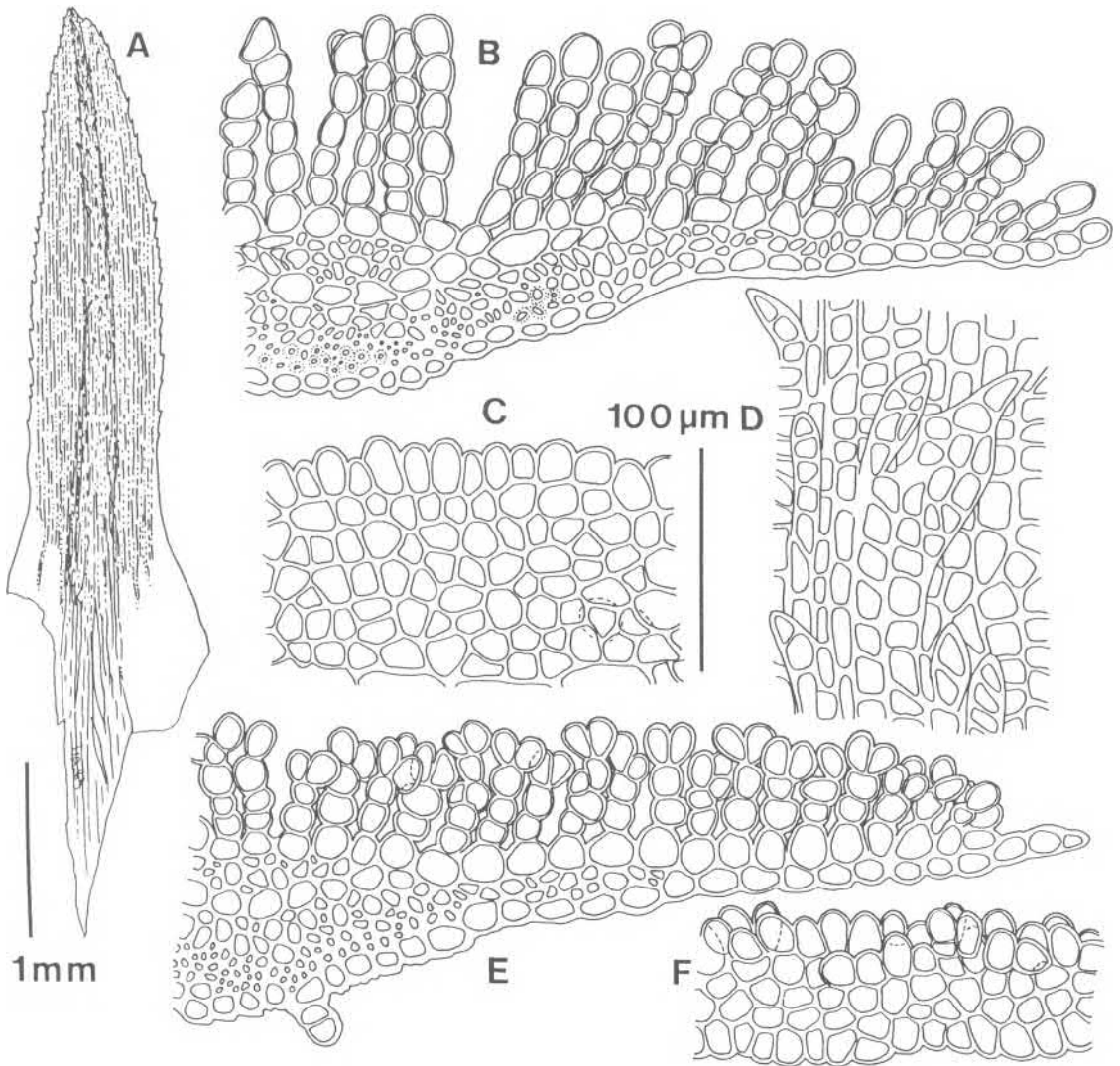


Fig. 16A-F. — A-D: *Pogonatum gracilifolium*. A. Leaf, B. Leaf cross-section, C. Lamella in side view and D. Dorsal teeth on costa (Newman et al. 525, MO). — E, F: *P. tahitense*. E. Leaf cross-section and F. Lamella in side view (Hoe 242, MO). — Use the 1 mm scale for A, and 100 µm scale for B-F.

small and rounded teeth on the leaf margin and the apical cells of lamellae are quite irregular. *P. tahitense* is distinguished by the ample geminations of the apical cells.

Pogonatum tahitense is a plant of open habitats growing on bare soil banks as well as on clay and rocks at 300–1 275 m. The plant has formerly been overlooked and misidentified as *P. neesii* in Asia. It has so far been found in Asia only on Java in Indonesia and on Taiwan, China.

Distribution — As 2: China; As 4: Indonesia; Oc: Hawaii, Marguesas and Society Islands.

Specimens examined (representative) — As 2: CHINA. Taiwan: Taityn, Baibara, 21.VIII.1926 Suzuki (H-BR!). — Oc: HAWAII. Maui: E Maui, road to Olinda Flume, between forest reserve gate and turn off to lower flume, on moist exposed recently disturbed ground at roadside, 20°49'N, 156°15'W, ca. 4 000 ft., 19.VII.1964 Crosby 1643; Oahu, along Wiliwili ridge trail, on disturbed earthen face of trail, S facing, 21°19'N, 157°46'W, 1 500–1 700 ft., Crosby 1573 (MO!).

47. *Pogonatum tubulosum** Dix. (Figs. 17A–C, 31 – map)

J. Bot. 80:34. 1942 (Jan.). — Type: Papua New Guinea. Central: above Port Moresby, Uniri River, rocks, ca. 2 000 m, 18.I.1936. Carr 15194 (BM!, holotype).

Pogonatum humile Bartr., Lloydia 5:291. 61. 1942 (Dec.) — Type: Indonesia. West Irian: Jayawijaya, Mt. Wilhelmina, Middlecamp, stones along small river, open place, 3 400 m, IX.1.1938 Brass & Myer-Drees 9690 (FH!, holotype). — Synonymized by Hyvönen (1986).

The small size and the extremely narrow, incurved leaves with proportionally wide costae make *Pogonatum tubulosum* easily identifiable and distinguishable from *P. neesii*. Another diagnostic character is the totally smooth apical cells of the lamellae which are somewhat irregularly crenate in side view. In this way, they resemble the SE Asian *P. microphyllum*, which has wider leaves with apical cells of the lamellae more irregularly crenate. From the

closely related *P. gracilifolium* and *P. tahitense*, the species is distinguished by its narrow blade with fewer lamellae with at least some of the apical cells retuse.

Pogonatum tubulosum has in the past been largely overlooked and not distinguished from other, more common species of the area such as *P. neesii*. It has so far been found only on the island of New Guinea and in northern Australia, in Queensland. It has been collected at a wide range of altitudes from 400 to 3 400 m and is a plant of fairly open habitats growing on soil and soil-covered cliffs.

Illustration — Hyvönen 1986: 126 (fig. 11).

Distribution — As 4: Indonesia, Papua New Guinea; Austr 1: Australia.

Specimens examined (representative) — As 4: INDONESIA. West Irian: Jayawijaya, Star Mts., Sibil valley, 1 200–1 300 m, 26.IV.1959 Zanten 76c. — PAPUA NEW GUINEA. Morobe: along road Lac–Bulolo, ca. 1/2 mile S of bridge

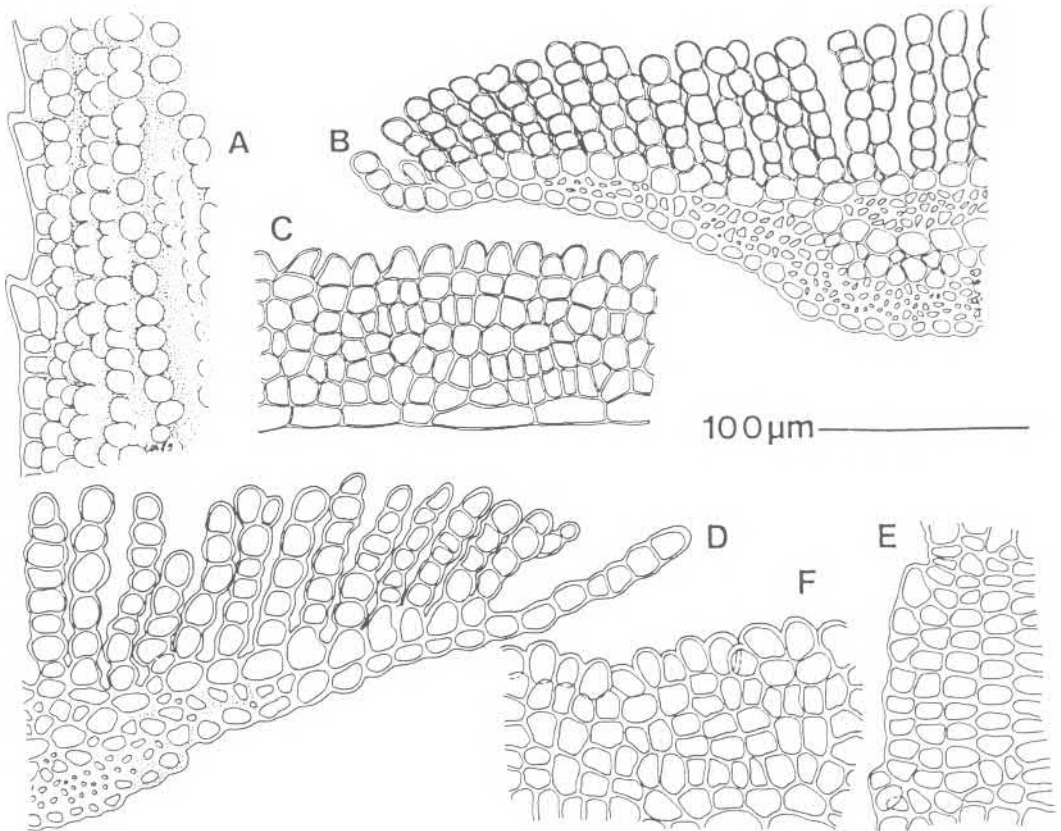


Fig. 17A–F. — A–C: *Pogonatum tubulosum*. A. Marginal teet as seen above, B. Leaf cross-section and C. Lamella in side view (Streimann 23284, H). — D–F: *P. minus*. D. Leaf cross-section, E. Marginal teeth of blade and F. Lamella in side view (Xu 77105, isotype H). — Use the 100 µm scale for all figures.

across Gurakor creek, on lateritic soil of steep roadside bank, 600 m, 15.III.1975, *Touw 14741* (L!); Southern Highlands: 14 km NW of Ialibu, Munia logging area, *Nothofagus* and Podocarpaceae dominated forest, on bare ground, 6°11'S, 143°55'E, 2 300 m, 8.IX.1982 *Streimann 23284* (H!, LAE, NICH, NY); Western Highlands: 9 km E of Mt. Hagen, Kagamuga forestry station, station grounds, on bare ground, 5°50'S, 147°18'E, 1 580 m, 13.VI.1982 *Streimann 20510* (H!, LAE, NICH). — Austr 1: AUSTRALIA. Queensland: ca. 90 km NW of Cairns, near Mossman, Mt. Lewis, below summit, on half-shaded, loamy streambank in rainforest, 1 200 m, 28.VII.1968 *Zanten 681179* (L!).

48. *Pogonatum minus* Xu & Xiong (Figs. 17D–F, 31 – map)

Acta Bot. Yunnanica 4:51. 1. 1982. — Type: China. Yunnan: Xundian, on soil of wall, pH 5, 2 120 m, 7.XI.1977 *Xu 77105* (YUNU, holotype; H!, KUN, isotypes).

Pogonatum minus is known only from type material distributed very sparsely outside China. The original description by Xu and Xiong (1982) is, however, furnished with exceptionally good figures illustrating all the important features of the plant. The closest relatives of *P. minus* are probably *P. gracilifolium*, *P. tubulosum* and *P. tahitense*. They all share small, rounded marginal teeth and excurrent, fairly wide costa. *P. minus*, however, has many unique features such as the extremely narrow blade with only a few, very high lamellae. The plants are also extremely small as indicated by its appropriate epithet.

The type specimen was collected on soil of a wall at about 2 000 m. The species is probably limited to such adverse and open habitats where competition with larger species is not significant. The plant is comparable in size to species with persistent protonema such as *Pogonatum spinulosum* and *P. brachyphyllum*. However, according to the original description as well as study of an isotype, the protonema of *P. minus* is fugacious.

Illustration — Xu & Xiong 1982: 52 (fig. 1).

Distribution — As 2: Endemic to Yunnan, China.

49. *Pogonatum belangeri** (C. Müll.) Jaeg. (Figs. 18G, H, 30 – map)

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873–74: 256. 1875 (Adumbratio 1:718). — *Polytrichum belangeri* C. Müll., Syn. Musc. Frond. 1:222. 1848. — Type: Mauritius, *Bélanger* (H-BR!, isotype fragment).

Pogonatum brachythecium Besch., Ann. Sci. Nat. Bot. sér. 6, 10:250. 1880, *syn. nov.* — Type: Réunion (île Bourbon), *Frappier* (PC!, isotype).

Pogonatum hildebrandtii C. Müll. in Wright, J. Bot. 26: 265. 1888, *nom. nud.* — *P. brachythecium* var. *hildebrandtii* Thér., Recueil Publ. Soc. Havraise Études Diverses 1924(1):

93. 1924. — Original collection: Madagascar, Imerina, An-drangoloaka, XI.1880 *Hildebrandt* (PC!).

Pogonatum parisii Thér. in Ren., Prodr. Fl. Bryol. Madag. Suppl. 62. 1909, *syn. nov.* — Type: Madagascar, Nossi Comba, *Marie* Herb. Bescherelle (H-BR!, isotype).

Pogonatum brachythecium var. *madagassum* Card. in Grand., Hist. Madag. 39:318. 1915, *syn. nov.* — Type: Madagascar, forêt du versant oriental, 1899 *Girod Guet 588* (PC!, holotype).

Pogonatum waterlotii Thér., Recueil Publ. Soc. Havraise Études Diverses 1923(2): 21. 1923, *syn. nov.* — Type: Madagascar, Tananarive, II.1914 *Waterlot* (H-BR!, isotype).

?*Pogonatum confusum* Thér., Recueil Publ. Soc. Havraise Etud. Div. 1924: 92. 1924, *nom. nud.* — Original collection: Madagascar, Tananarive, talus humides *Decary*; Ankatso *Decary*; Ambohimanga *Decary*.

Pogonatum confusum var. *longisetum* Thér., Recueil Publ. Soc. Havraise Études Diverses 1932(1): 148. 1932, *nom. inval.* — Original collection: Madagascar, Moramanga, *Decary*; Madagascar, Montaso, bordure est des Hauts-Plateaux, 1 400 m, 12.XI.1929 *Decary* (FH!, PC!, syntypes).

Pogonatum theriotii Demaret & Leroy, Explor. Parc Nat. Albert 6:61. 68–72. 1944. — Type: Zaire, Congo belge, entre Lubero et Butembo, talus argileux dans la forêt, 1 800 m, II.1938 *Lebrun 9880* (BR!, PC!, isotypes). — Synonymized by De Sloover (1986).

Pogonatum belangeri is a widespread and common plant in tropical Africa. The plant is fairly variable and, accordingly in herbaria, specimens of *P. belangeri* can be found under many different names.

Because *Pogonatum belangeri* lacks any unique features, the identification is in many cases difficult. Some specimens growing in shady and moist habitats have exceptionally low lamellae (3–4 cells) and wide unistratose margins. These might easily be mistaken for *P. usambaricum*, but the latter species is generally larger, with longer stems and remotely set leaves which are contorted in the dry condition. The marginal teeth are sharper and more patent than in *P. belangeri* and the sheath is not much wider than the blade. In *P. usambaricum* the fairly wide unistratose leaf-margin is always distinct even on the uppermost leaves. On the other hand, depauperate forms of *P. belangeri* might be difficult to distinguish from *P. capense*. The latter species has persistent protonema but this character is not always clearly visible in herbarium specimens. *P. capense* normally has almost entire leaf-margins with small teeth restricted to the apical portion. The apices of the leaves are also wide and rounded and the ventral stereid is very weak or lacking.

Pogonatum belangeri has been collected by roadsides and similar open habitats on ground at 100–2 200 m.

Illustrations — De Sloover 1986: 289 (figs. 358–394).

Distribution — Afr 2: Burundi, Cameroun, Kenya, Malawi, Ruanda, Tanzania, Uganda, Zaire; Afr 3: Madagascar, Mauritius, Réunion; Afr 4: South Africa.

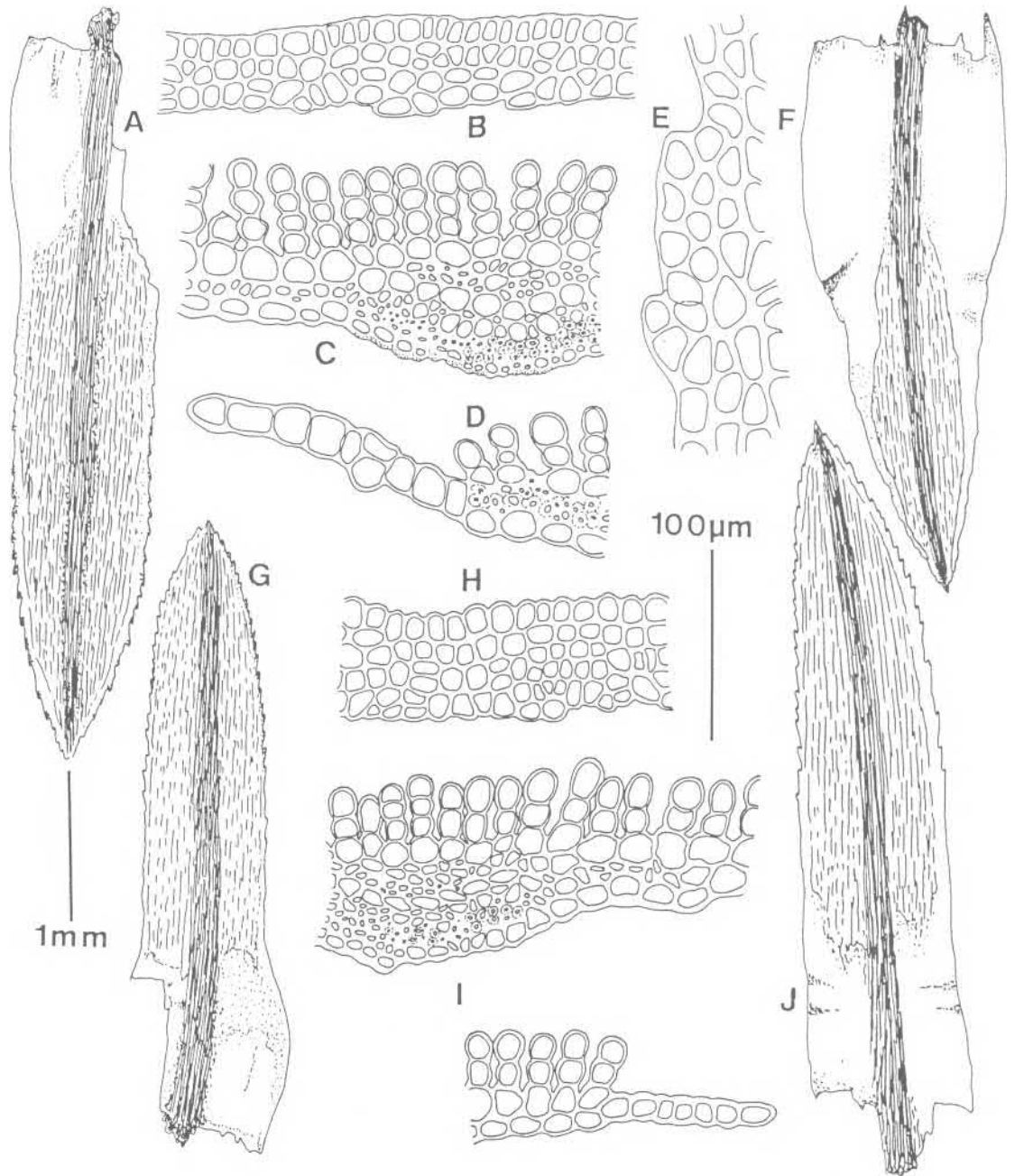


Fig. 18A-J. — A-C: *Pogonatum subulatum*. A. Leaf, B. Lamella in side view and C. Leaf cross-section (Streimann 5265, H). — D-F: *P. congolense*. D. Leaf cross-section, E. Marginal teeth of blade and F. Leaf (Louis 6675, BR). — G, H: *P. belangeri*. G. Leaf and H. Lamellae in side view (Crosby 7189A, MO). — I, J: *P. usambaricum*. I. Leaf cross-section and J. Leaf (Crosby 8277, MO). — Use the 1 mm scale for A, F, G and J, and 100 µm scale for B-E, H and I.

50. *Pogonatum usambaricum* (Broth.) Par. (Figs. 18I, J, 30 – map)

Ind. Bryol. 990. 1898. — *Polytrichum usambaricum* Broth., Bot. Jahrb. 20:194. 1894. — Type: Tanzania, Usambara, Maramu-Station, überall Erdflächen in dichten Rasen überziehend, 15.III.1893 *Holst 2503* (H-BR!, holotype; M!, isotype).

Polytrichum holstii Broth., Bot. Jahrb. Syst. 20:194. 1894, *syn. nov.* — *Pogonatum holstii* (Broth.) Par., Ind. Bryol. 981. 1898. — Type: Tanzania, Usambara, XI.1891 *Holst 126*; *Holst 1074* (H-BR!, syntypes).

Pogonatum flexibilibifolium C. Müll. ex Par., Ind. Bryol. 980. 1898, nom. nud. — Original collection: Camerun, in montibus Camerunensibus prope Bomanam pagum in rupibus basalticis adesis (an Fälsen von verwittertem Basalte), 30.XI.1890 *Dusén 18* (H-BR!, M!, UPS!).

Pogonatum usambaricum is a plant of fairly shaded and moist habitats. Many of its characters seem to be adaptations to this kind of environment. The unistratose margins are wide and the dorsal stereid band is reduced. The blade is very gradually narrowed to a long sheath. The lamellae are only 1–3(–4) cells high. The blade of some plants have colenchymatous cells with fairly thin walls. Some specimens of *P. belangeri* with exceptionally low lamellae are extremely difficult to distinguish from *P. usambaricum*. For diagnostic features see the discussion above under *P. belangeri*. *P. convolutum* is a species of similar habitats restricted to islands off the east coast of Africa. This species is larger and the partly bistratose leaf-margins are much narrower than those of *P. usambaricum*.

Pogonatum usambaricum is chosen from the two simultaneously published names for the species. Its type specimen is more representative, and the name indicates the collection locality. The original collection of *P. flexibilibifolium* is a plant with an exceptionally round leaf-apex, a weak dorsal stereid band and a very narrow sheath. Similar forms have also been observed in the Asian *P. subtortile*, and I regard the variation represented by the type of *P. flexibilibifolium* to be induced only by environmental factors.

Pogonatum usambaricum has been collected at 285–3 000 m.

Distribution — Afr 2: Kenya, Ruanda, Sao Tome, Tanzania, Zaire; Afr 3: Reunion; Afr 4: South Africa.

Specimens examined (representative) — Afr 2: RUANDA. Butare, parc de l'INRS, paroi verticale d'une excavation, 1 700 m, 18.VII.1974 *De Sloover 18472*. — TANZANIA. W Usambara, Mazumbai Univ. forest reserve, by the road Mazumbai-Mtai, submontane forest, on vertical bank, 1 500 m, 8.III.1984 *Pocs 8433/AP*. — Afr 4: SOUTH AFRICA. Transvaal: ca. 10 km WNW Tzaneen, Woodbush forest reserve, indigenous forest W of dam, on earthen bank, 23°48'S, 30°03'E, ca. 3 000 ft., 9.I.1973 *Crosby 7545* (MO!).

51. *Pogonatum congolense* Card. (Figs. 18D–F, 30 – map)

Rev. Bryol. 36:20. 1909. — Type: Zaire, Congo belge, Lazaret de St-Jean Berck, à terre, *Vanderyst 1908* (BR!, isotype).

Pogonatum congolense var. *subintegrifolium* Thér. & P. Vard., Bull. Soc. Bot. France 72:357. 1925, *syn. nov.* — Type: Gabon, à Mabaga, Mayoungou, 10.V.1916 *Le Testu 4902* (PC!, holotype).

Pogonatum semilamellatum Leroy, Bull. Jard. Bot. État 18:197. 20. 1947, *syn. nov.* — Type: Zaire, Congo belge, District Forestier Central, km 30 de la route Stanleyville-Banalia, sur terre, IV.1935 *Leroy 61* (BR!, holotype).

Pogonatum congolense is hardly to be mistaken for any other species of the genus. Some specimens with well-developed blades have the leaves contorted in the dry condition, and thus may resemble other African species such as *P. belangeri*. Small plants more closely resemble some species of *Oligotrichum* and *Notoligotrichum* G.L. Sm. The plicate, often arcuate capsules with mammillose exothecium are, however, typically those of the genus *Pogonatum*. *P. congolense* has a much reduced blade which gradually widens to a proportionally large sheath. The dorsal cells of blade are large and the dorsal stereid band is exceptionally wide, filling almost the entire leaf-width. Its leaves have unistratose margins with indistinct, very small teeth. The size of plants, length of blade, as well as the size of marginal teeth, all show fairly pronounced variation. However, recognition of more than one species or separation of subspecific taxa is not warranted as the observed variation is not discrete. Many intermediate forms can be found in regard to the characters given above.

As with other species of the genus, *Pogonatum congolense* is a pioneer plant of bare soil. It has been collected at 470–1 500 m only in the rain forests of central Africa.

Illustrations — De Sloover 1986: 277 (figs. 225–251), 280 (figs. 252–275 as *Pogonatum semilamellatum*).

Distribution — Afr 2: Cameroun, Gabon, Zaire.

Specimens examined (representative) — Afr 2: CAMEROUN. Bipinde, Urwaldgebiet, 1911 *Zenker 4099b*. — ZAIRE. Piste Lilanda-Yambao, suos bois forêt primitive, sur le paroi verticale d'une termitière, 470 m, 13.XII.1937 *Louis 6998*; Yangambi, plantation d'Hévées de 1911, sur le paroi verticale d'une termitière coupée le long de la route, ca. 470 m, X.1938 *Louis 13302* (BR!).

52. *Pogonatum subulatum* (Brid.) Brid. (Figs. 18A–C, 30 – map)

Bryol. Univ. 2:122. 1827. — *Polytrichum subulatum* Menz. ex Brid., J. Bot. (Schrader) 1800(1): 287. 1801. — Type: New Zealand, *Nelson* (E!, holotype).

Polytrichum nano-urnigerum C. Müll., Hedwigia 36:340. 1897. — *Pogonatum nano-urnigerum* (C. Müll.) Par., Ind. Bryol. Suppl. 278. 1900. — Type: New Zealand, North Island, 1882 Reader, misit 1892 ex Dimboola Victoriae. — Synonymized by Dixon (1926).

Pogonatum subulatum is the only indigenous species of *Pogonatum* in New Zealand. In Australia, the very widespread *P. neesii* is also present, as well as *P. tubulosum*, thus far found only in New Guinea and Queensland. *P. neesii* has been described under many different names from Australia (see the synonyms above). Many of these have formerly been assumed to be conspecific with *P. subulatum*. Recently the presence of *P. neesii* has been ignored almost totally although it is easily distinguished from *P. subulatum* by the retuse and finely papillose apical cells of lamellae. The leaves of *P. subulatum* have more remote and generally lower lamellae, giving a softer appearance to moist leaves. Its leaves are also wider than in *P. neesii*.

In New Zealand, European *P. aloides* is an introduced, weedy plant. The distinction of *P. aloides* and *P. subulatum* is difficult. Close study reveals several usually reliable characters, but in some cases distinction of the two is practically impossible. The basic leaf-form in *P. subulatum* is normally different from that of *P. aloides* as its sheath is not widened as much. The lamellae in both plants are fairly similar, but they are generally lower in *P. subulatum*, and the apical cells are essentially smooth and mostly regularly crenate in side view. In *P. aloides*, at least some of the apical cells are finely papillose and

essentially straight, or only slightly crenate in side view. The costa in the latter species is stronger, excurrent with numerous dorsal teeth. The latter species has a persistent protonema whereas this has not been observed in native *P. subulatum*.

Some plants of the SE Asian *Pogonatum subtortile* greatly resemble *P. subulatum*. The clearest difference can be seen in less pronounced marginal serration of *P. subtortile*, with its teeth less patent than in *P. subulatum*. The blade is also shorter in the Asian plant, and the dorsal stereid band is weaker and narrower.

Pogonatum subulatum has been collected from sea level to 1 050 m, mostly on roadside banks on open ground. Unlike *P. neesii*, *P. subulatum* is restricted to SE Australia and New Zealand, and it has not been found in areas with tropical and subtropical climates such as Queensland.

Distribution — Austr 1: Australia; Austr 2: New Zealand.

Specimens examined (representative) — Austr 1: AUSTRALIA. New South Wales: 27 km NNE of Kyogle, Wian-garee state forest, Brindle creek, Gunoniaceae-Lauraceae dominated forest with varied & well-developed shrub layer, exposed road cutting, red clay, 28°07'S, 153°06'E, 750 m, 3.IX.1978 Streimann 6073 (H!, L, NICH); Victoria: 15 ESE of Strath-bogie, Strathbogie Ra., wet sclerophyll forest gully, on creek bank, 730 m, 12.I.1978 Streimann 3380 (H!, L, MO, NICH); Tasmania: Penguin, creek at Ferndene, along McBrides creek, wet sclerophyll forest, moist diffusely lit soil on upturned stump, 41°09'S, 146°02'E, ca. 150 m, 2.II.1974 Norris 33987 (H!). — Austr 2: NEW ZEALAND. North Island: Auckland, Waitakare Ra., shaded clay bank in forest, 600 ft., 24.IX.1972 Linzey (MO!).

VII. PHYLOGENY AND GENERIC RELATIONSHIPS

A. POLYTRICHACEAE

Using cladistic methods to infer the phylogeny of such a plesiomorphic group as the Polytrichaceae (Mishler & Churchill 1984) is problematic, as only poor resolution is obtained at certain points. However, it still provides a better framework for rigorous study of phylogeny and a sound basis for the ensuing classification than traditional, mostly phenetic methods do. It should be noted, however, that the present distribution and results of the cladistic analysis are incompatible in certain points as discussed in more detail below. Nevertheless, the results of the cladistic analysis are presented unaltered and are tentatively accepted. In this study, specimens were studied only by traditional methods and consequently the suite of characters is rather small. More detailed study may reveal many new characters suitable for inferring the phylogeny of the genus and permit a new analysis

to be undertaken. One such character set might be the spores and their ultrastructure. Smith (1974) subdivided the family on the basis of the structure of the spore surface. According to Mishler and Churchill (1984), Tetrarhizaceae and Andreaeaceae are the two nearest outgroups of the Polytrichaceae, but unfortunately no SEM micrographs are available of the spores of Tetrarhizaceae. The spores of Andreaeaceae have an irregularly granulose surface (Murray 1986), resembling that of most genera of Polytrichaceae, as well as that of many other groups of acrocarpous and pleurocarpous mosses (Boros & Jarai-Komlodi 1975, Sorsa 1976, Ireland 1987). The spores of both Tetrarhizaceae and Andreaeaceae are more than 10 µm in diameter and consequently, it is assumed that the smaller spores with conical surface projections, which occur in some genera of the Polytrichaceae represent an apomorphic character state.

Ireland (1987) showed that spore size and surface structure can be used to distinguish infrageneric groups of *Plagiothecium* B.S.G. Similar studies should be made in *Pogonatum*. Accordingly, studies by Menzel (1986a, b, 1987) showed variation in the exine structure of *Pogonatum*. Size of spores might also prove to be a useful character, and only spores larger than 15–20 µm in diameter are in my study considered as a discrete character state. Further study, including the potential out-groups might, however, prove that distinction of more precise size classes is possible.

Smith (1971) presented a dendrogram with assumed phylogenetic trends of the whole family Polytrichaceae, and these results were further refined in his study of epiphragm structure and spore morphology (Smith 1974). Unfortunately, his conclusions were not summarized. In overall structure, *Microdendron* Broth., *Dendroligotrichum* (C. Müll.) or *Polytrichastrum* would seem to be most closely related to *Pogonatum*. Species such as *Polytrichastrum alpinum* and *Polytrichum sphaerothecium* (Besch.) C. Müll. have even been assigned to *Pogonatum* by such authors as Osada (1965), Crum (1983) and Noguchi (1987). However, neither of these species possesses any of the three apomorphies (see below) typical of the genus *Pogonatum*, and consequently they are excluded and accommodated in *Polytrichastrum* and *Polytrichum*, respectively. If the tendency to form compound peristome teeth is taken as an apomorphy shared by *Pogonatum* and *Polytrichastrum*, the latter can be assumed to be the nearest outgroup of *Pogonatum*. The peristomes of the two, however, differ in their pigmentation, and Smith (1971) considers the production of compound teeth in *Polytrichastrum* possibly to be regulated by environmental factors. It is naturally inappropriate to use such characters to infer phylogenies. Consequently, *Polytrichastrum* is assumed to share a common ancestor with those other genera of the Polytrichaceae which have hinge-tissue in their leaves (see discussion below) — a feature not possessed by most species of *Pogonatum*.

For the construction of my cladograms three monophyletic groups are tentatively distinguished in the Polytrichaceae. The dendroid Polytrichaceae, *Dendroligotrichum* and *Microdendron* are taken as the nearest outgroup of *Pogonatum*, and assumed accordingly to share common ancestor with the latter genus, not shared with other genera of the family. The strong pigmentation of the peristome teeth is viewed as synapomorphy, linking the three genera. It is, however, only an assumption that *Microdendron* has such a peristome, as sporophytes of the single species in the genus are still unknown. If the

relationship of dendroid genera and *Pogonatum* is accepted, one has also to assume that the calyptra lost its hairy covering several times during the evolution of the family. This is a character state shared by *Dendroligotrichum* with some other genera of the family, but not with *Pogonatum*. The latter genus is assumed to have retained the more primitive character state (calyptra covered with long hairs). One of the two other lineages of the family is assumed to include all genera with essentially naked calyptrae and 32 peristome teeth (*Atrichum*, *Oligotrichum* and other closely related small genera, *Bartramiaopsis* tentatively included in a basal position in this group) and the other one including the genera characterized by the hinge-tissue and the essentially dentate margins as their synapomorphies (e.g. *Polytrichum*, *Polytrichadelphus* (C. Müll.) Mitt., *Dawsonia* R. Brown). For inferring the ancestral character states for the genus *Pogonatum*, the species of the nearest outgroup have the strongest affect, but in the Polytrichaceae the relationship of the three lineages remains unresolved because of the lack of shared apomorphies and consequently one has to study three possible tree topologies, which are all equally possible for this unresolved trichotomy.

B. POGONATUM

Manual Hennigian argumentation, according to the methods briefly outlined by Mishler and Churchill (1984) and discussed in detail by Wiley (1981), was used to infer the cladograms. A short presentation of the procedure is given in the chapter "Material and methods" above. I have tried to find the cladogram which requires the fewest hypotheses of convergence and reversals, i.e. steps requiring character state change when the whole family Polytrichaceae is incorporated. However, other genera are inadequately studied, and more detailed study of each group might prove some of the assumed solutions not to be the most parsimonious.

The results as discussed below are in most cases compatible with the phylogenetic trends presented by Smith (1971). Loss and apparent reduction of certain structures are given equal value with true structural novelties. In Table 1 all apomorphic character states, along with corresponding plesiomorphic states, employed to construct the cladograms, are listed. The significance and reliability of each character is discussed below. Unfortunately, many of the nodes are supported only by a single character, and this naturally gives only weak support for the phylogeny as presented. One of the advantages of cladistic argumentation is, however, flexibility and the capacity to incorporate new and improved data (Wiley 1981).

Table 1. *Plesiomorphies and apomorphies of the genus Pogonatum*. Different characters of the gametophyte generation are marked with capital letters from A to X plus those of sporophyte with numbers 1–7. Apomorphies are defined in the cladogram only with this letter if there is only one character state evaluated. When there is more than one possible apomorphic state this is indicated by the addition of an appropriate letter (a–e) or in a few cases with additional “ ’ ” after the capital letter indicating the character. Reversals are marked in the cladogram with +. Different apomorphies do not necessarily form any transformation series and in some characters, uniting apomorphies under the same letter (e.g. characters E and O), is a mere technical solution without any connotation about relationship of the particular character states.

Plesiomorphy	Apomorphy		Plesiomorphy	Apomorphy	
A. Plants medium-sized	Plants robust	a	P. Ventral lamellae covering practically whole blade	Number of ventral lamellae reduced	a
	Plants tiny	b		Lamellae restricted to ventral side of costa (and just adjacent part of blade)	b
B. Stems simple	Branching regular			Lamellae absent	c
C. Protonema fugacious	Protonema persistent			Number of ventral lamellae reduced, bistratose portion of blade retained	d
D. Polytrichoid central strand	Stems without well defined central strand		Q. Lamellae of medium height (4–6 cells)	Lamellae low (1–3 cells)	a
E. Radial symmetry	Stems dorsiventral	a		Lamellae high (>6 cells)	b
	Plants anisophyllous	b	R. Apical cells solitary	Apical cells geminate	a
F. Leaves loosely incurved or contorted when dry	Leaves with tightly coiled apices			Apical cells fused	b
G. Blade mostly multistratose	Blade anomalous	a	S. Apical cells not differentiated	Apical cells retuse	a
	Blade narrowed	b		Apical cells widened	b
	Blade reduced	c		“Auxiliary” apical cells present	c
	Blade absent	d		Apical cells subquadrate	d
H. Blade lanceolate (long and fairly narrow)	Blade short and wide	a	T. Apical cells of lamellae with thin or firm walls	Apical cells with incrassate walls	a
	Blade basally constricted	b		Apical cells with extremely incrassate walls	b
I. Apex of blade acute	Apex wide (and rounded)	a		Apical cells with incrassate outer wall	c
	Apex cucullate	b		Apical cells distinctly notched	d
J. Leaves without hinge-tissue between blade and sheath	Hinge-tissue present		U. Apical cells smooth or finely papillose	Apical cells coarsely papillose	
K. Sheath wide	Sheath narrowed	a	V. Lamellae straight or slightly crenate as seen in side view	Lamellae (deeply) crenate	
	Sheath elongated	b		Lamellae irregularly crenate	b
L. Margins of sheath entire	Margins of sheath serrate	a	W. Leaves with 2 stereid bands	Ventral stereid band reduced	a
	Upper margins of sheath crenate by bulging cells	b		Ventral stereid band essentially absent	b
M. Margins bistratose	Margins reduced to unistratose	a	X. Cells of stereid bands with firm to incrassate	Cell-walls thin to firm walls	
	Margins multistratose	b			
N. Margins serrate	Margins dentate	a			
	Marginal teeth reduced	b			
	Margins essentially entire	c			
O. Dorsal teeth on costa numerous	Dorsal teeth on costa few	a			
	Dorsal teeth on blade in oblique rows	b			

(Contnd.)

Table 1. *Contnd.*

Plesiomorphy	Apomorphy	
Y. Central cells with thin to firm walls	Central cells with extremely incrassate walls	
Z. Dorsal cells of blade sub-quadrate, with firm walls	Dorsal cells enlarged	<i>a</i>
	Dorsal cells with incrassate walls, lumen transversely ovate	<i>b</i>
	Dorsal cells with extremely incrassate walls, lumen small and round	<i>c</i>
	Dorsal cells collenchymatous	<i>d</i>
	Dorsal cells with thin walls	<i>e</i>
Ä. Outer wall of dorsal cells incrassate	Outer wall of dorsal cells thin to firm	
1. Seta smooth	Seta scabrous	
2. Urn length moderate	Urn elongated	<i>a</i>
	Urn shortened	<i>b</i>
3. Exothecial cells essentially smooth	Exothecial cells mammillose	
4. Stomata present	Stomata absent	
5. Peristome with 64 simple teeth	Peristome with 32 compound teeth	<i>a</i>
	16 compound teeth	<i>b</i>
6. Peristome teeth obtuse < 250(-300) µm, evenly colored, oblong	Peristome teeth lanceolate up to 300-400 µm, with only median coloration	
7. Spores <15(-20) µm Ø	Spores >20 µm Ø	

quite clearly at an early stage of development and in the apical part of the urn. Often there is a geographic cline in the height of the mammillar salients: the exothecial cells of northern plants being less mammillose than those of more southern latitudes.

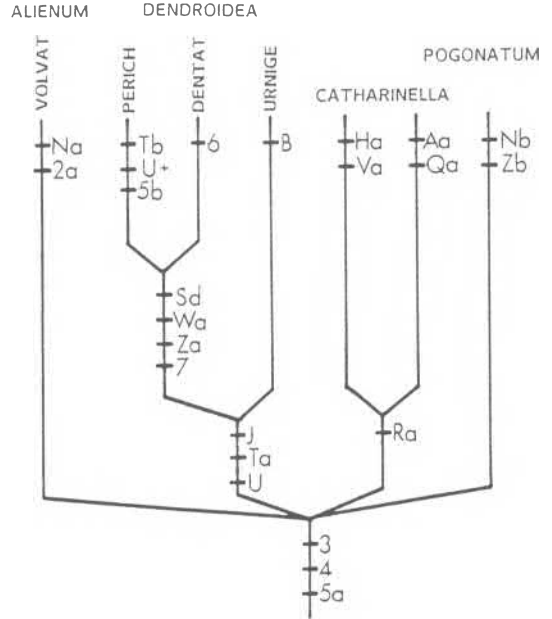


Fig. 19. Cladogram of the genus *Pogonatum*. For the explanation of the terms in all cladograms see Table 1 and discussion in Chapter VII (Phylogeny and Generic Relationships).

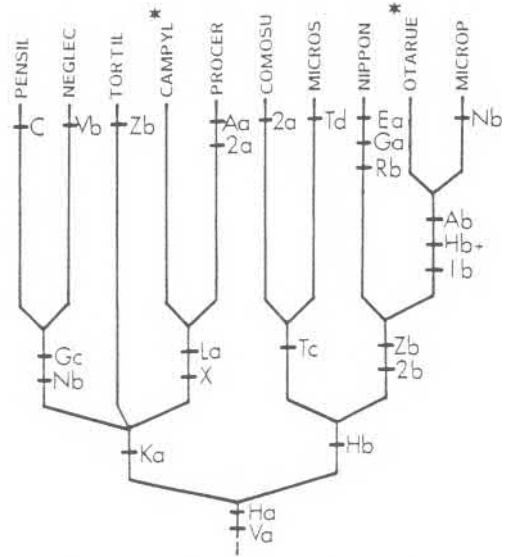


Fig. 20. Cladogram 1 of the subg. *Catharinella*.

Three synapomorphies define the genus *Pogonatum* as a monophyletic group (numbers and letters in italics refer to the cladograms in Figs. 19-22 and accompanying table with explanations). Numbered Figs. indicate the plate where the characters have been illustrated.

3. *Mammillose exothecium* (Fig. 14B). — Exothecial cells in all other genera of the family are essentially smooth or they may be only convex with a median pit as in *Polytrichum*. In *Pogonatum* they are clearly mammillose and this character is seen even in the old capsules of most species. Species whose mature capsules are low mammillose may show the character

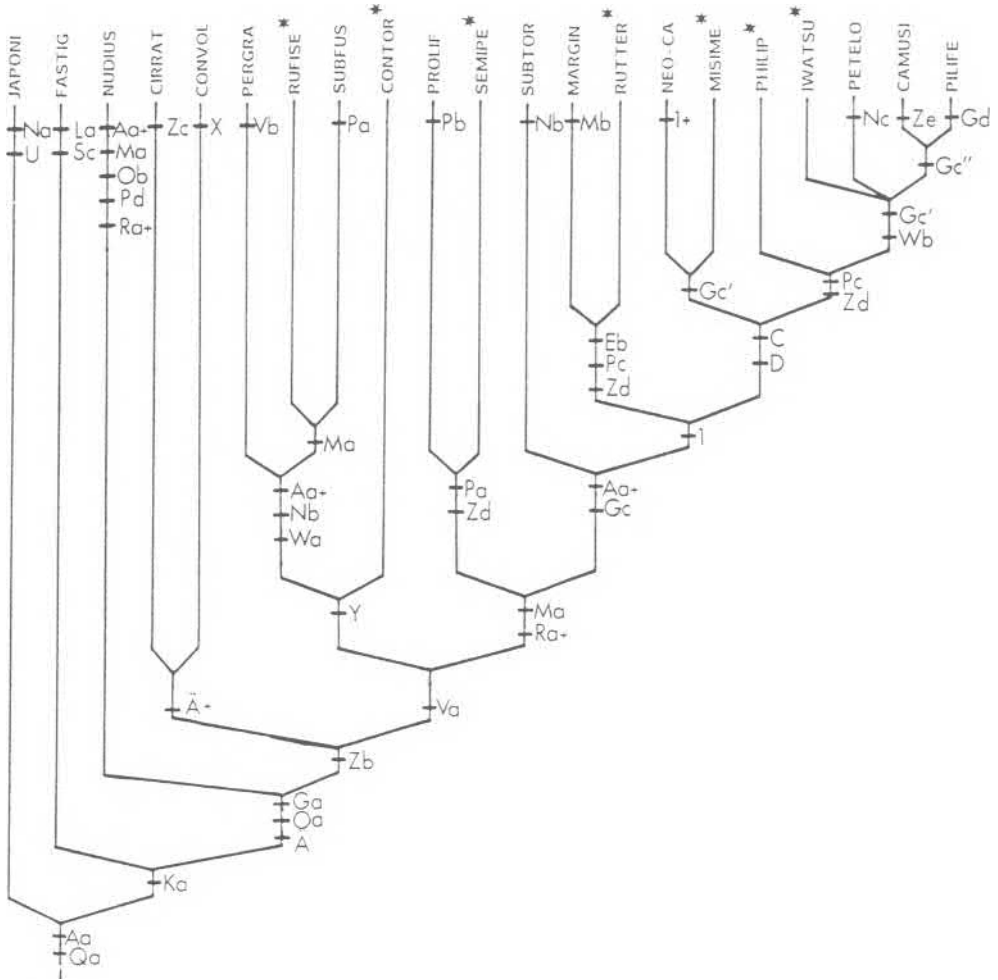


Fig. 21. Cladogram 2 of the subgenus *Catharinella*.

A relevant example of this variation is in the SE Asian *P. neesii* and *P. cirratum*. The European *P. nanum* also has low mammillae and they may even be essentially absent.

4. *Absence of stomata.* — Stomata are present in all genera of the Polytrichaceae except *Atrichum*, *Pogonatum* and *Itatiella* G.L. Sm. The three genera are, however, so different from one another by their other characters, that it is more parsimonious to assume that stomata have been independently reduced in each.

5a. *32 compound peristome teeth with strong pigmentation* (Fig. 14D). — In some species of *Oligotrichum* similar compound teeth are encountered, but

the median sinus in the teeth is more conspicuous than in *Pogonatum*, and the development of compound teeth in some species of *Oligotrichum* is not consistent. Those species of the latter genus which have 32 compound teeth are assumed to be derived from species with 32 simple teeth. Species of *Pogonatum*, however, are assumed to have derived from species with 64 teeth (Smith 1971). As given above, the strong pigmentation of the teeth is assumed to have evolved in the common ancestor shared by *Pogonatum* with the denroid Polytrichaceae.

Delimited by these three characters, the genus comprises 52 species including species previously placed in *Racelopus*, *Racelopodopsis* and *Pseudoracelopus* (sect. *Racelopus* in *Pogonatum* by Touw, 1986.

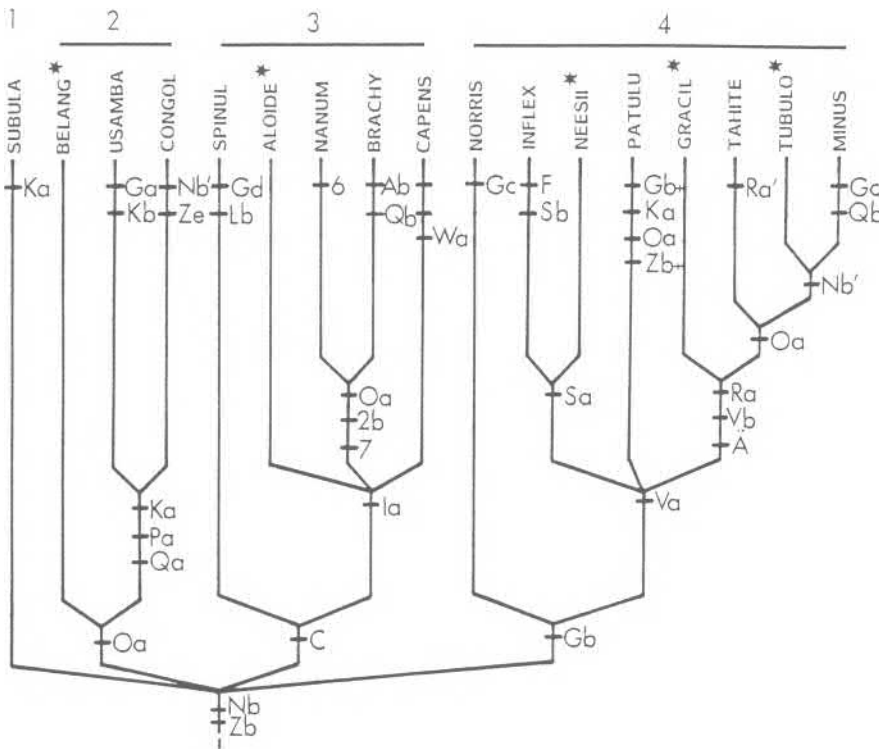


Fig. 22. Cladogram of the subgenus *Pogonatum*.

As already illustrated by the diagnostic apomorphies of the genus, the sporophytes in all species show only moderate variation but there is remarkable diversity in the gametophyte generation. Consequently species and supraspecific taxa in the genus are based mainly on gametophytic characters, and those characters are also the bases of most of the cladograms as discussed below.

C. SUBGENUS ALIENUM

A new subgenus *Alienum* is described to accommodate one single species, *Pogonatum volvatum*. It is characterized by two synapomorphies, extremely long capsules (2a; Fig. 1H) and dentate margins (Na; Fig. 1G). As illustrated by Smith (1975b), by its leaf margins it resembles species of *Polytrichum*, rather than most other species of *Pogonatum* with compound marginal teeth of blade (Figs. 11B, 12C). In its overall habit with stout and firm leaves *P. volvatum* resembles species of subgenus *Dendroidea*, plus such species of its geographic area as *P. comosum*. Its apical cells of the ventral lamellae are, however, undifferentiated unlike in the species given above.

D. SUBGENUS DENDROIDEA

Pogonatum urnigerum, *P. dentatum* and *P. perichaetiale* differ from other species of the genus in that the specialized apical cells of lamellae have much more incrassate walls than do the lower cells (Ta; Figs. 1B, 2E and 3E). All the three species are further characterized by possession of a group of specialized cells (hinge or swelling tissue) at the transition between the blade and the sheath (J; Fig. 1C and E, 3H). The hinge tissue is even more distinct in species of *Lyellia*, *Polytrichadelphus*, *Polytrichum*, *Dawsonia* and *Polytrichastrum*. If it is assumed that the common ancestor of *Pogonatum* and the genera given above already had this specialized structure, one has to presume that it was secondarily lost in all other species of *Pogonatum*. The structure is also absent in the genera *Microdendron* and *Dendroligotrichum*. It is, thus, more parsimonious to interpret these structures in the three *Pogonatum* species only as convergent with other, derived genera of the Polytrichaceae.

Pogonatum perichaetiale has a scattered distribution in the mountains of southern Asia, Africa and South America. Unlike other species of the genus,

both *P. dentatum* and *P. urnigerum* are widespread in northern latitudes. The latter species is found also in the tropics but only at high altitudes. *P. dentatum* shares four apomorphies with *P. perichaetiale* — dorsal cells of blade are similarly lax and large as seen above (*Za*; Figs. 2D and 3G), the ventral stereid band is very weak (*Wa*), the apical cells are similarly subquadrate as seen in cross-section (*Sd*; Figs. 2E and 3E), and spores are generally larger ($> 20 \mu\text{m}$ \varnothing) than in other species of the group (7). The present distribution of the two does not suggest a common origin. In this case, one is tempted to violate parsimony and interpret synapomorphies shared by *P. dentatum* and *P. perichaetiale* as homoplasies, as the distributional data would suggest that *P. urnigerum* and *P. dentatum* share common ancestor not shared by *P. perichaetiale*. Enigmatic also is the total absence of *P. urnigerum* in South America. However, the genus *Lyellia* has a distribution pattern comparable to that of *P. perichaetiale* and *P. dentatum* — *L. aspera* (Hag. & C. Jens.) Frye is found only in arctic areas, and the three other species are restricted to the Himalayan mountains. Parallel examples are found also in *Oligotrichum* (Smith 1972).

Regular branching of stems (*B*; Fig. 1A) distinguish *Pogonatum urnigerum* from its closest relatives. The peculiar flakes and platelets of epicuticular wax on the apical cells of lamellae in *P. urnigerum* might also be a unique feature in the genus, but it is not known whether *P. dentatum* and *P. perichaetiale* share that condition and thus that character cannot be accepted as an autapomorphy of *P. urnigerum*. Study of all three species in regard of this character might give additional information of the possible relationship of the two with each other and with *P. urnigerum*.

The peristome of *Pogonatum dentatum* differs markedly from that of other species in the group. Its teeth are long and slender, and the brown coloration is restricted to the median part. Its basal membrane is essentially absent. This is taken as an autapomorphy of *P. dentatum* (6).

Pogonatum perichaetiale is characterized by two unique apomorphies. The apical cells of the lamellae show extremely strong incrassation of all walls (*Tb*; Fig. 3C, E), and the peristome has 16 compound teeth (*5b*; Fig. 3F) instead of the 32 which typify all other species of the genus. However, the structure of the teeth reveals that they were formed by fusion of 32, already compound teeth. The extremely thick cell walls of apical cells of *P. perichaetiale* are assumed to have further developed from firm cell walls typical for *P. dentatum* and *P. urnigerum*, and the capitate papillae of the latter two are assumed

to be secondarily lost (*U+*) or laterally fused to form the extremely thick cell-walls.

Over twenty *Pogonatum perichaetiale*-closely related taxa have in the past been described, but as discussed in more detail in the systematic part, further cladistic analysis of the group is inappropriate until the characters are better understood. Characters such as sexuality, entire leaf-margins and elongation of the urn are potentially useful in this analysis.

E. SUBGENUS CATHARINELLA

The papillae on the apical cells of the ventral lamellae in *Pogonatum japonicum* are of approximately the same size as in *P. urnigerum*, although they are lower and not capitate. The structure of epicuticular wax is, however, strikingly different in these two, as it forms flakes and platelets on the apical cells of *P. urnigerum*, resembling those of *Dawsonia* and *Polytrichadelphus*. In contrast, the wax granules of *Pogonatum japonicum* more closely resemble those found in other species of *Pogonatum*. Other species with coarsely papillose apical cells of the lamellae are some species of *Polytrichastrum*, as well as *Dendrologotrichum squamosum* (Hook.f. & Wils.) Card. In the latter species, however, the papillae are formed by large granules of epicuticular wax and are thus not homologous with the papillae of *Pogonatum* (Clayton-Greene et al. 1985). The papillae of *Noto-logotrichum australe* (Hook.f. & Wils.) G.L.Sm. and *Polytrichastrum* (sect. *Polytrichastrum*) appear to be homologous with those of *Pogonatum*. If they are assumed to have been present already in a common ancestor of the three, it requires one to accept several reversals and thus it is taken as a homoplasy.

Several species of the genus have geminate apical cells of the lamellae (*Ra*; Figs. 5A, 6E, 8B etc.). In some small species of *Pogonatum* with irregular apical cells, the geminations seem only to be analogous with those encountered in larger species. In the latter geminations are assumed to be born by auxiliary vertical division of cells (Smith 1971). The matter is, however, not rigorously studied, and it is not yet clear whether or not geminate apicals are homologous with each other. Geminate apicals are rare in other genera of the family and are found only in *Dendrologotrichum squamosum*, plus certain species of *Polytrichum* and *Lyellia* (Smith 1971). Other characters suggest, however, that these taxa are only distantly related, and it is more parsimonious to interpret gemination of the apical cells as a homoplasy. The presence of apical geminations is, however, taken as a synapomorphy for the subgenus *Catharinella*, including fairly diverse species by their other charac-

ters. The assembly can be further divided by their general habit in the dry condition.

A group of mostly American species (termed tentatively as *Microstomum* species group in the following discussion) have similarly firm leaves, only slightly altered in the dry condition like those in species of subg. *Dendroidea*. They are characterized by crenate margins of the ventral lamellae with high apical cells (*Va*; Fig. 6D, H) and of proportionally wide blade (*H*; Figs. 5C, 6B and F).

Pogonatum nipponicum, *P. microstomum* and *P. comosum* are all characterized by an exceptional basal constriction of the blade (*Hb*; Figs. 6B, F and 7D). *P. microstomum* and *P. comosum* both have unusually high apical cells of the lamellae with an incrassate outer wall (*Tc*). The general shape of cells is similar, but in the former species they can be exceptionally high and notched, more or less bottle-shaped (*Td*; Fig. 6H), whereas in the latter species the incrassate outer wall is present but the cells are not distinctly pointed (Fig. 6D). The latter species is characterized by elongated capsules (*2a*), resembling those of *P. perichaetiale* and *P. volvatum* from the same geographic area. *P. nipponicum* is distinguished from other species by five apomorphies: a narrowed stereid band with the consequence that the wide bistratose portion of the leaves is wide (*Ga*; Fig. 7C), dorsal cells of blade with incrassate walls (*Zb*), clearly dorsiventral stems in dry condition (*Ea*; Fig. 7E), very short capsule (*2b*; Fig. 7F) and partly united apical cells of the lamellae (*Rb*). In *P. comosum*, dorsal cells of blade which have incrassate walls are also encountered. In this species, however, the basic primitive, more or less quadrate form of the cells is still clear (Fig. 6C), whereas the cells of *P. nipponicum* have transversely ovate lumens due to uneven incrassation of cell walls (Fig. 7A). The form of the apical cells of the lamellae (Fig. 7C) suggests that some of them were formed by fusion of two, notched cells. Alternatively, it can be suggested that the apical cells of *P. nipponicum* represent a primitive type, where division of cells is partially expressed. However, the form of geminate cells in related taxa suggest that they were primitively undifferentiated and not notched, and thus the peculiar form in *P. nipponicum* is interpreted to be the result of the fusion of two cells.

Pogonatum otaruense and *P. microphyllum* are small species confined to volcanic areas and characterized by small size (*Ab*), rigid leaves with a wide dorsal stereid band and by distinctly cucullate leaf-apices (*Ib*; Fig. 7I). Typically geminate cells are more common in *P. otaruense*. *P. microphyllum* is further characterized by small marginal teeth (*Nb*), while *P. otaruense* is left as a metaspecies (*) lacking charac-

teristic apomorphies. Synapomorphies shared by the two species and *P. nipponicum* are the short, small capsule, and the dorsal cells of the blade which have incrassate transverse walls. They are tentatively included in the *Microstomum* species group although one must hypothesize a reduction of the basal constriction of blade (*Hb+*) — a feature typical for many other species in the group.

Four other species of the *Microstomum* group — *Pogonatum campylocarpum*, *P. procerum*, *P. neglectum* and *P. pensilvanicum* — share a fairly narrow sheath with indistinct shoulders (*Ka*; Figs. 4D, G and 5C, F). In contrast, other species of the group have the blade widest near the apex and their sheath is broadened. Both *P. campylocarpum* and *P. procerum* are further characterized by the dentate margins of the sheath (*La*; Fig. 5C, F) and by the reduction of stereid bands (*X*). The number of stereid cells is somewhat reduced, and most of them have only slightly incrassate cell-walls (Fig. 5A, G). Both species generally have capsules with distinct striae unlike *P. comosum*, but *P. procerum* resembles the latter species in having an elongate urn (*2a*). *P. procerum* is further characterized by its extremely robust size (*Aa*), with stems up to almost 50 cm long. *P. campylocarpum* is left without apomorphies and thus it must be accepted as a metaspecies. This is not surprising as its position and relationship to *P. comosum* is problematic (see discussion in systematic part).

The position of species with extremely reduced structures is always problematic. The reduced gametophyte does not offer many characters to evaluate. The reduction of the blade (*Gc*; Fig. 4D, G) is a shared synapomorphy of *Pogonatum neglectum* and *P. pensilvanicum*. It is taken as indication of neoteny, which is further exemplified by the persistent protonema of *P. pensilvanicum* (*C*). In both species, geminate apical cells are not as common as in other species of the group, but lamellae are typically crenate along their upper margins, and in *P. neglectum* the crenation is more irregular (*Vb*; Fig. 4E) than in other species of the group. The two species are also characterized by small marginal teeth (*Nb*; Fig. 4F).

The position of *P. tortile* is similarly puzzling as it also has much reduced and simplified structures. It is tentatively included in the group as in some specimens apical cells are typically geminate (Fig. 4B), and the blade of leaves is wide from a fairly narrow sheath (Fig. 4A). It must be noted, however, that the apical cells are crenate but not high, and in most specimens apical geminations are rare or essentially absent. The only autapomorphy is the dorsal cells of blade with typically incrassate walls (*Zb*).

All other species of subg. *Catharinella* have the leaves typically contorted in dry condition. Many species of the group (termed *Cirratum* species group in the following discussion) have a fairly narrow dorsal stereid band (*Ga*; Fig. 9E) as compared with species possessing firm and incurved leaves. This is probably the main reason for the contortion of the leaves, and such contortion is also allowed for by the reduction in the height of the ventral lamellae (*Qa*; Figs. 9A, G, H, etc.). Both characters are interpreted as part of the "anomalous phenomenon" (Smith 1971). The presence of isolated stereids between the cell layers of the bistratose part of the blade in species such as *Pogonatum cirratum* (Fig. 9G and H) is assumed to be evidence of former, more primitive, much broader nerve. Similar reduction is apparent also in some species of other subgenera, as well as in other genera of the Polytrichaceae, but it is more parsimonious to interpret these as homoplasies. Reduction of the dorsal stereid band is accompanied by a decrease in the number of dorsal teeth on the costa (*Oa*). However, two robust species — *P. japonicum* and *P. fastigiatum* — are assumed to belong to this same group despite the fact that they lack two of the synapomorphies given above. With other species of the group they share such synapomorphies as low lamellae (*Qa*; Fig. 8E) and robust size (*Aa*). Bistratose margins of leaves and robust size can be interpreted as an indication of progressive development in a different direction than the anomalous reduction of stereid bands. Bistratose margins are, however, also typical of species of e.g. *Dendroligotrichum* and *Microdendron*, and consequently cannot be used at this level to designate the group.

Pogonatum japonicum has coarsely papillose apical cells of the lamellae (*U*; Fig. 8B), which resemble those of *P. urnigerum* and *P. dentatum*. However, it is more parsimonious to assume that the characters shared with the latter species — papillosity of the apical cells and more or less dentate margins like in *P. volvatum* (*Na*; Fig. 8A) — are only examples of convergence and they are autapomorphies of *P. japonicum*. *P. fastigiatum* differs markedly from *P. japonicum* as it has a much narrower sheath (*Ka*) than the former species. The character is shared by all other species of the *Cirratum* group and is taken as a synapomorphy segregating the species from *P. japonicum*. *P. fastigiatum* differs further from other species of the *Cirratum* group in possessing apical cells of lamellae which are normally much smaller than the mostly geminate lower cells. These "auxiliary" cells are assumed to have developed secondarily on original apical cells (*Sc*; Fig. 8E). Another characteristic feature of the species is the serrate margins of the sheath (*La*; Fig. 8F).

Pogonatum nudiusculum is an enigmatic, very small plant, and its relationship with other species of *Pogonatum* has been in dispute. It was assigned by Smith Merrill (1987) to the monotypic genus *Pseudotrichum*, a genus originally described by Reimers (1941). He drew attention to the dorsal teeth on the blade arranged in oblique rows (*Ob*; Fig. 8I), like those of many species of *Atrichum*. The same character is found also in some specimens of *Pogonatum microstomum*, and dorsal teeth on the blade are occasionally present in some other species as well. Smith Merrill (1987) did not study the calyptra, which, in the Taiwanese material, is similar to that of other species of *Pogonatum*. The species also possesses all the other characters defining the genus, including mammillose exothecial cells. Consequently, separation as a distinct genus would be excessive. The type of reduction in *P. nudiusculum* is not shared by other species of the genus with a reduced number of lamellae. In *P. nudiusculum* the bistratose part of the leaf has been retained even after the apparent loss of the lamellae (*Pd*; Fig. 8G). This kind of reduction is also encountered in species of *Alophosia* Card., *Bartramiopsis* and *Lyellia*. As part of the reduction, the large size and the geminate apical cells are assumed to be lost (*Aa+*, *Ra+*). The species is further characterized by unistratose margins (*Ma*), the thin outer wall of the dorsal cells of blade (*Á*), the reduced number of dorsal teeth on the costa (*Oa*) and narrow stereid bands in the costa (*Ga*). The latter three are synapomorphies shared with other species of the *Cirratum* group. When *P. nudiusculum* is placed in a basal position in the group, one has to accept several cases of convergence. That solution is, however, more parsimonious than to assume that several other characters arose twice in separate lineages. It must be kept in mind that many of the characters are reductions, and thus *P. nudiusculum* might best be placed in its own subgenus. However, it is provisionally included in subg. *Catharinella*.

All other species of the subgenus are characterized by dorsal cells of the blade with incrassate transverse walls (*Zb*; Fig. 9D) and pale cell-walls of the stereid bands. The latter character is seen also to some extent in *P. nudiusculum*. It might be an indication of halted development of the stereids as similarly pale, incrassate walls are seen in young leaves of the species, which in their mature form have stereids with normal coloration. In such species of the group as *P. subtortile* and *P. rutteri*, some of the cells in the stereid bands in some specimens have walls with typical reddish brown coloration. These examples can be interpreted as local reversals of the reductional trend. However, the characters are not useful as apomorphies as assessment in

out-groups is not decisive. Rigorous study of the development of stereids, and chemistry of the cell-walls would be necessary before this character could be evaluated with certainty.

Pogonatum fastigiatum and *P. japonicum* still have the dorsal cells of blade undifferentiated, without incrassation of the transverse walls. The largest species of the genus, *P. cirratum*, is characterized by dorsal cells of the blade with transverse walls so incrassate as to leave the leaf lumen small and round (Zc; Fig. 9D). As discussed in more detail in the systematic part above, three subspecies are tentatively distinguished in *P. cirratum*. The structure of the complex is, however, not clear and consequently it is treated as an unresolved aggregate. The African *P. convolutum* is characterized by a reduced ventral stereid band with mostly thin walls (X; Fig. 9K). The two species do not have dorsal cells of blade with fairly thin outer walls (\bar{A} ; Figs. 10A, B and F) typical for other species of the *Cirratum* group, which are further characterized by the crenate upper margin of the ventral lamellae as seen in side view (Va; Fig. 10C, E and H). Accepting reversal ($\bar{A}+$) rather than convergence (cf. *P. nudinsculum*) gives better resolution in this point, although both alternatives are parsimonious.

Pogonatum pergranulatum, *P. rufisetum*, *P. subfuscatum* and *P. contortum* share the peculiar incrassation of the walls of the central cells (Y; Fig. 10A), and they are segregated from other species. All species except *P. subfuscatum* are very soft and delicate and easily disintegrate when treated even with a very dilute KOH-solution. This might point to a shared chemical structure of cell-walls. *P. contortum* also has very reduced stereid bands with cells characterized by thin and pale walls. However, this cannot be used as an autapomorphy as assessment of the character is equivocal, and thus *P. contortum* is left as a metasppecies. *P. rufisetum*, *P. subfuscatum* and *P. pergranulatum* are all very small species and are characterized by several synapomorphies such as small marginal teeth (Nb), and by a ventral stereid band consisting of only a few cells (Wa; Fig. 10A, B and F). The latter species is further characterized by the irregularly crenate upper margins of the lamellae (Vb). This is a unique feature in subg. *Catharinella*, but is encountered in some similarly small species of other subgenera. *P. rufisetum* and *P. subfuscatum* both share unistratose margins (Ma) which are assumed to be reduced from originally bistratose margins. The latter is further characterized by the reduced number of ventral lamellae (Pa), but *P. rufisetum* does not have any apomorphies and consequently should be marked as a metasppecies.

Bistratose margins, as well as absence of geminate apical cells, are assumed to have been secondarily lost as a part of the anomalous reduction also in the common ancestor for the rest of the *Cirratum* group. A reduced ventral stereid band is a character shared by *Pogonatum proliferum* and *P. semipellucidum*. The species also share deeply sinuose margins of the blade, along with conspicuous conical tooth-cell in the apex of all teeth. These, however, cannot be used as synapomorphies of the two species as similar teeth are also found in *P. cirratum*, and consequently, the estimate of the character state of the common ancestor is not decisive. Reduced incrassation is also found in more basal taxa (e.g. *P. convolutum* and *P. contortum*). Both *P. proliferum* and *P. semipellucidum* are, however, further characterized by collenchymatous dorsal cells of the blade (Zd; Fig. 11B) and restriction of the lamellae to the central part of the leaves as part of the anomalum phenomenon (Pa; Fig. 11A and C). In *P. proliferum* this is further enhanced as the lamellae in most plants are restricted to the ventral side of the costa (Pb). *P. semipellucidum* is left as a metasppecies without characteristic apomorphies. Assemblage of the above two species is based on apparent reductional trends, and it is not certain whether their common ancestor already was that much reduced. It might well be that they only show convergence (Menzel 1987). It is nevertheless clear that both species belong to subg. *Catharinella*.

Smith (1971) and Touw (1986) supposed the reduced species of the *Racelopus* group to have evolved from SE Asian species of the genus *Pogonatum*, closely related to *Pogonatum macrophyllum* (= *P. cirratum* var. *macrophyllum*). Touw (1986) incorporated depauperate species formerly accredited to three different genera, *Racelopus*, *Racelopodopsis* and *Pseudoracelopus*, along with *P. neo-caledonicum* to form sect. *Racelopus*. Species of the group illustrate a reductional sequence of the gametophyte concluding with the extremely neotenous *Pogonatum piliferum*. All have a more or less scabrous seta (I). In all species of the group, as well as in *P. subtortile* — the species assumed to be most closely related to the group — there are incrassate transverse walls on the dorsal cells of the blade. They are all, however, small or minute plants, and if they are incorporated in the group it would be most parsimonious to assume they share a common ancestor with two other small species, *P. rufisetum* and *P. pergranulatum*. The species of the two groups are, however, so markedly different that it is highly unlikely that they have a common ancestor. Consequently, one has to accept that the size of plants was reduced twice.

Pogonatum subtortile is the most plausible of all the species of the genus to have a common ancestor with the group. It shows the same variation of leaf-apices as seen in species of the *Racelopus* group. Some specimens have the gradually narrowed apices typical of, for example, *P. rutteri*, and some plants especially common in New Guinea, have obtuse, wide leaf apices resembling *P. philippinense*. A character shared with species of the *Racelopus* group is the slightly reduced lamina as compared with other species of subg. *Catharinella* (*Gc*; Fig. 11E). An autapomorphy characterizing *P. subtortile* is the small marginal teeth (*Nb*; Fig. 11D). Unlike the species of the *Racelopus* group, the ventral stereid band of *P. subtortile* has only moderately incrassate walls. The imputation of such a character to a common ancestor is equivocal and thus it cannot be taken as an autapomorphy.

All species of the *Racelopus* group, except *Pogonatum marginatum*, have unistratose leaf-margins (*Ma*). Consequently, one has to assume that bistratose margins were thrice independently reduced or that multistratose margins of *P. marginatum* arose, not directly from bistratose margins typical for *P. cirratum* and other related species, but from the ancestor that had already lost the character and had unistratose margins. The latter solution is more parsimonious and accepted here.

Pogonatum rutteri and *P. marginatum* are both characterized by anisophyllous stems (*Eb*) and collenchymatous cell-walls (*Zd*). Their leaves are also totally without the ventral lamellae (*Pc*). As mentioned above, *P. marginatum* has peculiar and unique multistratose margins (*Mb*) resembling those of some species of genus *Diphyscium* Mohr. *P. rutteri*, on the other hand, does not have any apomorphies and is thus left as a metaspecies.

All other smaller species of the group have persistent protonema (*C*) and the central strand of the stems is lacking (*D*). *Pogonatum misimense* and *P. neo-caledonicum* have cells with incrassate walls whereas other species of the group have cells with thin walls and more or less conspicuous corner thickenings (*Zd*). *P. misimense* and *P. neo-caledonicum* are characterized by further reduction of the blade (*Gc'*). The latter species has the seta scabrous only basally and this is taken as a reversal (*I+*) and a reduction from an originally scabrous seta. *P. misimense* is left a metaspecies without characterizing apomorphies. This is not surprising as the relationship of the two species is somewhat in dispute and further study might even prove them to be conspecific.

The rest of the *Racelopus* group is characterized by the absence of ventral lamellae (*Pc*) and collenchymatous laminal cells (*Zd*). All species, except *P.*

philippinense, are characterized by the extremely reduced blade of the leaves (*Gc'*). The species are as well characterized by the reduced or absent ventral stereid band (*Wb*) and in *P. camusii* stereid bands are absent altogether. *P. piliferum*, on the other hand, is characterized by the total reduction of the blade (*Gd*). These two species are assumed to share a common ancestor not shared by the other two species, as they both have even more reduced blades (*Gc''*), compared with *P. iwatsukii* and *P. petelotii*. Leaf margins of the latter species are essentially entire (*Nc*). Unfortunately, *P. iwatsukii* has no apomorphies shared with either *P. petelotii* or *P. camusii* and *P. piliferum*, and consequently the cladogram is left as an unresolved trichotomy at this point.

F. SUBGENUS POGONATUM

There are four groups of species in the subgenus *Pogonatum*. However, there are no characters to justify further ordination of the groups and thus the cladogram is left basally unresolved, as a polytomy. Fig. 22 illustrates the cladogram of subg. *Pogonatum* with informal Groups 1–4. These groups are also referred to in the following discussion on the phylogeny of the subgenus.

More or less reduced marginal teeth (*Nb*) and dorsal cells of the blade with incrassate transversal walls (*Zb*) are typical features for species of subgen. *Pogonatum*. Marginal teeth might be reduced to only one rounded cell or the margins of the blade might even be essentially entire. There are, however, no characters shared with either of the three other subgenera, and thus the cladogram is left as a basally unresolved polytomy.

The species of the subgenus *Pogonatum* are predominantly fairly small or medium-sized plants. The bistratose part of the blade is wide in some species, but even then, the dorsal stereid band is proportionally not as narrow as in larger, but still reduced species in this respect. Resolution of the group is poor and only a few assemblies are characterized by more than one character. The group also includes exceptionally many metaspecies.

Eight, mostly small species, of the subgenus (Group 4, cf. Fig. 22) have a typically narrowed blade (*Gb*) with the bistratose part of the leaves reduced to a few cell rows, as compared with other species of the genus. Consequently, the number of ventral lamellae is generally small. In all species, except the Central American *Pogonatum norrisii*, the lamellae are deeply crenate as seen in side view (*Va*). The irregularity of the cells is further augmented in *P. gracilifolium*, *P. tahitense*, *P. tubulosum* and *P.*

minus, where the apical cells are remarkably irregular (*Vb*) and sometimes geminate (*Ra*; Fig. 17D). Such geminate apical cells are especially abundant in *P. tahitense* (*Ra'*; Fig. 16E). The margins of the lamellae give an impression of a development of accessory cells above the proper margin of the lamellae. *P. gracilifolium* normally has numerous teeth on the dorsal side of costa (Fig. 16D), but in *P. tahitense*, *P. tubulosum* and *P. minus* they are rare to almost absent (*Oa*). The two last species are characterized by the absence of marginal teeth, or if present they are extremely small (*Nb'*; Fig. 17A and E). *P. minus* has two further apomorphies — a reduced blade (*Gc*) and exceptionally high lamellae (*Qb*).

As mentioned above, all species of subg. *Pogonatum* have incrassate transversal walls on the dorsal cells of the blade. *P. patulum* exceptionally, has cell-walls only slightly incrassate. This species is further characterized by the reduced number of dorsal teeth on the costa (*Oa*), and the narrow sheath essentially without shoulders (*Ka*; Fig. 15F). It is tentatively included in the group although one has to accept one reversal (blade is not narrowed in *P. patulum*; *Gb+*). This, as well as the thin walls of dorsal blade cells (*Zb+*), is probably due to adaptation to a humid environment.

The widespread and common *Pogonatum neesii*, and the NE Asian *P. inflexum*, both have peculiarly retuse apical cells as seen in cross-section (*Sa*). These are much widened in the latter species (*Sb*; Fig. 15D). As elegantly illustrated by Osada and Noguchi (1962) and Osada (1965), *P. inflexum* is also characterized by distinctively tightly coiled apices of the dry leaves (*F*; Fig. 15E). *P. neesii* is left a metaspecies, without defining apomorphies, but this is not surprising for such a variable and widespread taxon.

Groups 2 and 3 are defined only by a few characters and they might well conceal some examples of convergence. *Pogonatum aloides* and *P. nanum* are two species native to Europe and to adjacent areas in the Northern Hemisphere. They are both characterized by a persistent protonema (*C*) and by wide leaf-apices (*Ia*). These characters are shared with the American *P. brachyphyllum* and with the African *P. capense*. The former is an even smaller plant with very reduced stems and only a few leaves (*Ab*; Fig. 13D). Characters such as absence of dorsal teeth on the costa (*Oa*), the very short, rounded urn (*2b*), and the large spores (*7*), suggest a common origin with *P. nanum*. *P. capense* is characterized by a diminutive ventral stereid band (*Wa*; Fig. 13A). *P. spinulosum* is tentatively included, as it shares one apomorphic character with the other species — persistent protonema. This tiny Asian species is characterized by the absence of a blade (*Gd*) and by peculiar, ir-

regular serration of the upper margins of the scale-like leaves (*Lb*; Fig. 13F). *P. nanum* is characterized by long peristome teeth (6) and *P. aloides* is left as a metaspecies without autapomorphies.

Group 2 consists of three African species characterized by only a few dorsal teeth on the costa (*Oa*). This is viewed as a character derived from one in which the dorsal teeth are numerous. Although, the evidence for this view is ambiguous, all possible resolutions of the polytomy in this part of cladogram favor the above assumption. *Pogonatum belangeri* does not have any apomorphies and thus it is left as a metaspecies. *P. usambaricum* and *P. congolense* are further characterized by a subpercurrent costa. Also typical for both species is the narrow sheath without shoulders (*Ka*; Fig. 18F and J), the low ventral lamellae (*Qa*) and the wide unistratose leaf-margins (*Pa*; Fig. 18D and I). The position of *P. congolense* is enigmatic, but it is provisionally put together with other African species based on shared characters. It has autapomorphies, such as essentially entire leaves (*Nb'*; Fig. 18F) and exceptionally large dorsal cells of the blade with only small corner thickenings (*Ze*; Fig. 18E). These are assumed to be reduced from formerly thicker walls as part of its adaptation to the ever-wet conditions of Central African rainforests. *P. usambaricum* has unusual characters, such as an exceptionally long sheath (*Kb*) and reduced stereid bands of the blade (*Ga*; Fig. 18I). The stereid bands in *P. congolense* are exceptionally wide and conspicuous for a plant of such humid habitats. The cell-walls are similarly thick and pale as in many species of subg. *Catharinella*. But as already discussed above, the character has not been rigorously studied and its use is thus avoided.

The Australian *Pogonatum subulatum* (= Group 1) has a narrow sheath without clear shoulders (*Ka*; Fig. 18A), and this is left as its only apomorphy.

G. DISCUSSION

Results of cladistic analysis, as presented in the cladograms, suggest division of the genus in four subgroups. It has been claimed that some of the three sections formerly accepted would even be worthy of recognition at a generic level. This might be true and is in congruence with other divisions of the family (cf. the nearest outgroup of the dendroids Polytrichaceae with two genera, *Dendrologotrichum* and *Microdendron*). The large, conglomerate genus is tentatively retained because the distinction of each of the four groups is based on only a few characters in each. Hopefully, further studies will reveal additional and more reliable synapomorphies and then division into discrete genera can be re-evaluated. At

this time, however, it seems appropriate to distinguish these four groups at a subgeneric level. Subg. *Dendroidea* will comprise species formerly assigned to sect. *Dendroidea* and *Cephalotrichum*. *P. volvatum* does not group well with any other species and it is therefore segregated as a subgenus of its own — *Alienum*. Species of two other subgenera were formerly all included in sect. *Pogonatum* along with a group of small species formerly assigned to three (Brotherus 1925) or two (Smith Merrill 1987) genera or as a section of the genus *Pogonatum* (Touw 1986). Distinction of the last group as two independent genera, or even as a section, is not supported by the cladogram as segregation of a large number of new genera would be required. Consequently, a new system with many genera would be much less infor-

mative than the old one with one conglomerate genus. Also, many of the groups are defined by only a few characters, and when new data are acquired these might well alter the cladogram and again force one to accept more taxonomic changes with concomitant increased complication. Accordingly, the former sect. *Racelopus*, although clearly monophyletic, is recognized informally as a species-group.

Subg. *Catharinella* is an appropriate name for the group where this species-group is accommodated. The fourth subgenus will therefore be named as subg. *Pogonatum*. This group is, however, the one with the most uncertain affinities between its members, and might prove to be only a "metagroup" (sensu Donoghue 1985).

VIII. HABITATS AND DISTRIBUTION

Species of *Pogonatum*, like nearly all other species of the Polytrichaceae are epigeic plants confined to more or less disturbed and open habitats. Some species such as the SE Asian *P. neesii*, may even be called weeds. It is an aggressive and successful colonizer of suitable open habitats in areas such as roadsides. Even when *Pogonatum* species grow on shady and closed forest floors, as *P. fastigiatum* and *P. microstomum* in oroboreal forests of SE Asian mountains, it is apparent that the populations originally occupied the site when it was barren of vegetation and the clones expanded only until the ground layer became closed. Consequently, most species of the genus can be assumed to benefit from human disturbance (Fagerstén 1977) even when it is quite extensive. For example, one sees extensive carpets of *Pogonatum*s growing with other weedy mosses and hepatics on road-sides and on soil in clear-cut and heavily eroded areas. Under natural conditions, such large-scale destruction occurs only infrequently after forest fires, landslides, storms and other rare destructive natural phenomena. In undisturbed forests, weedy colonizers are restricted to small patches on soil of eroded streamsides and similar sites. Species of the Polytrichaceae typically grow on bare soil thrown up by fallen trees. It is thus apparent that the mosaic formed by these patches is strikingly different from the situation in which several square kilometers of essentially bare ground become open for colonization. This difference in the size of clones may have some effect on population structure and diversity of weedy species of the genus. Sperm dispersal distances of mosses have been shown to be

extremely small, less than two meters even for the largest species of Polytrichaceae and much less for those with smaller stature (Wyatt 1985). Similarly, spore dispersal is mostly very localized as well, with a large proportion of spores falling in the near vicinity of capsules. Accordingly, genetic differentiation of small local populations will take place (Wyatt 1985). The situation is radically changed when large areas are cleared and colonized by these same species.

The size of a plant affects its role in pioneer vegetation. Tiny species of the *Racelopus* group are ecologically a very special group as they are all confined to bare soil of humid rainforests in SE Asia. They are rapidly growing plants with a persistent protonema and all grow on very unstable sites. They belong to a group of annual shuttle species (During 1979, Touw 1986). Other species with persistent protonema, such as *Pogonatum spinulosum* of temperate E Asia, seem to be more persistent, and their rapid growth may be important in the early stages of succession on bare ground by binding soil and retaining moisture, thus preventing wind and water erosion. Whether other bryophytes and seedlings of vascular plants benefit from the presence of persistent protonema, is, however, not yet demonstrated. The protonema might even prevent growth of other plants. These types of interactions are not well understood even in vascular plants.

As discussed above, all species of *Pogonatum* are confined to disturbed sites. It is, however, possible to divide them into groups according to their habitat preferences, and these groups differ from one another in habit and in pattern of water relations. The

ancestor of the group is assumed to have been well adapted to at least occasional periods of dryness. Clearly xeromorphic plants are represented in the subg. *Dendroidea*, and such plants also occur in other subgenera. Nevertheless, none of the species of *Pogonatum* resemble such plants as *Polytrichum juniperinum* and *P. piliferum* Hedw. whose highly specialized structures enhance survival even in severely dry conditions. In two other subgenera, species confined to open sites with regular desiccation are even less specialized (e.g. *Pogonatum microstomum* and *P. aloides*). The reduction of xeromorphic structures is apparent in many species of subg. *Catharinella* and is most pronounced in delicate plants of shaded, almost constantly wet forests such as *P. proliferum* of SE Asia and *P. contortum* of the wet coastal forests of the North Pacific area. Other species manifesting adaptation to such ever-wet environments include *P. procerum*, *P. nudiusculum* and *P. semipellucidum* of subg. *Catharinella* and *P. usambaricum* of subg. *Pogonatum*. The enigmatic African species, *P. congolense* is well adapted to grow in the humid rainforests of Central Africa.

The species best adapted to xeric conditions are also recorded highest in the mountains. *Pogonatum perichaetiale* has been collected at over 5 000 m in the Himalayas, and its Southern American subspecies grows almost equally high in the Andes (4 800 m). *P. urnigerum* may be found at elevations over 4 000 m. All are species belonging to subg. *Dendroidea*. *P. cirratum* subsp. *fuscatum* of the subg. *Catharinella* has also been collected at altitudes of over 4 000 m. It is confined to drier sites than other subspecies also when it grows at lower elevations. The large majority of species is, however, restricted to elevations between 2 000 and 3 000 m in the forested mountains of tropical and subtropical areas. These humid montane rainforests have a rich bryophyte vegetation with peak diversity at these latitudes (Richards 1984). Restricted to low elevations are only a few species such as *P. aloides*, *P. nanum*, and *P. brachyphyllum*. The last species is exceptional in being confined to the lowlands, mostly less than 300 m, of the southeastern United States.

All species of the genus seem to favor fairly acidic substrates and they are lacking or very rare in areas with predominantly calcareous rocks.

Smith (1972) presented several hypotheses, built upon current knowledge of the plate tectonics, to explain the present day distributions of the genera of Polytrichaceae. Several genera of the family are either restricted to, or have their main distribution, and the most plesiomorphic species in the Southern Hemi-

sphere. This suggests a Gondwanaland origin of the family. However, as noted by Schuster (1983), present-day distributions only partly reflect ancient land configurations. Fairly recent dispersal, as discussed below, might be an explanation for some of the present-day ranges. As pointed out by Schuster (1983), the most important factor determining the success of long-distance dispersal is not the spores but the availability of favorable, "empty" sites. Consequently, as all species of *Pogonatum* are pioneer plants of disturbed sites, they are likely to be more successful in their dispersal than plants forming the vegetation of the climax stage. Especially such species as *P. urnigerum* and *P. neesii*, which are able to grow in open habitats, are likely to succeed in establishing on a new site. On the other hand, species of the genus are almost exclusively dioicous, and consequently, at least two spores of the opposite sex should settle on the same site to ensure the sexual reproduction and further dispersal of the plant (Smith 1972). This happens probably very rarely, and thus long-range dispersal should be used cautiously as an explanation for the observed distributions.

Differentiation of two sections of the genus *Polytrichum* is assumed by Smith (1972) to have taken place as early as in the Jurassic Period, over 135 million years BP. There is no reason to assume that such a plesiomorphic genus as *Pogonatum* would have arisen and differentiated later than that. The ancient age of the species and subgenera is at least partly supported by their present distribution. The number of species in each part of the total range can be interpreted as an indication of the importance of the geologically active areas for the speciation. The largest number of species is to be found in geologically young areas such as the Himalayas, SE Asia in general, and the Andes in South America. The extremely rich flora of SE Asia is, however, partly due to composite nature of the area, including tectonic elements of diversely different origin (Audley-Charles 1987).

The results of the cladistic analysis can also be applied to infer explanations for the distribution of the species (Humphries 1981). As stated above, the analysis of *Pogonatum* presented here is based on a very small suite of characters. Consequently, I hesitate to make extensive biogeographical conclusions based on the analysis of only one genus.

The only species of subg. *Alienum* — *P. volvatum* — has a very limited range in the mountains of Central America. The area is geologically young and one is forced to hypothesize that the present range is a relict of former, wider range, probably in South America.

Subg. *Dendroidea* has a very scattered distribution with two species, *P. dentatum* and *P. urnigerum*,

widespread at high latitudes in the Northern Hemisphere (Figs. 23 and 24). The latter species is found also in high mountains of Australasia and Africa. It should be noted here that it has not been found in the Neotropics. The two species are exceptions in a genus of species with mostly tropical and subtropical distributions (cf. Fig. 25). Both are species of open areas, and with such species as *Polytrichum juniperinum*, they acquired the wide range at northern latitudes after the latest glaciation (Smith 1972). Whether they had such a wide distribution already before the Pleistocene is not known. However, one can hypothesize that ground left barren after the retreat of the glaciers offered favorable conditions for large-scale dispersal of these hardy pioneer plants. What the routes of dispersal from refugial areas were after the last glaciation is an open question.

Cladistic analysis suggests that *P. perichaetiale* and *P. dentatum* share a common ancestor. As already discussed above, their present distribution does not support this conclusion. Analogous patterns of distribution are, however, found in other genera of the Polytrichaceae (*Lyellia*, *Oligotrichum*; Smith 1972). If the implications of the cladogram are accepted, one would also expect *P. dentatum* and *P. urnigerum* to be more widespread in the Southern Hemisphere. However, neither of the two is present in South America, and the presence of the latter species in the high mountains of New Guinea is better interpreted as a recent intrusion. The major orogeny of the island dates back only to the Miocene, ca. 17 million years BP (Pieters 1982), and *P. urnigerum*, an aggressive colonizer as it is, might have attained its present range by step-wise dispersal to "empty" niches. *P. urnigerum* is known from Western Melanesia only in sterile condition (Hyvönen 1986) and this might be an indication of dispersal rather than of an older, disjunctive origin of the populations.

Pogonatum perichaetiale occurs sporadically in the high mountains of continental SE Asia, Africa, and South and Central America. It is the only species of the genus to occur in the tropical areas of all continents, except Australia. This is taken as an indication of its ancestry. There are no other species in the genus with such a "pantropical" range. Closely related species of the other groups have apparently differentiated after the disintegration of the former continuous range.

As described by Smith (1972), the species of subg. *Catharinella* were probably widespread in warm parts of western Gondwanaland before the southern continents were rifted apart. The *Microstomum* species group has two very closely related species, *Pogonatum microstomum* and *P. comosum*, on

different sides of the Pacific Ocean. It is enigmatic that no species of the group has been found in Africa. There is a dubious old report of *P. microstomum* from Ghana (De Sloover 1986), but it is surely an erroneous record, as it is highly unlikely that this species of Asian mountains could be found at low elevation in Africa (cf. similar record of *P. flexuosum* [= *P. cirratum* var. *macrophyllum*]). The cladogram of the group suggests that speciation has taken place already when the southern continents were still in near proximity of each other. Although not demonstrated by the cladogram, all American species of the *Microstomum* group might share a common ancestor different from that of the Asian species. Species of the group are especially diverse in America, despite the fact that the number of *Pogonatum* species is relatively low when compared with Asia. It can be postulated that species diversified to attain ecological niches occupied by species of the other groups in Asia and Africa.

Species of the *Cirratum* group are, with few exceptions, confined to SE Asia. *Pogonatum nudiusculum* and *P. fastigiatum* are restricted to the Himalayan area and *P. japonicum* is confined to NE Asia. All three species lack incrassate transverse walls on the dorsal cells of blade, a feature typical of the rest of the group. It might be postulated that they represent an older stock of the group brought in contact with Asia by the intrusion of southern Nepal and some other parts of Gondwanaland, long before the Indian subcontinent collided with the southern edge of the Eurasian plate (Audley-Charles 1987). However, it is probable that the group had already further evolved by that time and *P. cirratum* was introduced to Asia more than once. This would give some explanation for the very enigmatic geographical variation observed in this complex species.

Pogonatum contortum might have attained its range on both sides of the Pacific before the last glaciation by step-wise migration from Asia. Its present distribution is perhaps only a relict of former, much wider distribution along the North Pacific Arc (sensu Schuster 1983). The habitat preference of the species indicates that it belongs to the hyperoceanic flora element and shares similar distribution with several other species of bryophytes (Schuster 1983). The present distribution of *P. semipellucidum* and *P. proliferum*, and the synapomorphies they share, suggest that their common ancestor was already adapted to a similar environment as these modern species. Highly reduced species are, however, always problematic. The shared derived characters of the two might be only homoplasies.

Species of the *Racelopus* group are confined to Australasia. This is an extremely restricted range,

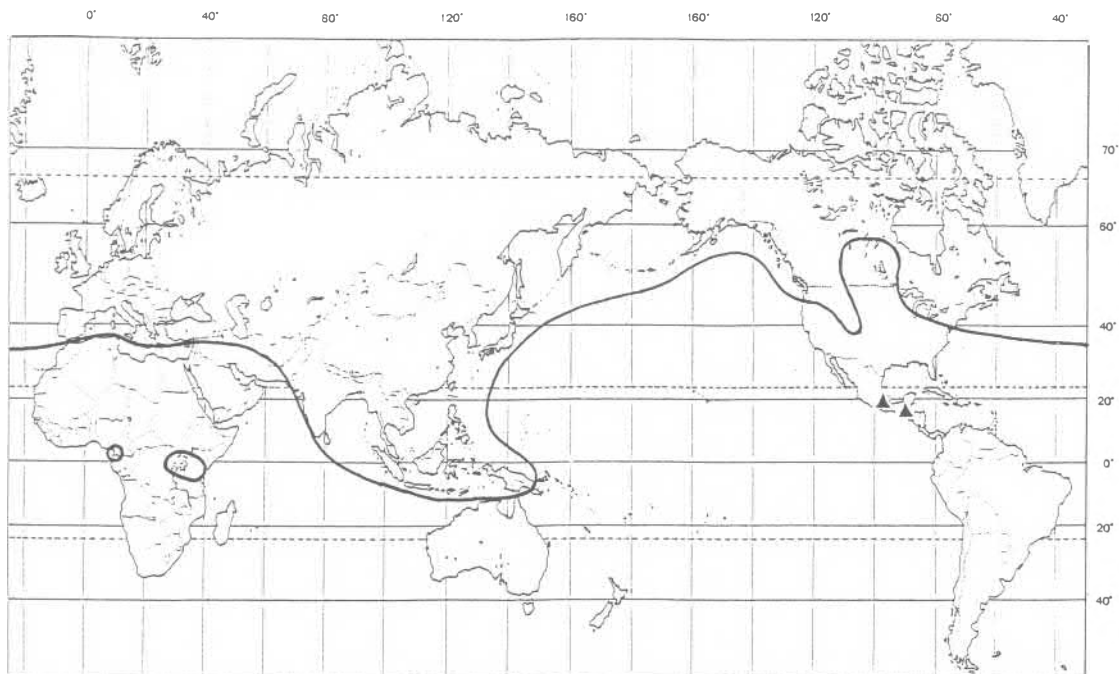


Fig. 23. Distribution of *Pogonatum urnigerum* (the continuous line indicates the southern boundary of the range, partly after Abramova et al. 1954, Osada 1966 and Long 1985) and *P. volvatum* (black triangles in Central America).

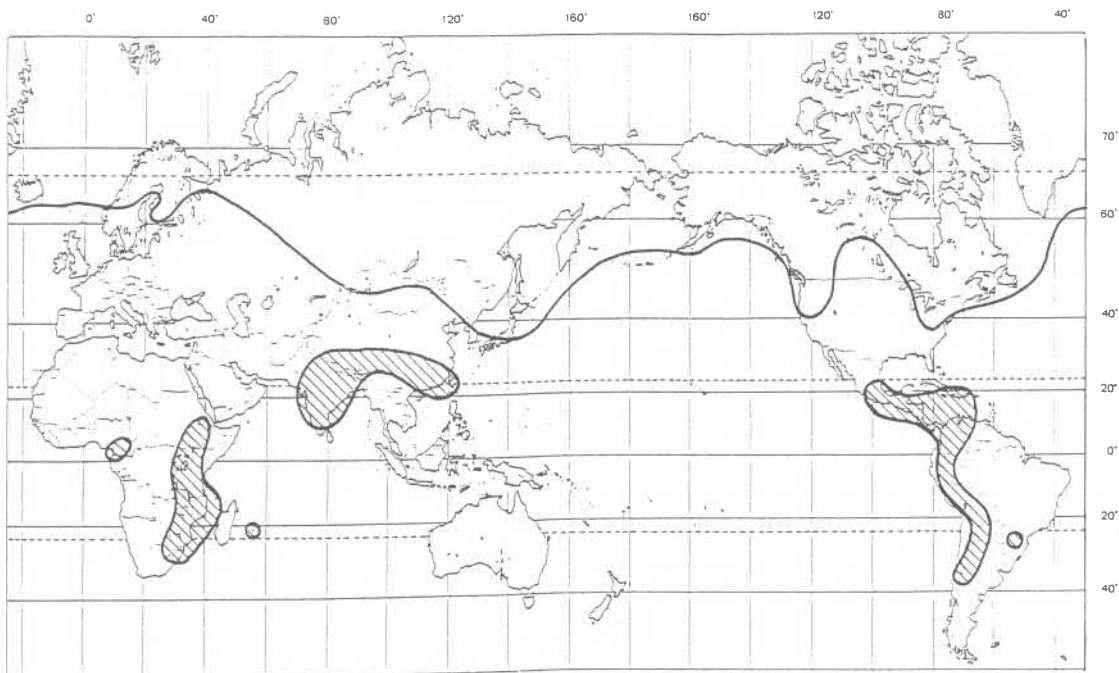


Fig. 24. Distribution of *Pogonatum dentatum* (the continuous line indicates the southern boundary of the range, mostly after Abramova et al. 1954, Vaarama 1967, Long 1985) and *P. perichaetiale* s. lat. (areas with diagonal toning, partly after Menzel 1986b and De Sloover 1986).

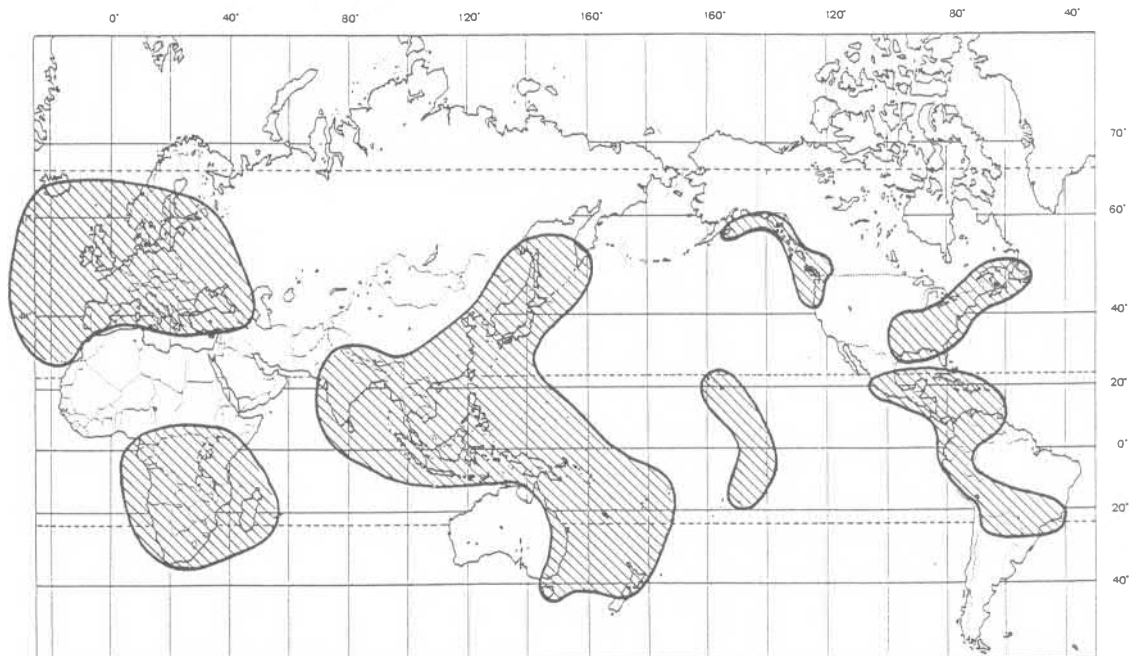


Fig. 25. Total distribution of *Pogonatum* subg. *Catharinella* and subg. *Pogonatum*.

when compared with other monophyletic groups of similar size. Consequently, it is interpreted as an implication of a relatively recent origin and fairly rapid speciation of the group. Touw (1986), on the other hand, concluded that the two lineages of the group have attained their present-day distributions from opposite directions. *P. marginatum* and *P. rutteri* are species with a mostly Asian distribution and the rest of the *Racelopus* group have the most plesiomorphic species, i.e. *P. misimense* and *P. neo-caledonicum* mostly on Pacific islands and New Guinea. This suggests that the origin is in another area to that of the two Asian species given above. If this latter view is accepted, the group has to be much older than assumed, if they are supposed to have attained the present range by dispersal totally from Asia. However, it should be noted that with both alternatives one has to assume that the species have acquired their range by prominent dispersal.

Only two American species, *Pogonatum norrisii* and *P. brachyphyllum*, belong to subg. *Pogonatum*. The latter species probably shares a common ancestor with the mostly Eurasian *P. aloides* and *P. nanum*, and the African *P. capense*. Biogeography would suggest *P. capense* to be more closely related to other species endemic to Africa, than to *P. aloides* and

its allies. This might be true, in which case, persistent protonema is the result of independent regression in several lineages. However, it is also possible that this group had a common origin at the northern edge of Gondwanaland adjacent to Europe and North America, and the taxa were separated and diversified from the beginning of the Mesozoic era as a consequence of gradual breakup of the formerly united Pangaea.

As discussed above under *Pogonatum volvatum*, one has to assume that the present distribution of *P. norrisii* is only a relict of a former, wider range. *P. norrisii* is endemic to geologically fairly young Caribbean islands, although the cladogram suggests that it diversified from other species of the group before the origin of the Caribbean islands. *P. neesii* is a widespread weedy species of Asia with a disjunct relict occurrence on the southeast coast of the Black Sea. Such species are also known of other bryophyte genera (Abramova & Abramov 1969). It is not difficult to accept the hypothesis that dispersal of *P. neesii* to Australia has taken place only recently, after the collision of Gondwana and Laurasia in late Tertiary, ca. 20 million years BP. It might belong to the group of post-Miocene intruders (Truswell et al. 1987), unlike *P. subulatum*, an endemic species of Australia and New Zealand. The presence of the last

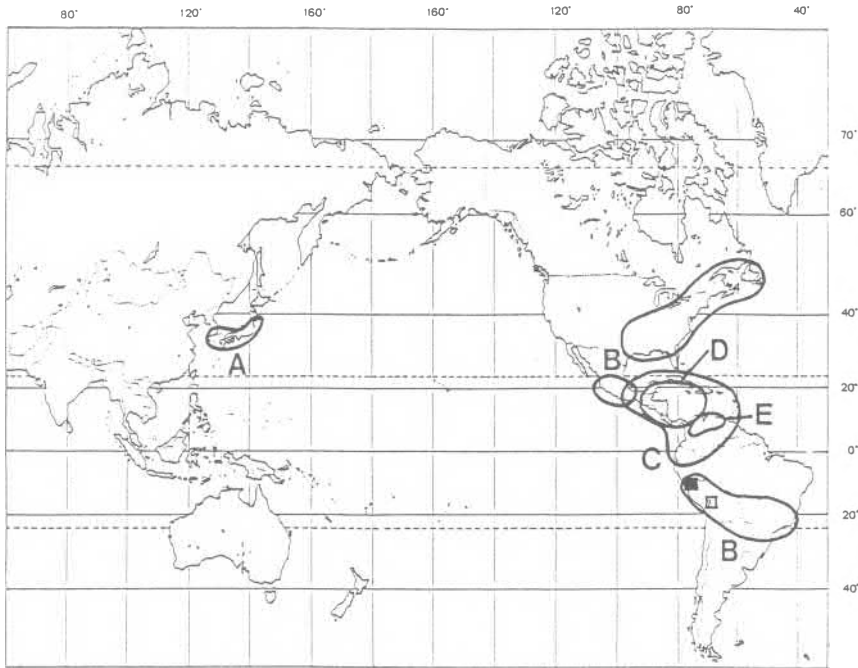


Fig. 26. Distribution of A. *Pogonatum nipponicum* (partly after Osada 1966), B. *P. pensilvanicum*, C. *P. tortile*, D. *P. procerum* and E. *P. neglectum*. The black square indicates the disjunct occurrence of *P. procerum* and open square that of *P. tortile*.

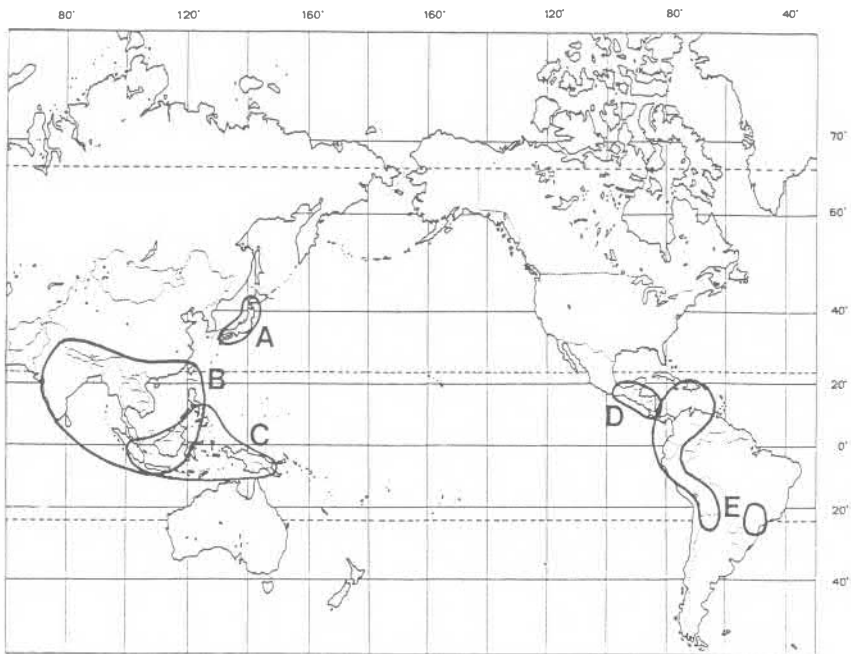


Fig. 27. A. Distribution of A. *Pogonatum otaruense* (partly after Osada 1966), B. *P. microstomum*, C. *P. microphyllum*, D. *P. comosum* and E. *P. campylocarpum*.

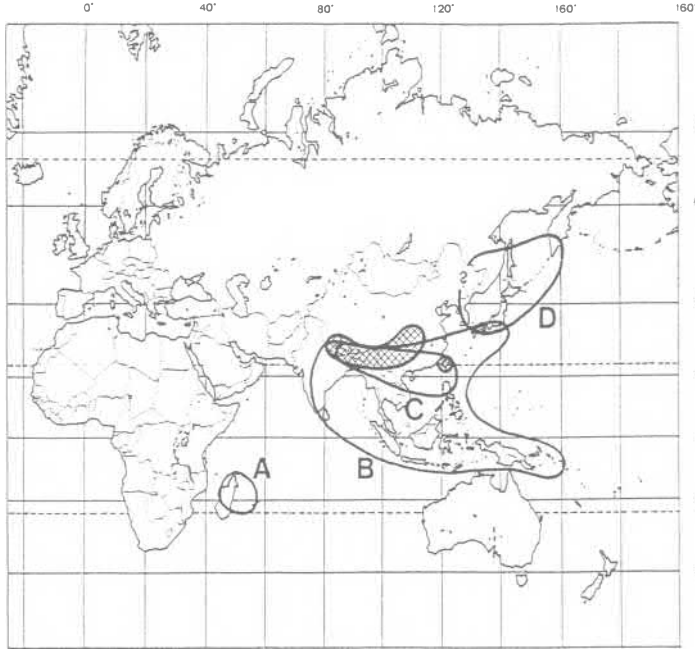


Fig. 28. Distribution of A. *Pogonatum convolutum*, B. *P. cirratum* s. lat. and C. *P. nudiusculum* and D. *P. japonicum* (partly after Abramova et al. 1954 and Osada 1966). The shaded area indicates the distribution of *P. fastigiatum* and the query the disjunct occurrence of *P. nudiusculum*.

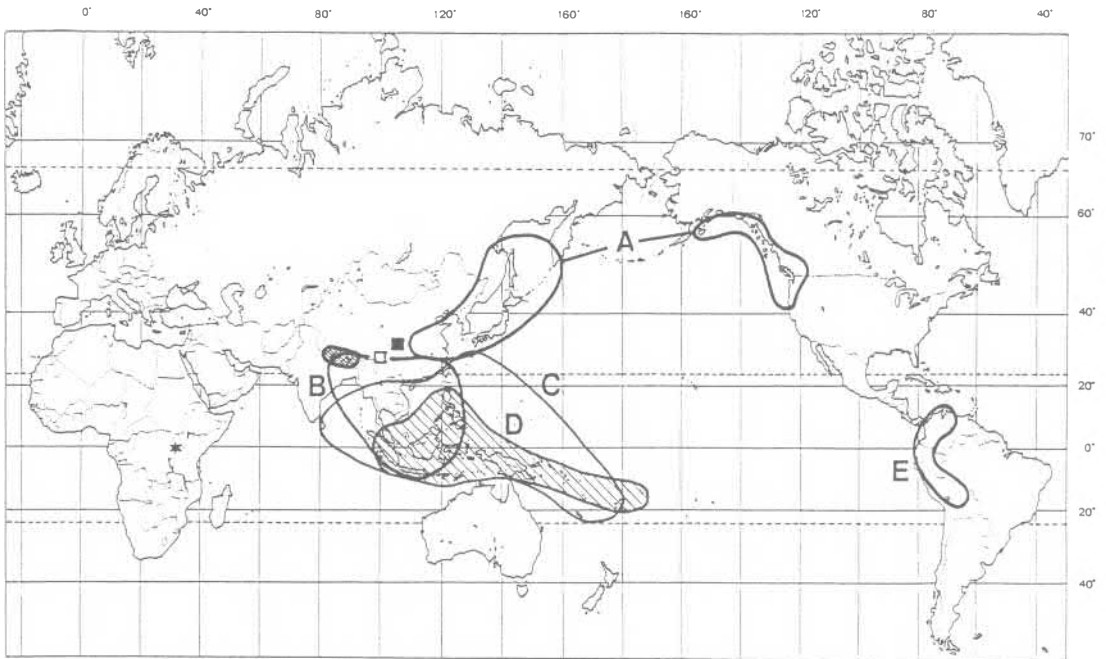


Fig. 29. Distribution of A. *Pogonatum contortum* (partly after Abramova et al. 1954 and Osada 1966), B. *P. proliferum*, C. *Racelopus* species group (after Touw 1986), D. *P. subtortile* (diagonal toning) and E. *P. semipellucidum* (partly after Menzel 1987). The black square indicates the only known locality of *P. pergranulatum* and the open square the one of *P. subfuscatum*. The shaded area indicates the distribution of *P. rufisetum* and the star the disjunct occurrence of *P. proliferum* in Africa.

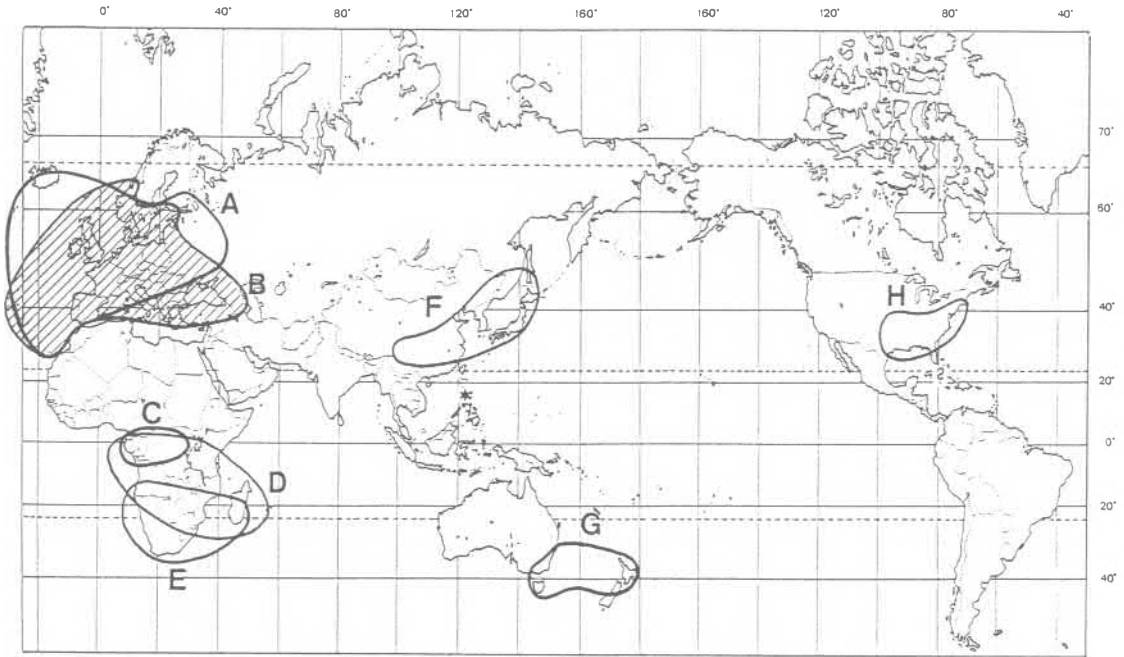
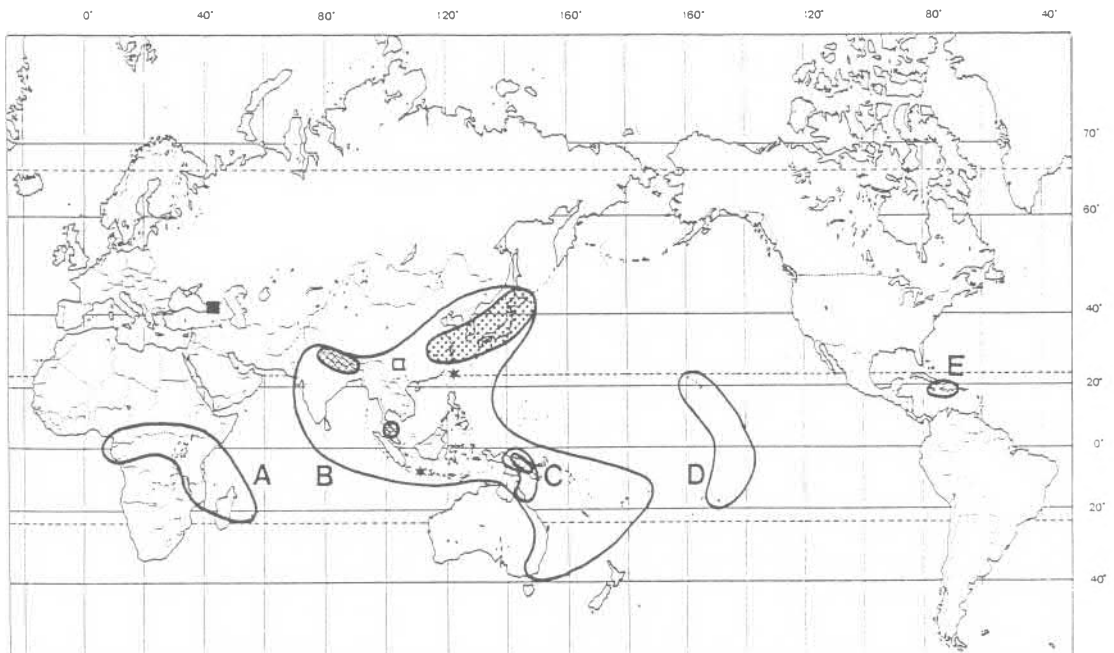


Fig. 30 (Above). Distribution of A. *Pogonatum nanum* (partly after Abramova et al. 1954 and Nyholm 1969), B. *P. aloides* (partly after Abramova et al. 1954 and Nyholm 1969), C. *P. congolense*, D. *P. belangeri* and *P. usambaricum* (ranges overlap approximately as drawn after collection localities), E. *P. capense* (partly after De Sloover 1986), F. *P. spinulosum* (partly after Abramova et al. 1954 and Osada 1966), G. *P. subulatum* and H. *P. brachyphyllum*. The query “?” indicates the doubtful report of the last species from Cuba in Crum & Anderson (1981) and the star the disjunct occurrence of *P. spinulosum*.



species in these southern areas is assumed to be of very ancient origin. The third species of the genus, *P. tubulosum*, is present in Australia and is restricted to northern Queensland and New Guinea. Its presence in Australia might also be of recent origin.

The biogeographical results of the genus *Pogonatum* support the theory of a Gondwanalandic origin of the family (Smith 1972). Highly specialized (most reduced) species of the *Racelopus* group have a restricted range in Australasia, whereas members of more plesiomorphic and apparently ancient assemblages have species in the Southern Hemisphere. The presence of the fairly plesiomorphic *P. subulatum* in Australia and New Zealand is illustrative of this

latter group. There are no *Pogonatum* species in southernmost South America and, as pointed out by Smith (1972), this might be an indication of cooler and unfavorable climates of eastern Gondwanaland. Thus, the most plausible site of origin of the genus, according to its present distribution, is the climatically rather warm northern margin of west Gondwanaland (Smith 1972). Cladograms suggest that speciation of some of the groups have taken place already before the breakup of Gondwanaland, i.e. before the Jurassic period. This is congruent with the age of the fossils (upper Carboniferous, Krassilov & Schuster 1984) which are assumed to be ancestors of the family.

IX. EXCLUDED AND DOUBTFUL TAXA

Most of the dubious names listed below will probably be reduced to synonymy when the types are studied. Some, however, have probably been destroyed and, as the information of the protologues is ambiguous or they are nomina nuda, their identity will remain in doubt.

The names are listed in alphabetical order according to the epithet and under the valid name of genera other than *Pogonatum*, if known.

Pogonatum abbreviatum Mitt.

J. Linn. Soc., Bot. 12:615. 1869. — Type: Colombia, Andes Novo-Granatenses, in declivibus ad viam inter Marta et Bucuramanga (6 000 ped.), *Weir 164*.

Polytrichastrum alpinum (Hedw.) G.L. Sm.

Mem. New York Bot. Gard. 21:37. 1971. — *Polytrichum alpinum* L. ex Hedw., Spec. Musc. 92. 19:2. 1801. — *Pogonatum alpinum* (Hedw.) Röhl., Ann. Wetterauschen Ges. Gesamte Naturk. 3(2): 226. 1814.

Polytrichum fasciculatum Michx., Fl. Bor. Am. 2:294. 1803, *syn. nov.* — *Pogonatum fasciculatum* (Michx.) P. Beauv., Prodr. Aethogam. 84. 1805. — *P. urnigerum* var. *fasciculatum* (Michx.) Brid., Bryol. Univ. 2:126. 1827. — Type: Canada, New Foundland (Terre Neuve) (PC!, holotype).

Pogonatum urnigerum var. *ovatum* Vilh., Act. Bot. Bohem. 2:49. 1923, *syn. nov.* — Type: Jugoslavia. Monte Negro: Durmitor, *Rohlena* (PRC!, holotype).

Polytrichastrum alpinum has repeatedly been mistaken as a species of *Pogonatum*, and it is thus not surprising that study of type material revealed some *Pogonatum* to be only synonyms of *Polytrichastrum alpinum*.

The type material of *Pogonatum urnigerum* var. *ovatum* consists of both *P. urnigerum* and *Polytrichastrum alpinum*. The protologue of the new variety name describes the capsules as ovate and these plants of the type material are typical *P. alpinum*. Consequently, the taxon is synonymized with the latter species and excluded from *Pogonatum*.

Pogonatum bisseti Par.

Ind. Bryol. 978. 1898, nom. nud. — Original collection: Japan. Honshu: Saitawa, Nikko, IV.1886 *Bisset 102*; Kanagawa: Ubago Hakone, V.1887 *Bisset 106* (H-BR!).

The identity of the plants is dubious as Müller (1900) describes it as resembling *Pogonatum himalayanicum* (= *P. urnigerum*) but the specimens in H-BR, which might be part of the original collection are clearly *P. contortum*.

Fig. 31 (Below left). Distribution of A. *Pogonatum gracilifolium*, B. *P. neesii*, C. *P. tubulosum*, D. *P. tahitense* and E. *P. norrisii*. The black square indicates the disjunct occurrence of *P. neesii*, shaded areas the scattered distribution of *P. patulum* and the open square the only known locality of *P. minus*. Stippled area is for *P. inflexum* and two stars for disjunct localities of *P. tahitense*.

Pogonatum brasiliense (Hampe) Jaeg.

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873-74: 266. 1875. — *Polytrichum brasiliense* Hampe, Vidensk Meddel. Naturhist. Foren. Kjøbenhavn ser. 3, 4:53. 1879. — Type: Brasilia australis, *Glaziou 5199*.

This species was compared with *Pogonatum commune* by Hampe (1879) and it is probably not a *Pogonatum* but more likely belongs to the genus *Polytrichum* as originally assigned by Hampe.

Pogonatum catharinelloides C. Müll. in Brühl

Rec. Bot. Surv. India 13(1): 128. 1931. nom. nud. — Original collection: India, Tenasserim, *Levier*.

Pogonatum geheebii Besch. in Geh.

Rev. Bryol. 24:75. 1897. — Type: New Caledonia, 1880 *Hughan* Herb. Melbourne.

Pogonatum gulliveri (Hampe) Jaeg.

Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877-78: 453. 1880 (*Adumbratio 2:717*). — *Polytrichum gulliveri* Hampe, *Linnaea* 40:315. 1876. — Type: Australia. Tasmania: Mt. Wellington, *Gullifer & Gullifer* (BM!, holotype).

Study of the type material of *Pogonatum gulliveri* (BM!) revealed it to be a species of the Rhizogoniaceae and not the Polytrichaceae.

Polytrichum juniperinum Hedw.

Spec. Musc. 89, 18 6-10. 1801.

Polytrichum maoriae C. Müll., *Hedwigia* 36:340. 1897, syn. nov. — *Pogonatum maoriae* (C. Müll.) Par., *Ind. Bryol. Suppl.* 278. 1900. — Type: New Zealand (H-BR!, isotype).

Polytrichum maoriae var. *robustum* C. Müll., *Hedwigia* 36:340. 1897, syn. nov. — *Pogonatum maoriae* var. *robustum* (C. Müll.) Par., *Ind. Bryol. Suppl.* 278. 1900. — Type: New Zealand. South Island: litore australis prope Greymouth, 1888 *Helms* (B, holotype, probably destroyed).

From study of a type specimen of *Pogonatum maoriae*, and according to the original protologue, it is apparent that both of the taxa described from New Zealand are not *Pogonatum* but instead are conspecific with the almost cosmopolitan *Polytrichum juniperinum*.

Pogonatum peruvianum Par.

Ind. Bryol. Suppl. 278. 1900. — *Polytrichum dentatum* Hampe ex C. Müll., *Linnaea* 42:266. 1879, hom. illeg. — Type: Peru.

Pogonatum polysetulum Par.

Ind. Bryol. 986. 1898, nom. nud. — Original collection: Himalaya sept. occid. (*Dehra-Doun*).

Pogonatum suburnigerum Dix. in Jongm.

Fossil. Cat. 2(13): 45. 1927, nom. nud?

Pogonatum tenellum (C. Müll.) Par.

Ind. Bryol. 988. 1898. — *Polytrichum tenellum* C. Müll., *Nuovo Giorn. Bot. Ital.* n. s. 4:18. 1897. — Type: Bolivia.

In the protologue the species is compared with *Polytrichastrum alpinum* and is probably conspecific with a species of either *Polytrichastrum* or *Polytrichum*.

ACKNOWLEDGEMENTS

I am indebted to Prof. Timo Koponen for originally introducing me to the subject, as well as for his guidance during the work. I thank Dr. Pekka Isoviita, Mr. Krister Karttunen, and Prof. Daniel H. Norris (Arcata) for their advice and valuable comments on the manuscript. Prof. Norris is also acknowledged for revising the language. Prof. Teuvo Ahti I thank for encouragement and advice. The staff of the Botanical Library is acknowledged for helping to obtain valuable literature. The Curators of B, BM, BR, C, CANB, CANM, COLO, E, FH, FI, GOET, GRO, HIRO, JE, L, LAE, M, MAK, MELU, MO, NICH, PC, PE, PRC, S, TNS and U are acknowledged for loaning specimens. I am also obliged to Dr. Marshall R. Crosby and Dr. Robert E. Magill for offering for my use the "master list" of the genus. Dr. Andries Touw and Prof. B.O. van Zanten offered me access to two unpublished studies which

included valuable information. Many colleagues in Taiwan and Japan, especially Dr. Ming-Jou Lai and Dr. Naoki Nishimura, are acknowledged for their kind hospitality and help during field trips in 1987-88. Dr. Li Xing-jiang (KUN) graciously helped me with some Chinese specimens of the Polytrichaceae. I also thank Ms. Ulla Ahola for some of the illustrations and Mrs. Sigbrith Launos for her patient technical assistance. The work was financially supported by the Emil Aaltonen and Alfred Kordelin Foundations and by the Academy of Finland, grant no. 01/681. Finally, I thank my wife, Ms. Soili Stenroos, for many helpful discussions on our studies, and for her professional technical help during the study, and I express my deepest gratitude to my parents, Mr. Paavo Hyvönen and Mrs. Helly Hyvönen for their dependable support.

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INDEX TO SPECIFIC AND INFRASPECIFIC EPITHETS

Accepted names of genus *Pogonatum* are in boldface. New synonyms and combinations are marked with *syn. nov.* and *comb. nov.*, and newly selected lectotypes with *lectot. nov.* An asterisk (*) after the epithet indicates a metaspecies. The page number refers to the systematic part of this treatment. Names given as dubious or excluded are in parentheses. For homonyms authors are also given. The list includes epithets of the genera *Neopogonatum*, *Plagioracelopus*, *Pogonatum*, *Pseudatrichum* and *Racelopus*. All combinations of the epithets in these genera are listed. Names excluded from the five genera by earlier authors and not treated in the systematic part are not incorporated in the following list.

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ADDITIONS AND CORRECTIONS

The following paragraph should be added to p. 16 under the heading 4c. *Pogonatum perichaetiale* subsp. *oligodus* and the epithet *polycarpum* var. *angustatum* should be added to the index of the epithets on p. 85.

?*Pogonatum polycarpum* Par. var. *angustatum* Schimp. ex C. Müll., Nuov. Giorn. Bot. Ital. 4:166. 1897, nom. nud. — Original collection: Bolivia, *Mandoni*.

The following paragraph replaces the one on p. 79 and should be moved to p. 18 under *P. pensilvanicum*. The epithet abbreviation on p. 83 should accordingly not be in parentheses.

Pogonatum abbreviatum Mitt., J. Linn. Soc., Bot. 12: 615. 1869, *syn. nov.* — Type: Colombia, Andes Bogotenses, in declivibus ad viam inter Marta et Bucuramanga, 6 000 ft., *Weir 164* (H-BR!, isotype).

Pogonatum manchuricum Horik. was assigned to genus *Polytrichum* by Gao & Chang (1983; Index muscorum Chinae boreali-orientalis. J. Hatt. Bot. Lab. 54:187–205) and accordingly it should be removed from p. 30 and excluded from the epithet list on p. 85. The query indicating the disjunct occurrence of *P. nudiusculum* in Fig. 28 is superfluous as well.

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UDK 582.32



104 000 1208

Distributor:

Akateeminen Kirjakauppa
(The Academic Bookstore)
Keskuskatu 1
SF-00100 Helsinki
Finland

ISBN 951-9469-32-X
ISSN 0001-5369

Vammalan Kirjapaino Oy 1989