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A revision of the moss genus *Lepidopilum* (Callicostaceae)

Churchill, Steven Paul, Ph.D.

City University of New York, 1988

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A REVISION OF THE MOSS GENUS LEPIDOPILUM

(CALLICOSTACEAE)

by

Steven P. Churchill

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Faculty in Biology in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy, The City University of New York

1988

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

A REVISION OF THE MOSS GENUS LEPIDOPILUM (CALLICOSTACEAE)

by

Steven P. Churchill

Advisor: Dr. William R. Buck

A revision of the moss genus Lepidopilum recognizes 30 species from the previously accepted 145 species. Lepidopilum is a mostly epiphytic genus in the family Callicostaceae with 28 species in the neotropics and two species in the paleotropics. Three informal phenetic groups are tentatively recognized based on gametophytic features. The Scabristeum Group contains 12 species: L. affine, L. apophysatum, L. brevipes, L. chloroneuron, L. cuspidans, L. grevilleanum, L. lastii, L. muelleri, L. pallidonitens, L. scabrisetum, L. subsubulatum and L. verrucipes. The second,

Longifolium Group, contains 8 species: L. amplirete, L. aurifolium, L. brevifolium, L. caviusculum, L. frondosum, L. erectiusculum, L. integrifolium and L. longifolium. The last, Polytrichoides Group, contains 10 species: L. arcuatum, L. cubense, L. curvifolium, L. diaphanum, L. inflexum, L. permarginatum, L. polytrichoides, L. stillicidiorum, L. surinamense and L. tortifolium. Several taxa of Lepidopilum are of questionable status and are discussed. Approximately nine types were not available for study.

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TABLE OF CONTENTS

APPROVAL PAGE.....	ii
ABSTRACT.....	iii
ACKNOWLEDGMENTS.....	v
TABLE OF CONTENTS.....	vii
LIST OF TABLES.....	viii
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
HISTORY OF LEPIDOPILUM.....	5
TAXONOMIC GROUPS.....	21
DISTRIBUTION.....	23
MORPHOLOGY.....	25
TAXONOMIC TREATMENT.....	40
Key to the species of <u>Lepidopilum</u>	46
Scabristeum Group.....	54
Longifolium Group.....	111
Polytrichoides Group.....	136
DOUBTFUL NAMES & EXCLUDED TAXA.....	184
FIGURES.....	189
LITERATURE CITED.....	291

LIST OF TABLES

Table 1.....	9

LIST OF FIGURES

Fig. 1. Gametophytic features of <u>Lepidopilum</u>	189
Fig. 2. Gametophytic features of <u>Lepidopilum</u> ; developmental sequence, from earliest (left) to later (right) juvenile leaves.....	191
Fig. 3. Gametophytic features of <u>Lepidopilum</u> ; reproductive asexual structures.....	193
Fig. 4. Gametophytic features of <u>Lepidopilum</u> ; calyptra morphology and anatomy.....	195
Fig. 5. Sporophytic features of <u>Lepidopilum</u> ; illustrating variation of seta, urn and operculum.....	197
Fig. 6. Sporophytic features of <u>Lepidopilum</u> ; morphology and anatomy of seta and capsule	199
Fig. 7. Distribution of <u>Lepidopilum</u> in the neotropics. <u>Lepidopilum muelleri</u>	201
Fig. 8. Distribution of <u>Lepidopilum</u> in the	

paleotropics. <u>Lepidopilum lastii</u> ,	
<u>L. verrucipes</u>	203
Fig. 9. Distribution of <u>Lepidopilum</u> in the	
neotropics. <u>Lepidopilum scabrisetum</u> , <u>L.</u>	
<u>apophysatum</u>	205
Fig. 10. Distribution of <u>Lepidopilum</u> in the	
neotropics. <u>Lepidopilum brevipes</u> , <u>L.</u>	
<u>chloroneuron</u>	207
Fig. 11. Distribution of <u>Lepidopilum</u> in the	
neotropics. <u>Lepidopilum affine</u> ,	
<u>L. brevifolium</u> , <u>L. grevilleanum</u>	209
Fig. 12. Distribution of <u>Lepidopilum</u> in the	
neotropics. A. <u>Lepidopilum longifolium</u> , <u>L.</u>	
<u>erectiusculum</u> . B. <u>Lepidopilum amplirete</u> ,	
<u>L. integrifolium</u> , <u>L. aurifolium</u> ,	
<u>L. caviusculum</u>	211
Fig. 13. Distribution of <u>Lepidopilum</u> in the	
neotropics. A. <u>Lepidopilum diaphanum</u> , <u>L.</u>	
<u>arcuatum</u> , <u>L. permarginatum</u> . B. <u>Lepidopilum</u>	
<u>tortifolium</u> , <u>L. stillicidiorum</u> , <u>L. inflexum</u>	
.....	213
Fig. 14. Distribution of <u>Lepidopilum</u> in the	
neotropics. <u>Lepidopilum polytrichoides</u> ,	
<u>L. curvifolium</u>	215
Fig. 15. Distribution of <u>Lepidopilum</u> in the	

neotropics. <u>Lepidopilum surinamense</u> ,	
<u>L. cubense</u>	217
Fig. 16. <u>Lepidopilum muelleri</u>	219
Fig. 17. <u>Lepidopilum muelleri</u>	221
Fig. 18. <u>Lepidopilum subsubulatum</u>	223
Fig. 19. <u>Lepidopilum scabrisetum</u>	225
Fig. 20. <u>Lepidopilum scabrisetum</u>	227
Fig. 21. <u>Lepidopilum lastii</u>	229
Fig. 22. <u>Lepidopilum lastii</u>	231
Fig. 23. <u>Lepidopilum pallidonitens</u>	233
Fig. 24. <u>Lepidopilum pallidonitens</u>	235
Fig. 25. <u>Lepidopilum apophysatum</u>	237
Fig. 26. <u>Lepidopilum chloroneuron</u>	239
Fig. 27. <u>Lepidopilum brevipes</u>	241
Fig. 28. <u>Lepidopilum verrucipes</u>	243
Fig. 29. <u>Lepidopilum grevilleanum</u>	245
Fig. 30. <u>Lepidopilum affine</u>	247
Fig. 31. <u>Lepidopilum affine</u>	249
Fig. 32. <u>Lepidopilum longifolium</u>	251
Fig. 33. <u>Lepidopilum longifolium</u>	253
Fig. 34. <u>Lepidopilum integrifolium</u>	255
Fig. 35. <u>Lepidopilum amplirete</u>	257
Fig. 36. <u>Lepidopilum erectiusculum</u>	259
Fig. 37. <u>Lepidopilum aurifolium</u>	261
Fig. 38. <u>Lepidopilum caviusculum</u>	263

Fig. 39.	<u>Lepidopilum frondosum</u>	265
Fig. 40.	<u>Lepidopilum brevifolium</u>	267
Fig. 41.	<u>Lepidopilum permarginatum</u>	269
Fig. 42.	<u>Lepidopilum stillicidiorum</u>	271
Fig. 43.	<u>Lepidopilum inflexum</u>	273
Fig. 44.	<u>Lepidopilum tortifolium</u>	275
Fig. 45.	<u>Lepidopilum arcuatum</u>	277
Fig. 46.	<u>Lepidopilum diaphanum</u>	279
Fig. 47.	<u>Lepidopilum curvifolium</u>	281
Fig. 48.	<u>Lepidopilum polytrichoides</u>	283
Fig. 49.	<u>Lepidopilum surinamense</u>	285
Fig. 50.	<u>Lepidopilum cubense</u>	287
Fig. 51.	<u>Lepidopilum cubense</u>	289

INTRODUCTION

The genus Lepidopilum is a rather large, speciose and variable group of 30 species, mostly epiphytic, with a distribution in tropical America and Africa with the greatest concentration of species in in the neotropics. The species occur in most vegetation zones within the tropics but attain their greatest diversity in the premontane to montane forest.

Lepidopilum can be characterized generally by its complanate habit forming mats or feather forms that are ascending or erect, the leaves mostly differentiated between lateral and median (ventral and dorsal). Lateral leaves are asymmetric and often erect-spreading to spreading, and median leaves symmetric and erect, both lateral and median leaves are mostly ovate- to oblong-lanceolate with margins bordered or not, serrate, a double costa, and cells fusiform to hexagonal. The production of propagula or deciduous leaves are a common means of vegetation, asexual reproduction. The sporophytes are typically erect, with the seta ornamented with papillae and/or spines, the capsules are (sub-)erect, and peristome double with the exostome papillose and appearing bordered, the endostome, somewhat longer than the exostome, is

lightly papillose, with a low basal membrane, cilia absent, and segments keeled and perforated; the spores are spherical, lightly papillose, the operculum is conic-rostrate, and finally the calyptra is mitrate-campaulate, plicate, hairy and laciniate at the base.

Prior to this study, no revisionary study existed for the some 145 species that were presently accepted in the genus. Revisions of such genera, like Lepidopilum, are critically needed for the tropics. Our concepts of diversity, evolution and distribution in the tropics are simply guess work until such revisions are at hand. Most inventory studies readily reflect this need by listing the most common or widely known taxa while listing only a few members of large and difficult genera, i.e., Cyclodictyon, Sematophyllum, etc. It was for this reason that the present investigation was undertaken.

This present study is offered as a taxonomic revision of the genus Lepidopilum. A distinction between a taxonomic and systematic revision should be clear to the reader. This study attempts only to delimit taxa at the species level. Such an alpha-taxonomic study is the first necessary step toward a systematic investigation, i.e., analysis of intra- and inter-relationships. However there are a number of

problems, such as the bordered aquatic species, or the "affine" group that warrent further investigation before the phylogenetic systematics of this genus can readily be undertaken. I make no apologies for the shortcomings of this present effort. Far more critical collections are needed. Richard Spruce is still, after well over one hundred years, the foremost eminent collector of neotropical Lepidopilum! Further regional floristic and, hopefully, populational level studies are needed to address aspects of variation, ecology, etc. Such field studies can rarely be satisfied by the mere visitation of the "plant collector", rather such needed studies will best be forthcoming by those residing in the tropics. The hypotheses presented here for the Lepidopilum species should be critically examined and tested.

The author's field experience with Lepidopilum is confined only to Colombia and Ecuador. In Colombia, over several years, in part in conjunction with the preparation of a moss flora, I have collected extensively in the Department of Antioquia. Further detailed collecting has been conducted in the Department of Valle, and to a lesser extent, in the Departments of Caldas and Choco. In Ecuador I have made collections in various areas and vegetational

zones with particular emphasis on the eastern side of the Cordillera Oriental, especially in the Amazonian region along the Rio Napo. During the course of field work both in Colombia and Ecuador I have observed and collected approximately one third of the species of Lepidopilum.

HISTORY OF LEPIDOPILUM

The history of Lepidopilum can be said to be one which resulted from the fact that it was easier to describe species than to search through the rather extensive and scattered literature, and to locate and examine original type material. Thus after nearly 190 years there are approximately 145 species of Lepidopilum described and presently accepted.

The genus Lepidopilum was first circumscribed by Bridel in 1827. Bridel's "character naturalis" included the following characterization: "Plantae pulchellae, exoticae. Habitus Pterigophylli. Folia disticha, diversiformia, oblongo-areolata. Theca cylindrica, subinclinata, pedunculo mediocri tuberculis scaberrimo. Sedes arborea. Patria aequinoctialis in altero terrarum orbe. Vita gregaria, perennis." and "character essentielles" : "Peristomium duplex. Exterius, dentes sedecium lineares erecti. Interius, cilia sedecium cum dentibus alternantia iisque aequalia, basi media fissa. Calyptra mitraeformis integra, frustulis s. paleis squamiformibus solutis scabra. Theca aequalis, exannulata." and finally the "character sexualis": "Flos monoicus, lateralis, gemmaceus.

Genitalia mascula circiter octo, paraphysibus paucis
filiformibus tenerrimis, foeminea cum paraphysibus
masculi, unico foecundo."

Three species were included in Bridel's Lepidopilum:
L. subnerve (= L. scabrisetum, though L. subnerve
still remains the name used for the typification of the
genus), L. binerve (= Callicostella scabriseta), and L.
polytrichoides.

Prior to Bridel's establishment of the genus
several taxa were described by Hedwig (1801) under
Hypnum, including H. diaphanum and H. polytrichoides,
and later a single species, Neckera scabriseta, by
Schwaegrichen in 1816.

Subsequent to Bridel but prior to the major
contribution of Mitten in 1869, just over a dozen taxa
were described, in particular by Hampe in 1863 and
1865.

The most significant single treatment of the 19th
century, or for that matter the 20th century as well,
was provided in Mitten's 1869 Musci Austro-Americani.
A total of 57 species of Lepidopilum are enumerated,
many of which were described as new to science. Many
of the described Lepidopilum species were based
on the extensive collections made by Richard Spruce in

South America, particularly in Ecuador and northern Peru. Mitten emphasized both sporophytic and gametophytic features in the recognition of Lepidopilum species. While characters such as seta length and ornamentation, and sexuality were employed, ultimately the majority of species were diagnosed by the shape of lateral leaves and their apices. The emphasis on lateral leaf characters would also be used extensively by subsequent researchers.

At the close of the 19th century nearly 100 species had been described. Carl Mueller described nearly as many new species as did Mitten during the 50 years prior to 1900 in a variety of European journals.

Approximately a dozen authors described additional Lepidopilum species in the first half of the 20th century. Most notable among these individuals is Brotherus, who based his descriptions on material collected by others from both the New and Old World, and Herzog (1916), who based his new taxa on personal collections from the middle Andes, particularly Bolivia.

The world-wide generic moss treatment by Brotherus in 1907 for Engler and Prantl's Die natürlichen Pflanzenfamilien enumerated 102 species, and later in the revised edition of 1925, the number increased to

111 species, with additional species listed as of uncertain status. A number of sectional and generic changes occurred between the works of Mitten and Brotherus, the most obvious being the raising of sectional ranks to genera (see Table 1).

Thus at the on-set of this study approximately 145 species of Lepidopilum were recognized in Index Muscorum (Wijk et al., 1964) with a few additional species described since then.

Regional Treatments

A few regional American treatments have appeared since the work of Mitten. Bartram's (1949) moss flora of Guatemala provided 10 descriptions of Lepidopilum. For its time, this was an important and general reference for Central America and the neotropics in general. Bartram had a fairly narrow species concept, at least for Lepidopilum, and apparently studied few type collections, perhaps due in large part to the difficulty of obtaining types during those times. Then, as now, this treatment is used to identify collections from many areas of the neotropics, and thus many collections were ascribed incorrect names.

TABLE 1. Comparison of the inter- and intra-classification of Lepidopilum by Mitten and Brotherus. Indented taxa are sections, all other are genera (in bold face). Numbers refer to the number of species recognized by authors.

MITTEN 1869		BROTHERUS 1907		BROTHERUS 1925	
<u>Lepidopilum</u>		<u>Lepidopilum</u>		<u>Lepidopilum</u>	
<u>Eulepidopilum</u>	46	<u>Eu-Lepidopilum</u>	92	<u>Eu-Lepidopilum</u>	108
<u>Peromilla</u>	1	<u>Peromilla</u>	1	<u>Peromilla</u>	1
		<u>Hemiragiella</u>	2	<u>Hemiragiella</u>	2
<u>Isodrepanium</u>	1	<u>Isodrepanium</u>	1	<u>Isodrepanium</u>	1
<u>Helicoblepharum</u>	5	<u>Helicoblepharum</u>	3	<u>Helicoblepharum</u>	3
<u>Actinodontium</u>	1	<u>Actinodontium</u>	5	<u>Actinodontium</u>	5
<u>Tetrastichium</u>	3	<u>Tetrastichium</u>	2	<u>Tetrastichium</u>	2
 TOTAL	 57		 116		 118

During the 1950's two further treatments appeared treating the mosses of two Greater Antillean islands. Crum and Steere (1957) recognized six species for Puerto Rico, and Crum and Bartram (1958) recognized three species for Jamaica.

The most extensive work is that by Welch in a series of regional floristic papers on the Hookeriaceae. The series treated only the Meso-American region; the number of Lepidopilium species given in each is as follows: Mexico, 14 species (Welch, 1966); Cuba, 8 species (Welch, 1969); Jamaica, Hispaniola and Puerto Rico, 11 species (Welch, 1971); Lesser Antilles, 14 species (Welch, 1972); Central America, 25 species (1974). These various articles were summarized in the series North American Flora, where 37 species were treated (Welch, 1976). While providing a summary of the Lepidopilium species for this region, little critical attention was given to resolving species problems either within the area covered or for adjoining South America.

Since that time several other regional treatments have appeared. In southern Brazil, Sehnem (1979) recognized 10 species of Lepidopilum. Two species were described as new: L. macrophyllum and L. stenodictyum; and L. plebejum C. Muell. was transferred to the genus

Lepidopilidium. Sehnem's species concept was likewise rather narrow, and apparently types were not studied. In the series Flora of Suriname, Florschütz-de Waard (1986) has treated seven species of Lepidopilum and recognized several new synonyms. This is the most critical regional study thus far, based on careful comparison of types and with descriptions that describe the variation for the area treated. Finally in the BRYOTROP-transect project in Peru Schultze-Motel and Menzel (1987) recognized 8 species with one new synonym.

**Previous classifications of the Hookeriales and
Lepidopilum**

Since the second edition of Brotherus (1925) two modern or recent treatments by Miller (1971) and Crosby (1974) have provided detailed discussion on the evolution and classification of the Hookeriales. Both of these studies will be given more detailed review here with their relevance to the placement of Lepidopilum.

Miller (1971) sought to provide a more balanced treatment of the Hookeriales by considering all characters, not just a few select features used in the

past. "If both sporophytic and gametophytic structures are taken into account, and if we allow reduction as an indication of advancement, the Hookeriaceae can be rearranged into several comparatively homogeneous groups with a common heritage" (p. 244). Miller then presented 23 principles for moss systematics (i.e., dicta). According to Miller the application of these principles resulted in the recognition of the order Hookeriales containing three suborders 1) Hookeriineae with six families: Pilotrichaceae, Hookeriaceae, Distichophyllaceae, Daltoniaceae, Symphyodontaceae and Leucomiaceae; 2) Ephemeropsidineae with a single family, the Ephemeropsidaceae; and 3) Hypopterygiineae with 2 families: Hypopterygiaceae and Cyathophoraceae.

Lepidopilum was placed by Miller into the family Hookeriaceae, subfamily Hookeriopsidoideae. Descriptive features used for this subfamily included 1) leaves with a double costa half or more of the lamina length, 2) leaves narrowly bordered or not, 3) cells smooth to unipapillose (papillae over cell lumina), 4) peristome double with exostome pale to hyaline and papillose, or red to brown and cross-striate, and 5) endostome pale yellow to brownish with a keeled, papillose membrane generally lacking cilia.

The following is the sequenced genera presented by Miller for the subfamily Hookeriopsidoideae:

1. <u>Amblytropis</u>	5. <u>Actinodontium</u>
2. <u>Cyclodictyon</u>	6. <u>Lepidopilum</u>
3. <u>Archboldiella</u>	7. <u>Hookeriopsis</u>
4. <u>Lepidopilidium</u>	8. <u>Callicostella</u>

No further discussion was provided for the sequencing of taxa. Finally Miller viewed the evolution of the Hookeriopsidoideae from "some Pilotrichaceous type" which exhibited a "long double costa, elongate seta, complanate foliage, and a pinnate habit." This then led via reduction to the Hookerioideae.

Crosby (1974) sought to employ the "Philibert-Dixon Principle": "In constructing a classification of the mosses, primary weight must be given to characters of the sporophyte, and particularly the peristome; mosses with similar gametophytes but different peristomes must not be grouped together but with mosses which have similar peristomes" (p. 133). Two major families resulted in the employment of the "Philibert-Dixon Principle": 1) Daltoniaceae which exhibits a papillose exostome, outer plates wider than inner, papillose endostome with a low or absent basal membrane, and

cilia absent. Further characters are mentioned: exothecial cells rectangular or subquadrate, and uniformly thickened; calyptra lacerate at base and often hairy. 2) Hookeriaceae which exhibits the typical "Hookeriaceous peristome", i.e., exostome cross-striate, furrowed or zig-zag median line, endostome with a high basal membrane, lightly papillose and with cilia absent.

Lepidopilum was placed within the Actinodontioid group of the Daltoniaceae by Crosby (1974). This group was characterized as having a double costa or costa absent, and cells lax. The following sequence given below was based on 1) increasingly complanate stems, and 2) reduction or loss of costae:

Actinodontium Schwaegr.

Lepidopilum (Brid.) Brid., nom. cons.

Stenodesmus (Mitt.) Jaeg.

Crossomitrium C. Muell.

?Isodrepanium (Mitt.) Britt.

A comparison of the recent treatments provided by Miller and Crosby shows little in common due in large

part to the fuzzy application of differing criteria to develop a classification. Concerning Lepidopilum, the only common element is the close placement of Actinodontium.

Recently another attempt has been made (Buck, 1987, 1988) to re-evaluate the Hookeriales. A similar opinion is expressed about his dissatisfaction of previous classifications "because apparently closely related genera are often placed in different families while, at times, very different genera are allotted confamilial status." As with Miller (1971), Buck sought to use both sporophytic and gametophytic characters. This is in contrast to the approach employed by Crosby (1974) where the emphasis was placed on peristome types (hookeriaceous vs. daltoniaceus). Buck (1987) suggested that the daltoniaceus peristome "represents the result of repeated modifications from the "hookeriaceous" peristome. Thus, while these modifications may have resulted from similar ecological pressures, the "daltoniaceus" peristome itself is polyphyletic." In addition to conventional characters, i.e., costa features and cell patterns of the lamina, Buck (1987) used "nontraditional characters" such as stem anatomy, pseudoparaphyllia, axillary hairs and calyptra features

to suggest groupings.

Buck (1987, 1988) recognized five families: Hookeriaceae, Daltoniaceae, Adelotheceaceae, Leucomiaceae, and Callicostaceae. The first three families are characterized by 1) leaf cells short, 2) axillary hairs 3-celled, and 3) plants little-branched. The last two families are characterized by 1) leaf cells elongate, 2) axillary hairs 2-celled, and 3) plants freely branched. Leucomiaceae is further defined as having a cucullate calyptra and fragile stems, and Callicostaceae as having a strong and double costa. Lepidopilum is placed in the Callicostaceae, and the 24 genera are simply sequenced alphabetically. All the genera of Miller's Hookeriopsidoideae, and Crosby's Actinodontioid group (with the exception of Isodrepanium) are contained in Buck's Callicostaceae.

Two major lines of evolution within the Callicostaceae are considered by Buck (1988). The first exhibiting a stem anatomy that lacks a hyalodermis, and where the exostome has undergone reduction from a hookeriaceous to a daltoniaceous type it appears only slightly bordered; this includes such genera as Callicosta and Schizomitrium. The second line of evolution exhibits a stem anatomy with a

well developed hyalodermis, and an exostome, where reduced, with a strong border; this group would include Lepidopilum.

The inherent weakness of these various studies has been the lack of using shared-derived characters (synapomorphies) to elucidate monophyletic groups at all levels. Buck's classification, as compared to those of Brotherus, Miller and Crosby, comes intuitively closer to a more "natural" system. However a critical evaluation of all characters is needed as well as attempting a higher level analysis that can establish character polarity based on an outgroup comparison or at least a functional outgroup(s).

The "naturalness" of Lepidopilum is still questionable. I certainly would have an easier conscience knowing that Lepidopilum exhibited several, or even one, unique character(s) that could establish its monophyly or at best paraphyly. There are several shared similarities to be found among possibly related genera for both gametophytic and sporophytic characters. The genus Lepidopilidium exhibits almost identical characters of the gametophyte with one or possibly two subgroups in the Scabrisetum Group of Lepidopilum. However Lepidopilidium exhibits a

hookeriaceous peristome, while Lepidopilum exhibits a daltonaceous peristome. If Buck's (1988) contentions are correct, that the hookeriaceous peristome type has been reduced to a daltoniaceous peristome type in several genera of the Callicostaceae, then it is likewise possible that Lepidopilum may be derived from another hookeriaceous peristomate ancestor on more than one occasion, and thus Lepidopilum, in part, is possibly polyphyletic. Another example of shared gametophytic features concerns the habit. In Actinodontium and Helicoblepharum, the first has an erect habit without notable differentiation of primary and secondary stems, however the seta is smooth and calyptra naked and smooth, though the peristome is daltoniaceous with a "border." Helicoblepharum has a spreading habit forming loose to dense mats, however the leaves often exhibit papillose cells by the projecting cell angles, and the peristome, daltoniaceous, appears reduced without a "border." Both forms are found in Lepidopilum, and in previous classifications have been placed together in Lepidopilum. Finally, among shared sporophytic characters, Stenodictyon has a sporophyte identical with Lepidopilum with a spinose seta and a daltoniaceous peristome (only one sporophyte is known,

with the type, and no other collections; observations are based on Mitten's description and illustration). Lastly, Amblytropis exhibits a spinose seta, and identical peristome and calyptra, though the urn is short oval-ovoid; however, the gametophyte is identical with Cyclodictyon. Immediate genera that I believe concern Lepidopilum and are possibly related, and thus should be closely examined, are: Amblytropis, Helicoblepharum, Lepidopilidium, Stenodesmus and Stenodictyon.

Any attempt at establishing the naturalness of Lepidopilum is similar to that found in most genera of mosses. Groups are defined by overall similarity (plesiomorphies + apomorphies). Thus we are confronted with taxa that are described by sets of combined characters, any one or several of which are never necessary to define a taxon, and any portion of these characters may be used to define other taxa in another combined form of character sets, as in Lepidopilum. Such polythetic groups have their origin in pre-evolutionary times (see Stevens, 1984, 1986 for a extensive review of this subject in botanical classifications). While many of the families and genera of mosses have been described and accepted after the theory of evolution, there is little or nothing

reflected in most classifications even into recent times of hierarchy, reflecting decent with modification.

Until there are hypotheses of monophyly for the Hookeriales, based on shared derived characters, the naturalness of all families and genera of this large pantropical order is open to question to my thinking. This situation holds for most groups of "bryophytes" (cf. Mishler, 1986; Mishler & Churchill, 1984).

The purpose of this study was to delineate the species of the genus Lepidopilum. While it is hoped that many of the species in this genus are monophyletic, some are likely not, and are paraphyletic or metasppecies. The species hypotheses put forth in this revision should and must be critically tested. This testing is a first necessary step before a phylogenetic analysis can be undertaken for the species. Likewise, however, polarity of character transformations will depend on a phylogenetic hypothesis at the next higher level, and this entails the related taxa, genera or subgenera, related to Lepidopilum.

TAXONOMIC GROUPS

I have recognized 3 informal groups of Lepidopilum species. Recognition of these groups are purely phenetic (with emphasis on the gametophyte), and are distinctly polythetic in their characterization. This is only a temporary grouping and no formal taxonomic status is intended. They may or may not have any phylogenetic significance. The sequence of groups and the species contained in each is followed in the Taxonomic Treatment.

1. Scabrisetum Group. This group includes those taxa that are usually strongly complanate with a strong differentiation between lateral and median leaves. The lateral leaves are asymmetric, and often falcate or falcate-sigmoid in shape.

The following taxa are included: L. muelleri, L. subsubulatum, L. lastii, L. scabrisetum, L. pallidonitens, L. apophysatum, L. chloroneuron, L. cuspidans, L. brevipes, L. verrucipes, L. grevilleanum, and L. affine.

2. Longifolium Group. Included in this group are species characterized by secondary stems that are

usually erect and radially foliate with little or no differentiation between lateral and median leaves. The leaves are often prominently recurved on one or both sides with a strong costa.

The following taxa are included: L. longifolium, L. integrifolium, L. amplirete, L. erectiusculum, L. aurifolium, L. caviusculum, and L. frondosum, and L. brevifolium.

3. Polytrichoides Group. This group includes species that exhibit weakly complanate to somewhat radially foliate secondary stems and branches that are often ascending or erect. Lateral and median leaves are differentiated; lateral leaves are not strongly asymmetric, falcate or falcate-sigmoid. Most species are limbate, that is, they have a weak to strong differentiated border of linear cells that differ from the inner lamina cells.

The following taxa are included: L. permarginatum, L. stillicidiorum, L. inflexum, and L. tortifolium, L. arcuatum, L. diaphanum, L. curvifolium, L. polytrichoides, L. surinamense, and L. cubense.

DISTRIBUTION

The distribution of Lepidopilum is tropical, as it is for many members of the family Callicostaceae. Only two species of Lepidopilum are restricted to the Old World, Africa and Madagascar, and both belong to the Scabrisetum Group discussed above. However, the greatest concentration of species occurs in the New World. Nearly a third of the species have a widespread distribution that includes the Caribbean, Central America and South America.

Within the neotropics, excluding widespread Lepidopilum species, the following distributions are observed: Central America and South America, L. brevipes, L. affine, L. cuspidans, L. permarginatum, L. stillicidiorum; Caribbean and South America, L. integrifolium; South American Andes and, in part, southern Brazil, L. arcuatum, L. aurifolium (Ecuador), L. brevifolium (Ecuador), L. caviusculum (Ecuador), L. chloroneuron (Ecuador), L. curvifolium, L. erectiusculum, L. frondosum (Colombia), L. grevilleanum (Ecuador), L. inflexum, L. subsubulatum; Central America, L. apophysatum; Caribbean: L. amplirete.

The distributional patterns of Lepidopilum,

particularly those with a restricted distribution or those considered "narrow endemics", may in fact reflect a restricted range of distribution, but just as likely it is a fact that many areas, particularly in South America, have been poorly collected. Thus, caution should be used in considering some of the present distributions of Lepidopilum and possible areas of endemism, especially when only represented by a few collections.

MORPHOLOGY

Gametophyte

Spores

The spores of Lepidopilum are spherical, pale green or yellow. In nearly all material examined, spore surface was ornamented with low papillae, but in a few cases the papillae are distinctly longer and the spores appear spinose with the use of a light microscope.

Rhizoids

Rhizoids are usually concentrated and clustered beneath primary stems and on prostrate secondary stems or where stems have contact with the substrate. In some cases they form a dense tomentum, e.g., in L. erectiusculum. The rhizoids appear smooth and rusty red in color using a light microscope.

Habit and Stems

Primary stems are creeping, long or short, and often

not readily observed. The leaves are mostly eroded or, if present, are reduced in some cases and are broadly ovate or nearly triangular and abruptly short to moderately acuminate; they often lack or have a reduced costa (Fig. 1). Secondary stems can be either prostrate and spreading forming mats or, more often, ascending and perpendicular or erect from the substrate. Branching is irregularly subpinnate, usually with few to several branches. In cross-section both primary and secondary stems of Lepidopilum typically exhibit a hyalodermis, i.e., a thin-walled epidermis, with the immediately subtending layer, the outer cortex, consisting usually of 2-5 rows of golden-yellow or rusty-golden, thick-walled cells. The inner cortical cells are usually largest, thin-walled and hyaline. As with most members of the Callicostaceae, a central strand is absent.

How well differentiated the stem cells are appears to be related, in part, to the environment and substrate. Some species associated with a very moist or aquatic environment exhibit cells of nearly equal size, and occasionally with cell wall thickness nearly equal (Fig. 1 B). Epiphytic species that often have ascending or erect stems often have a well differentiated outer cortex of very thick-walled cells

(Fig. 1 A).

Axillary Hairs

As in most taxa of the Callicostaceae, axillary hairs are found in the axils of stem leaves and consist of two cylindrical cells, the basal cell is short and brown or golden-brown, the terminal cell is elongate and hyaline (Fig. 1 C). Axillary hairs are most readily observed on terminal shoots among the developing leaves.

Pseudoparaphylla

The pseudoparaphylla on secondary stems and branches observed in Lepidopilum are foliose, short triangular or broadly lanceolate.

Leaves

Most of the variation observed in the gametophyte concerns the leaves, and thus much of the taxonomy and problems associated with species limits are related to this feature. Although Mitten (1869) used sporophytic or sexual features to separate large groups, most of

the 50 or more species recognized by Mitten were based on leaf characters, particularly the lateral leaves.

Leaves in Lepidopilum are arranged in 8 to 10 rows. A distinction is made between median (ventral and dorsal) and lateral leaves. Even within both median and lateral leaves there is a considerable amount of variation, particularly in shape, within individual plants and species.

Median leaves are usually appressed or erect(-spreading) on the stem, symmetrical, and most often ovate, ovate-lanceolate or lanceolate.

Lateral leaves are erect to erect-spreading or more often spreading or sometimes wide-spreading, symmetric or more commonly asymmetric, and vary greatly in shape from ovate to lanceolate, oblong, lingulate, obovate, or any possible combination of these descriptive terms because of the rotation or phyllotaxy of lateral leaves. There is, in some species, considerable variation in leaf shape. Another feature of some species is that the leaves can be subfalcate to falcate, and/or exhibit a distinctive sigmoid or S-shape, often associated with the L. scabriseta group.

The leaf apex is either long or short acuminate, acute or obtuse-rounded. Some variation exists with

lateral leaves in terms of apex shape, ranging, according to the phyllotaxic position, from acute to acuminate or other combinations.

Leaf margin also presents a number of features that have been useful in the circumscription of Lepidopilum species. A number of species exhibit a very distinct border of long linear cells juxtaposed to the intralaminar region that often has hexagonal or fusiform cells. The border is often composed of few to many rows of long linear cells along the margin which in some cases actually merge with the costa in the mid or distal region of the lamina and occasionally coalesce at the apex. In a number of species the border can be very indistinct or the result of laminar cells becoming progressively narrower toward the margin. Margins can be entire to weakly or strongly serrate. Occasionally the young developing leaves at the end of a shoot will have margins serrate but later exhibit entire or serrulate margins. Teeth along the margin can be simple, composed of a single cell, or composed of two cells abutting each other, as in L. frondosum.

Costae are always double, strong to weak and indistinct, usually of equal length on median leaves and generally unequal on lateral leaves. Costae can

vary from $1/5$ to $3/4$ of the lamina length. At the base of the leaf the costa can be set apart or joined. Particularly in lateral leaves both can be present. Costae usually gradually diverge, or are nearly parallel, although begin diverging at base.

Developmental sequence of leaves produced along vegetative branches were examined in Lepidopilum to note various character transformations found in the adult leaves along secondary stems and branches. It has been shown in a number of mosses, e.g., Atrichum, Fissidens, Mniaceae, Sphagnum, and Tortula, that the sequence of leaves produced along vegetative innovations is the same as the sequence via buds developing from protonemata (Churchill & Mishler, unpubl. data on the Mniaceae; Mishler, 1988). In Lepidopilum several species were examined, recording the development along shoots from juvenile to adult leaves. Two species discussed here include L. polytrichoides and L. tortifolium (Fig. 2). In both species the earliest juvenile leaves are symmetrical, short ovate-triangular with oblong-rectangular cells that become narrow toward the margin. In later development the juvenile leaves exhibit a weak double costa represented by 1-3 linear cells, each approximately $1/3$ the lamina length; also a weak border

along the margin can be observed, as well as weak marginal serration. These features suggest that the presences of a double costa, differentiation of a border and marginal serration are terminal additions (recapitulation). The question then can be asked, at what level do these various expressions enter in terms of phylogenetic transformations? Certainly in the Callicostaceae the double costa is widespread in all genera, thus in terms of Lepidopilum this character is irrelevant. This is likely true of marginal serration also. However, the border may have significance depending on the relative position of the Polytrichoides Group, and depending on the relationship of the various Lepidopilum groups to those taxa closely related. This feature, as well as other characters, may have a potential use once a phylogenetic hypothesis is developed for Lepidopilum. It is clear that the earliest juvenile leaves are similar to those thus far studied in various moss families and orders.

Perichaetia

The perichaetia are produced laterally on secondary stems and branches. Generally the perichaetia consist of perichaetial leaves that are ovate, ovate-

lanceolate, lanceolate or linear-lanceolate. Margins are serrate to entire, costae are absent, and cells are variously elongate. The archegonia are few and surrounded by few to many paraphyses. Once fertilized, the receptacle and archegonia enlarge, thus the perigynium elongates and contains, when fully developed, a whorl of several imbricating leaves. With the development of the perigynium, the basic leaf architecture remains the same. The basal region still still contains both old archegonia and paraphyses. When plants are autoicous, perichaetia may be distributed distally or proximally from the perigonia, or may be intermixed.

Perigonia

Perigonia are produced laterally on secondary stems and branches. These structures are bud-like in appearance. Perigonial leaves are generally ovate-lanceolate or oblong-lanceolate and are similar to perichaetial leaves, including the absence of a costa. Antheridia are few and are associated with few to many paraphyses.

Propagula

The presence of propagula has been observed in a number of Lepidopilum species. These are several- to many-celled cylindrical structures that are smooth (Fig. 3 A). Propagula are generally produced on secondary stems and branches, usually in the axils of leaves. In several cases the author has observed propagula produced on damaged stems. Propagula have also been observed along the adaxial costal region as in L. curvifolium, or on lamina apices as in L. cubense. Typical of tropical lowland, and in particular premontane to high montane forest mosses, the production of propagula is widespread in numerous families, unlike the situation found in the north temperate zone. Thus in general I do not regard the ability to produce propagula as particularly significant in the taxonomy of Lepidopilum and caution should be used when one species is described as having these structures present or absent.

Although not true propagula, deciduous leaves serve the same function in terms of asexual reproduction (Fig. 3 B). In a number of Lepidopilum species small deciduous distal branch leaves can be found. The most dramatic case of this is found in a form of L. scabrisetum that has been known under the specific epithet of L. stolonaceum and is most widespread in the

Caribbean region. Such plants are most common on leaf litter and rocks, and produce numerous short branches containing deciduous leaves. However this phenomenon is less common than the production of propagula among Lepidopilum species.

Calyptrae

The typical calyptra in Lepidopilum is one that is short mitrate or mitrate-campanulate, covering often half or more of the capsule (Fig. 4). The surface can be smooth or appearing somewhat plicate, and either rarely naked or more commonly hairy or "pilose" (Fig. 4). The ornamentation is composed of several structures - unicellular hairs, paraphyses, and aborted or sterile archegonia, and what I believe are multicellular modified paraphyses. However the ontogeny of these structures remains unknown in the mosses. In cross-section the calyptra is composed of 2-4 layers of cells (Fig. 4 C); in regions of the plicae it is 3-4 layers thick, the region between these are usually 2-celled. The cross-section of the base of modified paraphyses is 1-2 cells thick, and appears to be hollow or with several enlarged hyaline cells in the center. The base of the calyptra is generally lacinate

or appearing lobed, rarely erose.

Sporophyte

Setae

The setae in Lepidopilum vary from very short, equal to or shorter than the capsule, to elongate, many times longer than the capsule (Fig. 5). In most the seta is erect, but in some of the small epiphytic species the seta can be curved. Although in many species length of seta is diagnostic, it has also been observed in an equal number of species to vary intraspecifically. The majority of species are ornamented; some are smooth below, and a few are smooth throughout though often roughened below the urn (Fig. 5). Ornamentation of the seta surface is also an important feature between and within Lepidopilum species. Two basic types of papillae have been observed on setae and these can be found separately or mixed. Both are developed entirely from epidermal cells (Fig. 6 A). The first can be described as low papillae and are simply projections from the upper ends of epidermal cell walls; these can be bluntly rounded or somewhat spinose. The other type is an elongate spine that can be 3-5 times longer than

the low papillae and are always found associated on the same seta with the low projecting papillae. These spines can be rounded or sharp-pointed at the apex. In cross-section the setae can be seen to have a thick-walled epidermis and thick-walled outer cortical cells, often in 3-7 layers; the inner region, the central strand, is composed of weak, often collapsed hyaline cells (Fig. 6 A-B).

Capsules

The capsules in Lepidopilum are erect to suberect, rarely pendent. The urn is short- to long-ovoid or ovoid-cylindrical (Fig. 5), and when deoperculate often flask-shaped with a flaring mouth. The exothecial cells are usually short- to long-rectangular or oblong, equally thick-walled or occasionally collenchymatous (Fig. 6 D) In cross-section the walls are short-rectangular or quadrate and thick-walled.

Stomata

Stomata are usually found at the base of the urn in the neck region. In surface view the stomata appear immersed, with 4 or 5 cells surrounding the opening

(Fig. 6C). Often the stomatal area is somewhat bulging from the capsule surface, giving the appearance of an apophysis in a number of species (hence the name L. apophysatum Hampe).

Opercula

The opercula vary from conic to more commonly short- or long-rostrate, the latter being the most common in Lepidopilum (Fig. 5). Typically the cells at the base are oblate-rectangular, in mid region short rectangular and at the apex short- to long-rectangular. Annuli often remain attached to the opercular base.

Annulus

Although the Hookeriaceae s. l. has been described as lacking an annulus, there are differentiated cells at the junction of the urn mouth and base of the operculum (Fig. 6 D). In Lepidopilum the "annulus" is composed of several rows of rusty-red oblate-rectangular to somewhat quadrate, thick-walled cells. After the operculum is shed, the annuli remain attached to either the capsule mouth or to the base of the operculum.

Peristome

Lepidopilum exhibits a typical double peristome.

The exostome is composed of 16 teeth with each tooth appearing bordered in surface view (Fig. 6 F). In much of the material examined the exostome was fragile and readily lost; the endostome appears to be less fragile. The outer cell plates are thick and broad, and always lightly papillose (Fig. 6 F). The inner plate is several times thinner and also narrower than the outer plate (thus giving the impression of a border), and exhibits extended lamellae/trabeculae (Fig. 6 F).

The endostome has 16 segments with a low or absent basal membrane, and cilia are absent. The segments alternate with the exostome teeth. Each segment is long lanceolate, keeled (outwardly), and lightly papillose on both surfaces (Fig. 6 G). The endostome is often slightly longer than the exostome.

When dry the exostome typically arches back or becomes recurved with the distal portion lying adjacent to the urn mouth. The endostome remains erect or slightly appressed. When wet the exostome becomes erect and/or appressed to the endostome segments. The functional morphology of the exostome (recurved

when dry, erect or appressed when wet) has been described as a daltoniaceous peristome (see Crosby, 1974, Allen et al., 1985).

TAXONOMIC TREATMENT

LEPIDOPILUM (Bridel) Bridel, Bryol. Univ. 2: 267.

1827.

Type. Lepidopilum subenerve Bridel, nom. illeg. (=

L. scabrisetum (Schwaegrichen) Steere

Pilotrichum subgen. Lepidopilum Bridel, Mant. Musc.

141. 1819. Hookeria sect. Lepidopilum (Bridel)

C. Mueller, Syn. 2: 192. 1851. Lepidopilum

sect. Eulepidopilum Mitten, J. Linn. Soc., Bot.

12: 373. 1869, nom. illeg. = Lepidopilum

(Bridel) Bridel sect. Lepidopilum.

Trachypodium Bridel, Bryol. Univ. 2: 268. 1827,

nom. nud. in syn. Based on Trachypodium

subenerve Brid., nom. nud.

Campylotrichum Sikora, Beitr. Gesammt. Natur-

Heilwissenschaft 1: 283. 1836. Type:

Campylotrichum acuminatum Sikora, Nova

Hollandia (sic, now known to be Trinidad),

Sieber s.n. (FH-Schiffner) = Lepidopilum

polytrichoides (Hedw.) Brid. See Buck &

Churchill, 1989.

Lepidopilum sect. Peromilla Spruce ex Mitten, J.

Linn. Soc., Bot. 12: 372. 1869. Type.

Lepidopilum erectiusculum (Taylor) Mitten

Lepidopilum sect. Mniolepidopilum C. Mueller, Flora
58: 546. 1875. Type. Lepidopilum mniaceum C.
Mueller. Type not available.

Lepidopilum sect. Urolepidopilum C. Mueller, Flora
58: 548. 1875. Hookeria subsect.

Urolepidopilum (C. Mueller) C. Mueller, Bull.

Herb. Boissier 5: 205. 1897. Type.

Lepidopilum caudatum C. Mueller (= L.
polytrichoids (Hedwig) Bridel).

Lepidopilum sect. Barbatina Hampe, Vid. Medd.

Naturh. For. Kjoebenh. ser. 3, 9-10: 265.

1878, nom. nud. Based on Lepidopilum
albescens Hampe. Type not available.

Puiggaria Duby, Mém. Soc. Phys. Hist. Nat. Genève

27: 7. 1880. Type. Puiggaria ovalifolia Duby
(= Lepidopilum ovalifolium (Duby) Brotherus).

Lepidopilum sect. Hemiragiella Bescherelle, J. Bot.

(Morot) 8: 63. 1894. Type. Lepidopilum
cladorrhizans Bescherelle (= L. longifolium
Hampe).

Lepidopilum sect. Cyathophoridium C. Mueller,

Hedwigia 37: 246. 1898, nom. nud.

Cyathophoridium C. Mueller, Hedwigia 37: 246.
1898, nom. nud. Based on Lepidopilum

latifolium C. Mueller (= L. scabristeum
(Schwaegrichen) Steere).

Pseudolepidopilum Luisier, Broteria Cienc. Nat. 7:
127. 1938, nom. invald. desc. gall. Based on
Pesudolepidopilum virens (Cardot) Luisier.

Plants small to rather large and robust, dark to light green, yellowish-green or golden-yellow or brown, usually glossy; forming loose to dense mats or tufts, corticolous, ramicolous, less often epiphyllous or saxicolous. Primary stems usually short creeping, radiculose or radulose beneath, rhizoids rusty-red, leaves often eroded or reduced, short ovate-triangular, costae short and double; in cross-section hyalodermis well developed, usually outer cortical cells in several rows with thick, rusty-red walls. Secondary stems spreading or ascending and often erect and perpendicular to substrate, irregularly pinnately branched, branches few; in cross-section hyalodermis well developed, outer cortical cells thick-walled, rusty-red, in several rows; pseudoparaphyllia foliose, short lanceolate or triangular; axillary hairs 2-celled, basal cell short, brown, terminal cell elongate, hyaline. Secondary stem and branch leaves generally similar, the latter smaller, crowded or distant, radially foliate, secund or more often complanate,

smooth, undulate, cripate or flexuose, erect to wide-spreading; lateral leaves usually distinctly asymmetric or less often symmetric, linear-lanceolate, ovate-lanceolate, obovate, oblong to oblong-lanceolate, some falcate and/or distinctly S-shaped (sigmoid), acuminate, and occasionally channeled, or acute to obtuse-rounded, base folded because of leaf position, occasionally weakly auriculate or slightly decurrent on one side; margins plane, rarely recurved, elimbate or limbate, border distinct or not, entire or more often serrulate, serrate or spinose; costae double, strong to weak, often unequal in length, at base closed or set apart, $1/5$ to $3/4$ (or more) lamina length, usually diverging, rarely parallel; median cells linear or fusiform to broadly short or long hexagonal or rhomboidal, thin or thick-walled, smooth, porose or not, marginal cells similar but gradually smaller and narrower or forming a distinct border of often oblong-linear cells, lower and basal cells usually oblong or short- to long-rectangular, somewhat lax, often porose, insertion cells sometimes golden-brown or yellow; median leaves usually symmetric or slightly asymmetric, lanceolate or more often ovate, ovate-lanceolate or oblong-lanceolate, acuminate to acute or obtuse, elimbate or limbate, entire to

serrate, costae double, closed or set apart, $1/5-1/2$ lamina length, usually diverging, occasionally parallel, cells similar to those of lateral leaves. Propagula often present in leaf axils, rarely extending along one or both costae, uniseriate, usually with several to many short-cylindrical cells. Autoicous or dioicous. Perigonia lateral, leaves ovate-lanceolate or oblong-lanceolate, costae usually absent, margins entire or serrulate, median laminal cells elongate, paraphyses few or absent. Perichaetia lateral, if plants autoicous then distal on stems or branches, often above perigonia, leaves ovate-lanceolate or -subulate, margins entire or more commonly serrate, median lamina cells elongate, costae absent or weak. Setae short or elongate, reddish-orange or rusty-red, straight, rarely twisted, smooth or more commonly ornamented along entire length or smooth below, papillae uniformly low and projecting distally from cell ends or dimorphic with low papillae and long, nearly spinose ones perpendicular to seta surface or nearly so, tips bluntly rounded or sharply pointed; capsules generally erect or suberect, urn ovoid, or ovoid-cylindrical, mouth flared and contracted below when deoperculate; exothecial cells oblong or short- to long-rectangular, uniformly thick-walled or

collenchymatous, stomata appearing sunken, often indistinct, few to several at base of urn; annulus present, in several rows, often remaining attached to operculum or urn mouth, cells oblate-rectangular, thick-walled, dark rusty-red; operculum short to long rostrate; peristome double, exostome teeth 16, long-linear, when dry arching and recurved, erect and appressed to endostome when wet, appearing bordered, outer surface papillose, broader and thinner than inner surface, inner surface narrow, lamellae distinct and projecting; endostome basal membrane low, segments 16, linear, usually longer than exostome teeth, keeled, papillose, cilia absent. Spores spherical, smooth to more often lightly papillose. Calyptrae mitrate-campanulate, smooth to more often plicate, smooth or more often pilose, hairs often multicellular, hollow at base in cross-section (modified archegonia?), at base lobed or shallowly to deeply lacerated.

Etymology. *Lepidopilum*, from the Latin, *lepid-* (=scaly), and *-pilum* (= a felt cap, mitra); in reference to multicellular hairs on the calyptrae.

KEY TO THE SPECIES OF LEPIDOPILUM

1. Lateral leaves distinctly limbate with 2-8 rows or more of linear cells, inner laminal cells broadly rhomboidal-fusiform, rhomboidal or hexagonal, never linear or linear-fusiform; plants often radially foliate or loosely complanate
2. Plants lax, pale green or whitish to pale reddish green, often with an iridescent sheen; leaf cells large, 130-150 um long, 30-55 um wide, hexagonal to broadly fusiform **26. diaphanum**
2. Plants rigid or stiff, dark green to golden-yellow, glossy; leaf cells smaller, variously shaped
3. Leaves ovate-lanceolate; apex gradually long acuminate; costa 1/2 lamina length; seta short, 2-3 mm long, distal 1/2 papillose **28. polytrichoides**
3. Leaves ovate-oblong to oblong-lanceolate; apex obtuse-rounded, abruptly acuminate, apiculate or acute; costa 1/2-3/4 lamina length; seta short and papillose throughout or distal 1/5 rough, or elongate
4. Leaves short ovate-oblong to obovate, 2 x longer than wide
5. Leaf border of 1-3 rows of linear cells, often

inconspicuous; costa ca. 1/2 lamina length

6. Leaves obovate; primary stems conspicuously
tomentose; seta short, 2.5-3.0 mm long, smooth
or distally roughened **29. surinamense**

6. Leaves ovate, broadest near the middle; primary
stems not conspicuously tomentose; seta longer,
4.5-5 mm long, papillose throughout except at
base **27. curvifolium**

5. Leaf border 4 rows or more of linear cells; costa
2/3-3/4 lamina length

7. Leaves small, 2.0-2.6 mm long; seta short or
long, papillose or spinose

8. Leaf apices short apiculate; seta 8-12 mm long
24. tortifolium

8. Leaf apices sharply short acuminate; seta 1.8-
2.8 mm long **23. inflexum**

7. Leaves large, 4-5 mm long; seta elongate, 11-14
mm long, spinose **21. permarginatum**

4. Leaves long oblong-obovate to ovate-oblong, 3-4 x
longer than wide

9. Leaf apices bluntly acute or short acuminate;
marginal serration blunt **22. stillicidiorum**

9. Leaf apices sharply short acuminate or apiculate;
marginal serration sharp **25. arcuatum**

1. Lateral leaves elimbate or inconspicuously limbate,

inner lamina cells similar to marginal cells or gradually grading into marginal cells; plants radially foliate or more often strongly complanate

10. Lateral leaves symmetrical or nearly so, not falcate or falcate-sigmoid; lateral and median leaves not strongly differentiated
11. Costa $3/4$ lamina length or more
12. Lateral leaves oblong, 2.0-2.8 mm long; median cells hexagonal to fusiform-hexagonal, 100-150 μ m long **19. frondosum**
12. Lateral leaves lanceolate to oblong-lanceolate, 1.5-1.8 mm long; median cells linear-fusiform, 38-48 μ m long **17. aurifolium**
11. Costa $1/3$ - $1/2$ lamina length
13. Leaves small, 1.2-1.5 mm long; plants forming mats **20. brevifolium**
13. Leaves larger, usually 2 mm long or more; plants forming mats or wefts
14. Leaves broad, 1.5-2.2 mm wide; inconspicuous border of linear cells often present
15. Leaves broadly ovate-lanceolate, apices gradually long-acuminate; seta usually papillose in distal $1/2$ **28. polytrichoides**
15. Leaves broadly oblong or obovate, apices abruptly short acuminate or apiculate; seta

variously ornamented

16. Leaves obovate, broadest above leaf middle;
plants erect; primary stems often densely
tomentose; seta short, 2.5-3.0 mm long,
distally smooth or rough **29. surinamense**
16. Leaves oblong, broadest at leaf middle;
plants spreading, usually perpendicular to
substrate, not erect; rhizoids inconspicuous;
seta 4.5-8.0 mm long, papillose throughout
except at base **27. curvifolium**
14. Leaves narrow, usually 1.2 mm wide or less;
border absent
17. Plants forming rather dense mats, strongly
complanate; leaves often undulate, margins
plane **12. affine**
17. Plants ascending or erect, if forming mats
then loosely complanate, typically plants
appearing radially foliate; leaves smooth or
crispate, not undulate, margins often recurved
on one or both sides
18. Apices often twisted or forming propagula at
tip or along distal margin; seta papillose in
distal 1/2 **30. cubense**
18. Apices erect or recurved, propagula typically
forming in leaf axils; seta spinose or

papillose throughout

19. Leaf margins recurved throughout except at apex and base; seta smooth **14. integrifolium**

19. Leaf margins partially recurved on one or both sides; seta papillose or spinose

20. Leaf apices acute or broadly short-acuminate; leaves 2.2-3.0 mm long, usually broadest at leaf middle

21. Plants forming mats; leaves complanate, oblong, usually recurved on one side

15. amplirete

21. Plants erect; leaves radially foliate, ovate, usually recurved on both sides

18. caviusculum

20. Leaf apices gradually long acuminate; leaves 3 mm long or more, usually broadest below leaf middle

22. Leaf margins sharply serrate; lower secondary stems with leaves often distant, branches often conspicuously densely foliate and abruptly attenuate

16. erectiusculum

22. Leaf margins serrulate or entire; secondary stems densely foliate, branches not attenuate **13. longifolium**

10. Lateral leaves asymmetric, slightly to strongly falcate to falcate-sigmoid; lateral and median leaves differentiated, usually strongly so

23. Lateral leaves broadly oblong to obovate, often 2-3 x longer than wide

24. Lateral leaves monomorphic, broadly oblong; apices obtuse-rounded, apiculate

5. pallidonitens

24. Lateral leaves dimorphic, largest obovate, smaller oblong to oblong-lanceolate (usually on lower secondary stems and distal branches); apices short-acuminate or aristate

25. Plants rather course and stiff; largest leaves 4 mm or more long, and 1 mm or more wide; plants normally epiphytic

6. apophysatum

25. Plants rather lax and soft; largest leaves less than 4 mm long, and 1 mm or less wide; plants of mesic or aquatic habitats
(latifolium form)

4. scabrisetum

23. Lateral leaves oblong, ovate-oblong or oblong-lanceolate, often 4-5 x longer than wide

26. Lateral leaves strongly undulate, large, 4.5-5.5 mm long; seta 22-28 mm long

11. grevilleanum

26. Lateral leaves smooth, crispate or flexuose, less than 4 mm long; seta less than 15 mm long

27. Apices gradually long-acuminate

28. Lateral leaves ovate-lanceolate, 2.4-2.9 mm long, 0.5-0.7 mm wide; apices mostly narrowly long-acuminate or subulate; seta mostly 4-5 mm long

2. subsubulatum

28. Lateral leaves oblong-lanceolate, broadest at leaf middle, 3.0-4 mm long, 0.6-1.2 mm wide; apices broadly to somewhat narrowly acuminate, not subulate; seta mostly 5-9 mm long or more

29. Median cells broadly fusiform to rhomboidal-fusiform, 85-140 um long, 14-20 um wide; distal half of lamina broadly elongate and very gradually tapering, abruptly acuminate

3. lastii

29. Median cells somewhat narrower, 78-110 um long, 11-13 um wide; distal half tapering to a long acuminate apex

1. muelleri

27. Apices short-acuminate

30. Lateral leaves appearing distant on secondary stems; leaves clasping stem, base often auriculate on one side; seta 7-9 mm long

7. chloroneuron

30. Lateral leaves crowded to somewhat distant; leaves not clasping stem, base not auriculate or subauriculate; seta short or long

31. Plants medium sized, usually densely foliate;
lateral leaves commonly falcate-sigmoid;
deciduous branches or leaves often present;
seta mostly greater than 4 mm long

4. scabrisetum

31. Plants small and slender, not densely
foliate; lateral leaves falcate, occasionally
falcate-sigmoid; rarely producing deciduous
branches and leaves; seta less than 4 mm long
32. Lateral leaves small, 1.4-1.6 mm long;
plants of Old World

10. verrucipes

32. Lateral leaves larger, 2.0-2.7 mm long;
plants of New World

33. Calyptra densely hairy; seta 2.5-3.5 mm
long

8. cuspidans

33. Calyptra naked; seta 1.7-2.2 mm long

9. brevipes

SCABRISETUM GROUP

1. *Lepidopilum muelleri* (Hampe) Mitten, J. Linn. Soc., Bot. 12: 379. 1869. Hookeria muelleri Hampe, Linnaea 20: 84. 1847. Type. Venezuela. Moritz s.n. (isotypes, BM, S).

Figs. 16-17.

Hookeria deppeana C. Mueller, Syn. Musc. 2: 196.

1851, syn. nov. Lepidopilum deppeanum (C. Mueller) Mitten, J. Linn. Soc., Bot. 12: 383. 1869. Type. Mexico. Deppe. Type not seen.

Lepidopilum mohrianum C. Mueller, Linnaea 38: 649.

1874, syn. nov. Type. Mexico. San Cristobal, Sep 1857, Mohr (isotype, NY).

Lepidopilum sartorii C. Mueller, Linnaea 38: 649.

1874, nom. nud. in syn. Based on L.

mohrianum C. Muell.

Lepidopilum monilidontium Hampe, Vid. Medd. Naturh.

For. Kjoebenh. ser. 3, 6: 154. 1875, syn. nov.

Eriopus monilidontius (Hampe) Paris, Ind.

Bryol. Suppl. 144. 1900. Type.

Brazil. Rio de Janeiro, Glaziov 7091

(isotypes, H-BR, NY).

Lepidopilum goniothecium C. Mueller, Linnaea 42:

495. 1879, syn. nov. Type. Venezuela. Fendler 122a (lectotype, H-BR; isoelectotype, NY). See discussion section.

Hookeria haplociliata C. Mueller, Bull. Herb.

Boissier 5: 206. 1897, syn. nov. Lepidopilum haplociliatum (C. Mueller) Paris, Ind. Bryol. Suppl. 223. 1900. Type. Guatemala. Coban, 4400 ft, Dec 1885, Türkheim 6 (lectotype, H-BR). Syntype. Guatemala. Alta Vera Paz, 1310 m, 27 Nov 1891, Türkheim 6696 (H-BR).

Lepidopilum pringlei Cardot, Rev. Bryol. 37: 51.

1910, syn. nov. Type. Mexico. Vera Cruz: Near Jalapa, 4000 ft, 25 Jun 1908, Pringle 10499 (lectotype, PC; isoelectotypes, F, L, NY, US). Type chosen on the basis of duplicates in various herbaria.

Lepidopilum auriculatum Herzog, Biblioth. Bot. 87:

135. 1916, syn. nov. Type. Bolivia. Tablas, ca. 1800 m, May 1911, Herzog 4517 (holotype, JE).

Lepidopilum splendens Brotherus, Bot. Jahrb. 56

(Beibl. 123): 19. 1920. Type. Peru. Sandia:

Sandia, 2600-3000 m, Weberbauer 819 (holotype, H-BR).

Lepidopilum macrophyllum Sehnem, Pesquisas Bot. 33:

49. 1979, syn. nov. Type. Brazil. Rio Grande do Sul: Sao Francisco de Paula, Taimbé, 800 m, 17 Feb 1953, Sehnem 6414 (holotype, PACA; isotype, NY).

Plants medium sized to rather robust, dark green to yellowish-green or golden-yellow, glossy, corticolous, epiphyllous, lignicolous or ramicolous. Primary stems creeping; secondary stems spreading to ascending or suberect and perpendicular to substrate, to 6 cm long, several branched; in cross-section hyalodermis well developed, outer cortical cells in 2-4 rows, small, thick-walled, rusty-red, inner cortical cells several to many, large, thin-walled, hyaline. Leaves complanate, crowded, crispate or flexuose; lateral leaves erect-spreading to wide-spreading, asymmetric, ovate-lanceolate to oblong-lanceolate, usually broadest $1/3-1/2$ above base, 3-4(5) mm long, 0.7-1.2 mm wide, broad to narrowly long-acuminate, apices often channeled or erect; margins often recurved at base, elimbate, serrate in distal $1/3(1/2)$, occasionally serrulate or strongly serrate; costae set apart,

gradually diverging, $1/3-1/2$ lamina length; median cells linear, fusiform or fusiform-rhomboidal, 78-110 μm long, 11-13 μm wide, thin-walled or more commonly somewhat thick-walled, basal cells oblong-rectangular, porose or not; median leaves symmetric, ovate- to oblong-lanceolate, often abruptly short- to long-acuminate, 2-3 mm long, to 0.9 mm wide, costae ca. $1/3$ lamina length. Propagula often present in leaf axils, short to more commonly long cylindrical. Autoicous & ?dioicous. Perigonial leaves short ovate-lanceolate, 0.7-0.9 mm long, broadly acuminate. Perichaetial leaves ovate-long lanceolate or subulate, 1.0-1.2 mm long. Setae elongate, 5-13 mm long, reddish-orange to rusty-red, ornamented, papillose to more commonly spinose, spines to 90 μm long; capsules erect to suberect or rarely inclined, urn ovoid-cylindrical, 1.2-2.0 mm long; opercula conic-rostrate, 1.1-1.3 mm long; exostome 620-820 μm long, endostome 820 to 1110 μm long. Spores 13-15 μm in diameter, lightly papillose. Calyptrae mitrate-campanulate, 1.8-2.5 mm long, plicate, sparsely to densely hairy.

Etymology. Muelleri, named in honor of Carl Mueller (1818-1899); well known bryologist, particularly remembered for his abundant over-description of new

Distribution (Fig. 7). From Mexico south through Central America, and from Venezuela and Colombia south to Peru and Bolivia, with an apparent disjunct to southern Brazil. At elevations from 70-2400 m, most common in premontane to high montane forests; on branches and trunks of shrubs and treelets, less often encountered on logs and leaf litter.

Representative specimens examined. MEXICO. Mirador, Liebman s.n (NY). Chiapas: Trail between Pueblo Nuevo & Simojovel, 24 Dec 1962, Robinson 9805 (US). Oaxaca: 25 mi above Valle Nacional on Hwy 175 in Sierra Juarez, 25 Dec 1972, Sharp et al. 4714 (F). Veracruz: El Atoron 5.5 km N de Coatepec, carretera antigua Xalapa, 1265 m, 5 Dec 1975, Juarez G. 258 (B).

GUATEMALA. Alta Verapaz: Cobán, 1350 m, Jul 1908, Turckheim 7784 (H-BR); between Tactic and divide on road to Tamahu, 1500-1600, 1-7 Apr 1941, Standley 90773b, 91485 (F).

HONDURAS. Francisco Morazan: Cerro Uyuca, 1600-1800 m, 9 May 1947, Standley et al. 8046 (F); trail up Montana Uyuca, drainage of the Río Yequare, 1600-1850 m, 30 Nov 1975, Richards et al. 3590 (F).

COSTA RICA. Monteverde, 10 Jun 1966, James 15 (US).
 Limón: La Columbiana Farm of United Fruit Co., ca. 70
 m, 6-7 Mar 1924, Standley 36569a (US).

PANAMA. Chiriquí: Ca. Boquete, Holcomb Trail, 1000-
 1500 m, 20 Apr 1918, Cornman 3191a (F, US).

COLOMBIA. Andes Bogotenses, Bucaramanga, 7000 ft,
Weir 145 (NY). Antioquia: Municipio de Andes, ca. 2.7
 km SO de Santa Rita, 1790 m, 20 Jul 1986, Churchill et
al. 14516, 14545, 14556 (HUA, NY); Municipio de Jardín,
 Sur Jardín ca. 5-10 km, 2480 m, 4 Oct 1987, Churchill &
Marulanda 15719 (HUA, NY); Municipio de La Unión, Cerro
 San Miguel, sur San Miguel, 2460-2620 m, 6 Jul 1987,
Churchill et al. 15448 (HUA, NY); Municipio de Sonsón,
 de Sonsón hacia Nariño, Páramo de Sonsón, 7 Jul 1987,
Churchill et al. 15493 (HUA, NY); Municipio de Urrao,
 ca. 16 km NE de Urrao hacia Caicedo, 2400 m, 2 Jul
 1985, Churchill et al. 13444 (NY). Boyacá: Near
 Bocota, 2100 m, 22 Aug 1957, Grubb & Guymer B.357c, d,
361 (BM). Choco: Municipio de El Carmen, 8 km SE del
 borde entre Choco y Antioquia, 1970 m, 19 Jul 1986,
Churchill et al. 14516 (HUA, NY).

VENEZUELA. Caracas, Bishchell s.n. (NY).

ECUADOR. Antombos, Spruce 762 (BM, NY). Archedonia,
Jameson s.n. (NY). Chimborazo, Spruce 763 (BM, H-BR,
 NY). Río Blanco, Spruce 761 (BM, NY). Tunguragua,

Spruce 759 (BM, NY). Prope Granadilla, Nov 1910,
Allioni 493 (BM). Gualquiza: Yumasa, 30 Jan 1910,
Allioni 8481 (H-BR).

PERU. Huanuco: Huanuco, Chicochao, 1900-2000 m, 19
Aug 1967, Ferreyra 16948a (US).

BOLIVIA. Incacorral, ca. 2300 m, Jun 1911, Herzog
5019 (BM, FH, L, NY). Río Tocarani, 2200 m, Jul 1911,
Herzog 4081 (BM, H-BR). Talschlucht Tablas, 1800 m,
May 1911, Herzog 4581 (FH, L).

The collection by Fendler, No. 122, is a mixed
collection containing three taxa for which Mueller
described two species: L. goniothecium (Fendler 122a),
and L. aureo-fulvum (Fendler 122b), the latter is
Lepidopilidium portoricense (C. Muell.) Crum & Steere.
Furthermore some of Fendler's collection contain L.
longifolium Hampe, mixed or only with L. aureo-fulvum,
which led originally to some possible confusion as to
which taxon Mueller may have intended as a new species
but the original description clearly notes the marginal
serration and the affinity to L. muelleri.
The choice of the lectotype was based on a pure
collection under Fendler's 122a.

Lepidopilum muelleri is a highly polymorphic species
and the morphological limits are not well defined.

Considerable variation is found in the gametophyte, both in the size of leaves and shape. The basic leaf shape, broadest $1/3-1/2$ above the base and the tapering, generally long acuminate apices is all that readily characterizes this species, at least under the concept adopted here. Plants tend to be more robust with higher elevation, but variation appears to exist at all elevations between shape and size, particularly in the elongation of the lamina and marginal serration. Furthermore there appears to be no correlation between various lamina shapes or sizes and seta length or ornamentation. The extreme ends of this variation can readily be separated but there are numerous intermediates; further segregation may be warranted with more detailed studies and further collectings at all elevational ranges. The separation of L. subsubulatum from L. muelleri at times is difficult, particularly in the smaller forms of the latter. It may be that these two should be combined but at present I prefer to recognize L. subsubulatum.

2. *Lepidopilum subsubulatum* Geheeb & Hampe in Hampe,

Vid. Medd. Naturh. For. Kjoebenh. ser. 4, 1: 123.

1879. Type. Brazil. Prope Apiahy, 1879, Puiggari

53. (lectotype, G; isoelectotype, H-BR).

Fig. 18.

Puiggaria elegans Duby, Flora 63: 171.1880. 1880.

Type. Brazil. Sao Paulo: Apiahy, Puiggari
(G).

Lepidopilum subaurifolium Geheeb & Hampe in Hampe,
Flora 64: 405. 1881, syn. nov. Type. Brazil.
Rio de Janeiro, 1880, Glaziou 11736 (holotype,
G; isotypes, H-BR (2), possible type, NY).

Lepidopilum pycnodictyum C. Mueller, Hedwigia 39:
271. 1900, syn. nov. Type. Brazil. Santa
Catarina: Serra Geral, Jan 1890, Ule 862
(lectotype, H-BR).

Lepidopilum stenodictyum Sehnem, Pesquisas Bot. 33:
53. 1979, syn. nov. Type. Brazil. Rio de
Janeiro: Nova Friburgo, 1000 m, 5 May 1957,
Sehnem 7714 (lectotype, PACA; isoelectotype,
NY).

Plants small to medium sized, glossy olive-green to
yellow-green or golden-yellow, ramicolous or
epiphyllous. Primary stems short creeping; secondary
stems spreading or ascending to erect, perpendicular to
substrate, to 5 cm long, several branched; in cross-

section hyalodermis well developed, outer cortical cells in 2-3 rows, small, thick-walled, rusty-red, inner cortical cells few, thin-walled, hyaline. Leaves crowded, somewhat flexuose; lateral leaves spreading to wide-spreading, narrowly ovate- or oblong-lanceolate, 2.4-3.0 mm long, 0.50-0.75 mm wide, occasionally falcate, long and narrowly acuminate; margins slightly recurved below, elimbate, serrulate to serrate in distal 1/3; costae 1/4-1/3(1/2) lamina length, gradually diverging; median cells linear to fusiform, (55)78-120 um long, 6-11 um wide, somewhat thick-walled, basal cells oblong-rectangular, occasionally porose; median leaves appressed to erect, ovate- to oblong-lanceolate, 1.8-2.3 mm long, 0.5-0.7 mm wide, long acuminate. Propagula cylindrical, to 0.4 mm long. Autoicous. Perigonial leaves ovate-lanceolate, to 0.8 mm long, broadly acuminate. Perichaetial leaves ovate-lanceolate to linear, 1.0-1.3 mm long, long acuminate. Setae generally elongate, (2)4.0-5.5 mm long, reddish-orange to rusty-red, ornamented, papillose throughout, spinose except at base; capsules suberect to erect, urn ovoid-cylindrical, 0.9-1.2 mm long; exothecial cells irregularly subrectangular to rectangular; operculum conic-rostrate, 0.8-1.0 mm long exostome to 600 um long, endostome to 755 um long. Spores 14-

17 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, 2.0-2.2 mm long, plicate, sparsely hairy, occasionally almost naked.

Etymology. Subsubulate, from the Latin, sub- (somewhat, less than), subula (fine sharp point); in reference to the narrow acuminate leaf apex.

Distribution. Southern Brazil.

Representative specimens examined. BRAZIL. Minas Gerais: Caraca, Mar 1892, Ule 1467 (H-BR, US). Santa Catarina: Serra Geral, Jan 1891, Ule 1184 (H-BR). Sao Paulo: Prope Apiahy, 1880, Puiggari 192 p.p. (H-BR); In monte Jaragua prope Taipas, 800-1050 m, 1 Jun 1901, Schiffner 812 (H-BR); Ad flumen "Rio Branco" prope Santos, ca. 20 m, 12 Sep 1901, Schiffner 1505 (H-BR).

Lepidopilum subsubulatum is a small and slender species in comparison to that typically found in L. muelleri Hampe. Both species appear to be closely related, furthermore several intermediates have been observed; however, at present I prefer to retain L. subsubulatum until further material and types have been examined relating to the variation found in L.

muelleri.

3. *Lepidopilum lastii* Mitten, J. Linn. Soc., Bot. 22: 309. 1886. Type. Central Africa (Tanzania?). Usagara Mountains, Last s.n. (holotype, NY; isotype, H-BR). Fig. 21-22.

Lepidopilum dusenii C. Mueller in Brotherus, Bot. Jahrb. 20: 202. 1894, syn. nov. Type. Cameroon. Bomana, 660 m, Dusén s.n. (lectotype, H-BR). Syntype. Cameroon. Buea, Preuss 1089 (H-BR).

Lepidopilum callochlorum C. Mueller in Brotherus, Bot. Jahrb. 24: 259. 1897, syn. nov. Type. Cameroon. Dusén 258 (holotype, H-BR).

Lepidopilum filiferum Brotherus in Mildbraed, Wiss. Ergebn. Deutsch-Zentr. Afr. Exp. 2: 166, pl. 15, f. 37. 1910, hom. illeg. Type. Vulkan-Gebiet, Mildbraed 2038 (holotype, H-BR).

Lepidopilum carrougeaunum Thériot & Potier de la Varde in Thériot, Recueil Publ. Soc. Havraise, Études Diverses 91: 94. 1924, syn. nov. Type.

Madagascar. Southwest of Tananarive
(Antananarivo), 1922, Carrougeau s.n.
(holotype, PC).

Plants medium sized to somewhat robust, dark-green, yellowish-green to golden-yellow, glossy, ramicolous or corticolous, rarely saxicolous. Primary stems creeping; secondary stems spreading to ascending, perpendicular to substrate, few branched, tufts with several short ascending branches; in cross-section hyalodermis well developed, epidermal cells rather large, thin-walled, outer cortical cells in 2-3 rows, small, thick-walled, rusty-red, inner cortical cells numerous, larger, hyaline. Leaves crowded, loosely to strongly complanate, smooth to somewhat crispate; lateral leaves spreading to wide-spreading, asymmetric, ovate-oblong to oblong-lanceolate, usually falcate, (2.8)3.0-4.0 mm long, 0.6-0.8(1.1) mm wide, short to long acuminate; margins plane, elimbate, serrate in distal 1/3-1/2, occasionally strongly serrate, or serrulate to nearly entire; costae 1/4-1/2 lamina length, gradually diverging; median cells broadly fusiform to rhomboidal-fusiform, 85-140 μ m long, 14-20 μ m wide, usually + thick-walled, occasionally thin-walled, basal cells oblong-rectangular; lateral leaves

erect, symmetric, ovate-oblong to oblong-lanceolate, 3.0-3.5 mm long, 0.8-1.2(1.8) mm wide, acuminate, often abruptly so. Autoicous. Perigonial leaves ovate-oblong to oblong-lanceolate, 1.0-1.2 mm long, broadly acuminate. Perichaetial leaves ovate-lanceolate, 1 mm long. Setae elongate, (2.5)4-10(14) mm long, stout to slender, ornamented, spinose throughout or only papillose at base, spines short to long, to 85 μ m long; capsules suberect, occasionally horizontal, urn ovoid-cylindrical, 1.3-1.6 mm long; exothecial cells oblong-rectangular, thick-walled; opercula rostrate, 1.2-2.0 mm long; exostome to 770 μ m long, endostome to 880 μ m long. Spores 14-18 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, 2.0-2.5 mm long, plicate, smooth to sparsely hairy, rarely + densely hairy.

Etymology. Lastii, in honor of Joseph Thomas Last (1847/8-1933), the collector.

Distribution (Fig. 8). Cameroon to southern Ethiopia and south through eastern Zaire and Kenya to Malawi, and Madagascar; frequent at elevations from ca. 1500-2300 m. Low to mid montane forests; on branches and trunks of shrubs and treelets, also

lianas, occasionally on rocks.

Representative specimens. ETHIOPIA. Kefa: Bonga, near the Catholic Mission, 7 Jan 1973, Friis et al. B136 (MO).

CAMEROON. Fernanado Poo (Bioko): San Carlos, Nov 1911, Mildbraed 7031 (H-BR); Pic Clarence, 2000 m, Dec 1894, Newton s.n. (H-BR). Buea, 3000 ft, Jul 1891, Jungur s.n. (H-BR); Bomana, 19 Jul 1892, Dusén s.n. (NY).

ZAIRE. Between Tongo & Mukule, W of Rutshuru, 17 Dec 1914, Bequaert s.n. (NY).

RWANDA. Cyangugu: Uwinka, 2250 m, 12 Aug 1974, De Sloover 18838 (B, L, NY); 2300 m, 22 Aug 1974, De Sloover 19014 (B, BM, FLAS, H-BR, U). Gisenyi: Gikungu, 2100 m, 27 Jul 1974, De Sloover 18645 (H-BR).

KENYA. Aberdare Natl. Park, W side of mountain, 3300 m, 16 Jun 1970, Rasmussen et al. 14 (MO, NY).

TANZANIA. Morogoro: Uluguru Mountains, summit of Bondwa Peak, 9 km S by E of Morogoro, 2100 m, 13 Dec 1972, Crosby et al. 8685 (MO); Mwere Valley, near boundary of Forest Reserve, 8 km SSE of Morogoro, 1480 m, 14 Dec 1972, Crosby et al. 8706, 9093 (MO).

MALAWI. Mlanje District: Mlanje Mountain, Lucheny Plateau, 1820 m, 1 Jul 1946, Brass 16561, 16688 (L,

NY).

The gametophytic plants are somewhat variable in relative size, marginal serration and cell shape but the basic leaf shape is similar with the rather broad elongation in the distal half of the lamina, and generally the broad fusiform cells. In the tufted forms the leaves tend to be somewhat larger and often serrulate to nearly entire, furthermore the branches are abbreviated and often ascending but this is considered possibly only an environmental form of the typical weft form that is complanate spreading. Sporophytically, the seta varies considerably, within a collection and between collections. The type of Lepidopilum lastii exhibits short setae, 2-3 mm long, while at the other extreme, collections range from 8-14 mm long. However, more than a third of the collections examined varied by 3-7 mm in each sample; furthermore the ornamentation appears to vary from short to long spinose, and less often merely papillose.

Most plants examined were autoicous, and in most cases both the perigonia and the perichaetia could readily be located. The species L. filiferum was originally described as dioicous but an examination of the type revealed that the plants are autoicous.

A nice series of collections have been made by De Sloover and Crosby that further assisted with the variation in L. lastii. De Sloover (1975) has provided an excellent illustration of L. lastii and discussed the variation found in the Rwanada area.

Maintaining this species, separate from the New World species, may prove unacceptable. Lepidopilum lastii certainly has its affinities with the Scabrisetum Group (as does L. verrucipes Card.), and is similar to some forms of L. scabrisetum as broadly considered in this study, however I prefer at this time to retain L. lastii at the species level.

4. Lepidopilum scabrisetum (Schwaegrichen) Steere, Bryologist 51: 140. 1948. Neckera scabriseta Schwaegrichen, Suppl. Sp. Musc. 1 (2): 153. 1816. Pilotrichum scabrisetum (Schwaegrichen) Bridel, Musc. Recent. Suppl. 4: 141. 1819. Daltonia scabriseta (Schwaegrichen) Walker-Arnott, Mém. Soc. Linn. Paris 5: 296. 1827. Lepidopilum subenerve Bridel, Bryol. Univ. 2: 268. 1827, nom. illeg. incl. spec. prior. Trachypodium subenerve Bridel, Bryol. Univ. 2. 268, 1827, nom. illeg. Hookeria subenervis Hampe, Linnaea 20: 84. 1847,

nom. illeg. incl. spec. prior. Type. Guiana.

Richard (holotype, G; isotypes, BM, NY).

Figs. 19-20.

Hookeria intermedia C. Mueller, Syn. Musc. 2: 195.

1851, syn. nov. Lepidopilum intermedium (C.

Mueller) Mitten, J. Linn. Soc., Bot. 12: 377.

1869. Type. Trinidad. Monte Tocuche, 14 Mar

1847, Crüger s.n. (syntypes, BM, S); 28 Aug

1847, Crüger s.n. (syntypes, BM, S).

Hookeria latifolia C. Mueller, Syn. Musc. 2: 199.

1851. Lepidopilum latifolium (C. Mueller)

Mitten, J. Linn. Soc., Bot. 12: 380. 1869.

Type. Trinidad. Monte Tocuche, Crüger s.n.

(isotype, BM).

Lepidopilum oblongifolium Mitten, J. Linn. Soc.,

Bot. 12: 383. 1869, syn. nov. Type. Brazil.

Minas Geraes, Gardner 79 (holotype, NY).

Lepidopilum daltonioides Schimper ex Bescherelle,

Ann. Sci. Nat. Bot. sér.. 6, 3: 230. 1876.

Type. Guadeloupe, L' Herminier s.n. (isotypes,

H-BR, NY).

Lepidopilum livens Bescherelle, Bull. Herb. Boissier

2: 396. 1894, syn. nov. Type. Costa Rica.

Lehmann 1126 (holotype, G; isotype, US).

Lepidopilum stolonaceum C. Mueller, Hedwigia 37:

245. 1898, syn. nov. Type. Puerto Rico.

Manati, Apr 1887, Sintenis s.n. (isotype, NY).

Lepidopilum pterygophylloides C. Mueller, Hedwigia

37: 246. 1898. Type. Puerto Rico. Prope

Naguabo, Nov 1886, Sintenis s.n. (isotype, NY).

Lepidopilum ovatifolium Herzog, Beih. Bot.

Centralbl. 27: 351. 1910, syn. nov. Type.

Bolivia. Cochabamba: Incacorral, 2200 m, Jan

1908, Herzog s.n. (holotype, JE).

Lepidopilum michelianum Brotherus & Paris in Paris,

Rev. Bryol. 33: 56. 1906. Type. French Guiana.

Maroni, 1905, Michel s.n. (holotype, H-BR).

Lepidopilum malachiticum Herzog, Biblioth. Bot. 87:

135. 1916, syn. nov. Type. Bolivia. San

Miguelito, ca. 1500 m, Herzog 2746 (JE);

Sillar, ca. 1800 m, Herzog 2769 (JE).

Lepidopilum argutidens Brotherus, Rev. Bryol. 47:

39. 1920, syn. nov. Type. Ecuador. Oriente:

Gualaquiza, Río Salado, 800 m, Jun 1909,

Allioni 8283 (holotype, H-BR).

Plants small to medium or somewhat large sized,
glossy dark green, yellowish-green, golden-green, or
reddish-brown, ramicolous, corticolous, epiphyllous,

occasionally terricolous or saxicolous. Primary stems creeping, leaves generally ovate-acuminate but generally eroded, costae weak; secondary stems spreading, ascending to distinctly erect and perpendicular to substrate, to 5 cm long, branches few, often producing somewhat attenuate fragile branches with deciduous ecostate leaves ca. 1.0-1.5 mm long. Secondary stem leaves crowded, sometimes crispate, loosely or commonly strongly complanate; lateral leaves spreading, falcate, asymmetric, oblong to oblong-lanceolate and sigmoid, 2-3.7 mm long, 0.5-1.0 mm wide (occasionally lower secondary stem leaves distinctly larger, oblong-obovate, to 4.5 mm long, to 1.5 mm wide), usually short acuminate, apex occasionally pinched; margins plane below, often erect distally, occasionally recurved below on one side, serrate in distal $1/4-1/3$, often sharply so in upper $1/4$; costae set apart, $1/5-1/3(1/2)$ lamina length, gradually diverging; median cells linear-fusiform, 0.85-120(145) μm long, 10-15(17) μm wide, mostly thin-walled, occasionally lax, basal cells irregularly short- to occasionally long-rectangular; median leaves erect or appressed, suboval- or oblong-lanceolate, sometimes narrowly so, 1.7-2.5(3.2) mm long, 0.6-1.0(1.4) mm wide, acuminate, often pinched or channeled, distally

serrate, costae separate, ± parallel. Autoicous, synoicous (? dioicous). Perigonial leaves broadly short-ovate, to 1 mm long, concave, short acuminate. Perichaetial leaves lanceolate, 0.8-1.1 mm long, acuminate. Setae (4)5-9 mm long, reddish-orange to dark rusty red, ornamented throughout or occasionally smooth at base, papillae short to somewhat long and often spinose, to 125 μ m long; capsules erect to suberect, urn ovoid-cylindrical, 1-1.8 mm long, usually flared at mouth when deoperculate; exothecial cells oblong-rectangular, thick-walled; opercula conic-rostrate, 1.2-1.5 mm long; exostome to 750 μ m long, endostome to 820 μ m long. Spores spherical, 12-14 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, to 1.75 mm long, plicate, sparsely to rather densely hairy.

Etymology. Scabrisetum, from the Latin, scabri- (rough, scabrous), and setum (seta); in reference to the ornamentation of the setae.

Distribution (Fig. 9). Widespread from southern Mexico and the Caribbean south to Peru, Bolivia and Brazil. In low wet tropical to mid montane forests, from near sea level to 2600 m; commonly epiphytic on

trunks and branches of shrubs and treelets, less common on rocks, leaf litter and humus, and soil.

Representative specimens examined. MEXICO. Puebla: Cerro de Cuhuatepec, 3000 ft, 23 Nov 1944, Sharp 1360 (US). Oaxaca: 25 miles above Valle Nacional on Hwy 175, in Sierra Juarez, 25 Dec 1972, Sharp et al. 4340, 4358 (F).

GUATEMALA. Alta Verapaz: Chama, 900 ft, 19 Aug 1920, Johnson 339a, 446 (NY, US); 1.5-2 miles south of Cubilguitz, 300-350 m, 1 Mar 1942, Steyermark 44420 (F, NY).

COSTA RICA. La Fuente, 1200 m, 16 Feb 1934, Alfaro 72 (US). Cartago: Vicinity of Pejivalle, ca. 900 m, 7-8 Feb 1926, Standley 47174c (US). Cocos Island: 15 May 1958, Klawe s.n. (US), 3 Sep 1967, Klawe s.n. (US). Heredia: Volcán Barba, arriba de Sacramento, 2600 m, 6 Feb 1979, Griffin et al. D262 (FLAS). Limón: Cano La Palma, ca. 1 mile from Laguna Penitencia, 19-25 Jul 1968, Steere CR-134, CR-179, CR-184 (NY). Puntarenas: Monteverde, 1200-1500 m, Jan-Feb 1959, Palmer L3 (NY).

PANAMA. Chiriqui: Palo Alto, Boquete, 11 Aug 1977, Salazar A. 830 (NY). Cocle: Cope, 11 Aug 1979, Salazar A. 1477 (NY).

CUBA. Oriente: Slopes of La Bayamesa, ca.

Aserradero San Antonio de los Cumbres, 1500-1800 m, 21-24 Jan 1956, Morton 9260 (NY). Santa Clara: Trinidad Mountains, Arroyo Trinitario, Río Negro, 1-12 Mar 1910, Britton 5196a (NY). Santiago de Cuba: La Gran Piedra, 1.5 km SE of peak, 3 Apr 1982, Buck 7581 (HAC, NY).

JAMAICA. Portland: Seamen's Valley, 150-250 m, 14 Feb 1920, Maxon & Killip 45 (BM, F, NY); 7 mi NW of Muirton, trail to John Crow Mts., 350 m, 11 Apr 1981, Crosby 13729 (NY). St. Andrew: Hardwar Gap, 3800 ft, 2 Feb 1980, Griffin & Steere 8 (NY). St. Mary: Castleton Botanical Garden, 19 mi N of Kingston, 24 Apr 1981, Buck 5938 (NY). St. Thomas: Corn Puss Gap, ca. 9 mi N of Bath, 550 m, 9 Apr 1981, Buck 5547 (NY). Trelawny: Vicinity of Windsor Cave, 140 m, 21 Apr 1981, Crosby 13919 (NY).

HAITI. Grand'anse: Massif de la Hotte, 41 km S of Roseaux, 710 m, 13 Nov 1982, Buck 9098 (NY).

DOMINICAN REPUBLIC. El Seibo: 16 km S of Miches on road to El Seibo, 1400 ft, 28 Mar 1981, Buck 5045 (NY). La Vega: Vicinity of Piedra Blanca, 200-500 m, 12 Nov 1947, Allard 16869 (US); on top of Loma Campana, 1036 m, 1 Jan 1948, Allard 18583 (NY). San Cristobal: Mano Matuey, 12 km from Cambito Garabito on road to El Cacao, 1800 ft, 31 Mar 1981, Reese 15654 (NY).

PUERTO RICO. Alto de la Bandera, near Adjuntas, 14

Mar 1913, Britton & Marble 2204 (NY). Sierra de Cayey, Reserva Forestal Carite, 3 Mar 1981, Reese 14672 (NY). Sierra de Luquillo, old Catalina-Yunque trail, 4 Jan 1940, Steere 5914 (F, NY, US). Summit of La Torrecilla Barranquitas, 28 Oct 1937, Steere 4642 (FH). Toro Negro Mts., Dona Juana, 1000 m, 10 Jul 1962, Alain 9432 (NY). Vicinity of Alto de la Piedra, above Villalba, 750-950 m, 19 Feb 1922, Britton & Earle 6122 (NY).

LEEWARD ISLANDS. Guadeloupe: Vallie de St. Louis, 1906, Duss 69 (NY); Morne Gommier, 1906, Duss 74 (NY). Montserrat: Roches, on Poud Mountain, ca. 2000 ft, 13 Feb 1907, Shafer 834 (NY). Saba: Mount Scenery, Jun-Aug 1980, van Slageren 191M (NY, U). St. Kitts: Mt. Misery, Aructel s.n. (BM); s. loc., 1841, Breutel (NY).

WINDWARD ISLANDS. Martinique: L'Alma, N of bridge over River Blanche, ca. 500 m, 18 Apr 1969, Crosby & Crosby 4748 (F, FLAS, NY, US); Bois de Colson, 500 m, 28 Apr 1941, Stehle 3966 (NY). St. Lucia: King s.n. (NY). St. Vincent: Above Perseverance, 1400 ft, 12 Apr 1962, Cooley 8618 (FH); valley of north fork of Cumberland River, 400-600 m, 2-3 May 1947, Morton 5491 (US); upper valley of Richmond River, 330-540 m, 26-27 May 1947, Morton 6193 (NY, US); slope of Mt. St. Andrews, 2000 ft, 12 Feb 1891, Elliott 4 (BM).

COLOMBIA. Andes Bogotenses, 1863-1864, Weir s.n.

(FH, NY). Antioquia: Ca. 2.7 km SO de Santa Rita, 1790 m, 20 Jul 1986, Churchill et al. 14586-b (HUA, NY). Magdalena: Parque Nacional de la Sierra Nevada, Río Buritaca, 1600-1700 m, Jul-Aug 1977, Griffin et al. 50.032 (U), 1500 m, Jul-Aug 1977, Griffin et al. 50.205 (FLAS). Meta: Colonia Penal y Agrícola de Oriente, 1120 m, 9 Aug 1981, van Reenen & Schulte F. 129 (U). Valle: San Antonia, km 17, NO de Cali, 21 Jun 1987, Churchill et al. 15119 (NY).

VENEZUELA. Aragua: Parque Nacional "H. Pittier", Rancho Grande, 1100 m, 31 May 1966, Steyermark et al. 95834 (US). Bolivar: Río Grande, Reserva Forestal, Imataca, 266 m, 5 May 1979, Bermudez V-1213 (FLAS). Falcon: Cerro Santa Ana, ascensión del lado sur desde el pueblo de Santa Ana, 800-850 m, 24 Jan 1966, Steyermark & Braun 94568 (US). Isla Margarita: Cerro Copey, 900 m, 19 Mar 1983, Sugden 1128 (NY). Mérida: Dist. Campo Elias, road to La Azulita and Jaji, 1700 m, 10 Oct 1981, Fransén 1143 (FLAS). Lara: Terepaima, 600-1200 m, 1 Aug 1976, Bermudez & Lobo V-1205 (FLAS). Zulia: San José de los Altos, 1600-1800 m, 7-24 Jul 1975, Griffin 191 (FLAS).

TRINIDAD. Arima Valle, Spring Hill, 1200 ft, 6 Jul 1960, Fleming s.n. (NY); Mount Tocuche, 3-5 Apr 1920, Britton et al. 1411 (NY); Guayaguayare road, Ortoire

River, 25 Mar 1921, Britton 2560 (FH).

TOBAGO. S. loc., Broadway 2382 (NY).

GUYANA. Bartica, 18 Jan 1924, Linder 4 (FH, NY).

Upper Mazaruni: Jawalla, at confluence of Kukui and Mazaruni Rivers, 500 m, 6-7 Feb 1985, Gradstein 4867 (U). Essequibo River, Moraballi Creek, near Bartica, ca. 0 m, 1929, Richards 104 (BM, NY).

SURINAM. Marowijne River, trail to Nassau Mountains, 28 Feb 1949, Lanjouw & Lindeman 2398 (U); Mountains in Southern borderland, 12 Apr 1952, Geijskes s.n. (U). Nickerie: Area of Kabalebo Dam project, line E from road near km 114, 50 m, 13 Nov 1981, Florschutz-de Waard & Zielman 5510 (FLAS).

FRENCH GUIANA. Montagne de Kaw, Camp Caiman, 250 m, 13 Jun 1979, Cremers 5790 (U); Mont Galbao, 650 m, 13 Dec 1976, Cremers 4710 (FLAS); 40 km SE of Cayenne, 200-300 m, Mar 1985, Gradstein 5907 (U).

ECUADOR. Esmeraldas: East of San Mateo, "Mt. Zapallo", ca. 500 m, 17 Sep 1982, Steere & Balslev 25616 (NY). Napo: Hotel Jaguar, on Río Napo, ca. 50 km below Puerto Misahualli, ca. 400 m, 11 Jan 1981, Steere E-114 (NY); 8 km SE of Tena, 1500 ft, 22 Sep 1960, Grubb et al. 2955 (BM). Pichincha: Nanegal-Nanegalito road, ca. 3 km S of Nanegalito, ca. 1650 m, 7 Oct 1984, Steere 27536 (NY). Pichincha/Napo: 1.6 km NE of

Borija, Cerro Antisana, 5600 ft, 14 Aug 1960, Grubb et al. 2847a (BM). Pastaza: Ca. 5 km SE of Puyo on road to Macas, ca. 1000 m, 23 Jul 1985, Churchill & Sastre 13668 (NY).

PERU. Loreto: Soledad, on Rio Itaya, ca. 110 m, 20-22 Sep 1929, Killip & Smith 29788 (NY).

BRAZIL. Amapá: Município de Oiapoque, 109 km SSE of Oiapoque on road between Oiapoque and Calcoene, 5 Dec 1984, Mori et al. 17208 (NY). Amazonas: Along BR 307 from São Gabriel da Cachoeira to Cucui, just N of Igarapé Ia-Mirim, 17 Jul 1979, Buck 2587 (INPA, NY); along road to Balbina hydroelectric dam project from Manaus-Caracarai Road (BR-174), 8 Aug 1979, Buck 2695A (INPA, NY); from Igarapé Arabu of the Rio Curicuriari to summit of Cerro Curicuriari, ca. 450 at summit, 9-12 Jul 1979, Buck 2487 (INPA, NY). Roraima: Boca da Mata, 216 km N of Boa Vista, ca. 2 km N of Rio Surumu, 30 Nov 1977, Buck et al. 2006 (FLAS, INPA, NY).

The concept presented here of Lepidopilum scabrisetum is modified and expanded from previous treatments of the species. I view the species as fairly polymorphic after examining considerable material. Two major points of variation concern the deciduous branch and leaf forms previously known as

L. stolonaceum C. Muell. on the one hand, and L. latifolium (C. Muell.) Mitt. on the other.

Lepidopilum stolonaceum typically is a somewhat smaller form with the "key character" of attenuate branches that produce deciduous leaves (Fig. 3B). This form is most distinctive and common in the Caribbean region, but occurs throughout the range of L. scabrisetum. I consider this as only a form that is commonly associated with marginal habitats, i.e., substrates of leaf litter, decaying logs, etc. Gametophytically, except for the deciduous leaves (and branches), the secondary stem leaves are almost identical to "typical" L. scabrisetum in variation throughout Latin America. Within the neotropics, pleurocarpous mosses commonly produce vegetative means of reproduction, especially in the premontane to high montane forests, at least in Colombia. Given the frequency that this phenomenon occurs within Lepidopilum and among other pleurocarps, it seems questionable whether taxonomic rank should be assigned to such forms.

Lepidopilum latifolium is a more robust form that is often associated with very mesic or semi-aquatic habitats and often found on rock or occasionally on soil. The larger leaves are often oblong-obovate and

short- to somewhat long-acuminate, but more typical leaves are found usually on distal secondary stems and branches. This form is readily bridged by intermediates, including L. intermedium (C. Muell.) Mitt., a most appropriate name. It is obvious that previous students of Lepidopilum had difficulty as evident in the inconsistent naming of collections between the transition from L. scabrisetum s.s., to L. intermedium and to L. latifolium.

In South America, particularly the Andes, there appear to be further modifications in general shape and marginal serration. However, these forms, and those mentioned appear to maintain the general falcate-sigmoid leaf shape.

Lepidopilum pallidonitens (C. Muell.) Par. may be confused with the "latifolium" forms, but has uniform leaves that are broadly oblong-obovate, never with smaller falcate-sigmoid leaves, with a short apiculate apex, never long acuminate.

Lepidopilum daltonioides Schimp. ex Besch. had been previously considered a synonym of L. robustum Mitt. (= L. longifolium Hampe) by Crum & Steere (1957). However the type collection proved to be a synonym of L. scabrisetum.

5. *Lepidopilum pallidonitens* (C. Mueller) Paris, Ind.

Bryol. Suppl. 223. 1900. Hookeria pallidonitens

C. Mueller, Nuovo Giorn. Bot. Ital. n. ser. 4:

132. 1897. Type. Bolivia. Cochabamba, prope

Choquecamata, Jun 1889, Germain s.n. (isotype,

NY).

Fig. 23-24.

Lepidopilum quadrifarum Herzog, Beih. Bot.

Centralbl. 61B: 589, f. 18. 1942, syn. nov.

Type. Costa Rica. La Palma, 1500 m, 30 Apr

1928, Valerio 45 (holotype, JE).

Lepidopilum attenuatum Bartram, Rev. Bryol.

Lichénol. 33: 11. 1964, syn. nov. Type.

Ecuador. 8 km SE of Tena, Cerro Antisana, ca.

1500 ft, 27 Sep 1960, Grubb 2939 (isotype, US).

Plants medium sized to rather large, usually glossy green or yellowish-green, saxicolous. Primary stems short to rather long creeping; secondary stems spreading to ascending, to 9 cm long, few to several branched, branches occasionally attenuate, and with deciduous leaves; hyalodermis well differentiated, outer cortical cells in 2-3 rows, small, thick-walled, inner cortical cells numerous, large, hyaline. Leaves

strongly complanate, crispate or not; lateral leaves erect-spreading to spreading, asymmetric, broadly oblong to oblong-obovate, 3.5-4.0 mm long, 1.0-1.3 mm wide, subfalcate, obtuse-rounded, apiculate; margins plane, elimbate to limbate with 2-4 rows of linear cells, serrulate to serrate in distal $1/4-1/3$; costae closed to set apart, diverging, $1/4-1/3$ lamina length, rather weak; median cells long fusiform, thin-walled, basal cells oblong-fusiform, weakly porose; median leaves appressed to erect, + symmetric, shorter, broadly short oblong or obovate. Propagula in leaf axils, short cylindrical, to 0.3 mm long. Dioicous? Perichaetial leaves ovate-lanceolate or -subulate, 1.2-1.7 mm long, acuminate, serrulate. Setae elongate, 6.0-9.2 mm long, yellowish-red, papillose and spinose throughout, spines to 100 μ m long; capsules suberect, urn ovoid-cylindrical, to 1.6 mm long; opercula conic rostrate. Calyptrae mitrate-campanulate, 2.2-2.4 mm long, hairy.

Etymology. *Pallidonitens*, from the Latin, *pallidus* (pale) and *nitens* (shining); in reference to the color of the leaves.

Distribution. From Costa Rica south to Bolivia; at

elevations from 500-1500 m. In wet lowland to mid montane forests; associated with aquatic habitats.

Specimen citation. ECUADOR. Tungurahua: Along trail from Rio Pastaza up to village Río Verde, 1507 m, 16 Jul 1975, Fantz B359 (NY).

Given the too few collections it is difficult to provide a thorough characterization of this species. It appears closely related to the latifolium form of L. scabrisetum with the broadly oblong leaves, however the leaves are uniform in shape in L. pallidonitens whereas in the latifolium form they vary from obovate to oblong and usually falcate-sigmoid.

6. *Lepidopilum apophysatum* Hampe in Bescherelle, Mém.

Soc. Sci. Nat. Cherbourg 16: 229. 1872. Type.

Mexico. Cordova (Cordoba), Mar 1866, Bourgeau 2137 (isotype, NY).

Fig. 25.

Plants rather robust, glossy olive-green, ramicolous or corticulous. Primary stems short creeping, rhizoids inconspicuous; secondary stems ascending, usually perpendicular to substrate, to 5.5 cm long, few-

branched; in cross-section hyalodermis well differentiated, outer cortical cells small, in 3-4 rows, thick-walled, rusty-red, inner cortical cells larger, numerous, hyaline. Leaves crispate, lateral leaves erect-spreading to spreading, asymmetric, obovate to oblong-obovate, 3.0-4.2 mm long, 0.9-1.2 mm wide, abruptly short acuminate; margins plane, elimbate, serrate, rather sharply so, in distal $1/3-1/2$; costae closed to separate at base, diverging, $(1/3)1/2$ lamina length; median cells rhomboidal to hexagonal, 45-70 μm long, 20-26 μm wide, somewhat thick-walled, basal cells oblong-fusiform or -rectangular; median leaves symmetric, ovate to obovate, acuminate, 1.4-1.8 mm long. Propagula not observed. Autoicous. Perigonial leaves broadly ovate to oblong-lanceolate, to 1.5 mm long, acuminate, margins entire to serrulate, costae absent. Perichaetial leaves lanceolate, to 1.3 mm long, narrowly acuminate, costae absent. Setae elongate, (4.5)5.0-6.5 mm long, reddish-orange, papillose throughout except at base, papillae low; capsules erect to suberect, urn ovoid-cylindrical, 1.4-1.8 mm long; exothecial cells quadrate to short rectangular, somewhat collenchymatous; stomata several at base, swollen; opercula rostrate, ca. 1.5 mm long. Spores 15-17 μm in diameter, lightly papillose.

Calyptrae mitrate-campanulate, ca. 2.5 mm long, plicate, sparsely hairy.

Etymology. Apophysatum, from the Greek, apophysis (offshoot, prominense); in reference to the swelling about the stomata region at the base of the capsule.

Distribution (Fig. 9). East-central Mexico, along the eastern slopes of the Sierra Madre Oriental, at elevations to 2150 m. In montane forests, on tree or shrub branches and trunks.

Specimens examined. MEXICO. Chiapas: Along road from Pueblo Nuevo Solistahuacan to Rayon via Rincon Chomula, 2150 m, 30 Dec 1959, Sharp M5982 (F). San Luis Potosi: Tamasopo Canon, 9 Jun 1891, Pringle 763 (F, H-BR, L, NY, US). Veracruz: Orizaba, 1870, Hahn s.n. (L, NY).

The robust habit of the plant and the somewhat long obovate leaves are distinctive features not to be confused with any other species in Mexico, except possibly L. scabristeum (Schwaegr.) Steere which typically has falcate-sigmoid leaves.

7. *Lepidopilum chloroneuron* (Taylor) Hampe & Lorentz,

Bot. Zeit. 26: 816. 1868. Hookeria chloroneura
Taylor, London J. Bot. 5: 61. 1846. Type.
Ecuador. Pichincha, Jameson s.n. (holotype, FH;
isotypes, BM, NY). Fig. 26.

Plants small, green to yellowish-green, ramicolous. Primary stems short-creeping; secondary stems erect, slender and somewhat delicate, several-branched; in cross-section hyalodermis well developed, outer cortical cells in 3-4 rows, small, thick-walled, rusty-red, inner cortical cells numerous, larger, somewhat thick-walled, hyaline. Leaves crowded to commonly distant with stem often exposed, flexuose; lateral leaves wide-spreading, from a clasping base, asymmetric, short ovate-lanceolate, gradually long acuminate to oblong, abruptly-short acuminate, 2.0-2.6 mm long, 0.5-0.8 mm wide; margins recurved on one or both sides below, elimbate to weakly limbate on oblong-lanceolate leaves, serrate in distal 1/4; costae gradually diverging, 1/3-1/2 lamina length; median cells fusiform-rhomboidal, 44-75 μ m long, 11-15 μ m wide; median leaves somewhat asymmetric, short ovate-to oblong-lanceolate, 1.4-1.7 mm long, 0.5-0.7 mm wide, acuminate. Apparently dioicous. Perigonia not observed. Perichaetial leaves narrowly ovate-

lanceolate or subulate, 1.4-1.8 mm long, irregularly serrate. Setae elongate, 7.0-9.0 mm long, dark rusty-red, smooth to lightly papillose below, distal 1/2 short spinose, spines to 70 μ m long; capsules erect to suberect, occasionally appearing pendent, urn short ovoid-cylindrical, (6)0.8-1.2 mm long; exothecial cells short rectangular, not strongly thick-walled; opercula conic-rostrate, ca. 1 mm long; exostome to 520 μ m long or more, endostome to 710 μ m long. Spores 16-18 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, 2.0-2.2 mm long, hairs few and scattered, occasionally with a few aborted archegonia, plicate, laciniate at base.

Etymology. Chloroneuron, from the Latin, chloro- (green), and -neuron (nerve); in reference to the green costa.

Distribution (Fig. 10). Presently known only from Ecuador. Probably from low to mid montane forests, to about 2000 m; on shrub or treelet branches.

Specimens examined. ECUADOR. Chimborazo: Chimborazo, Spruce 739 (BM, F, FH, G, NY). Morona Santiago: Lucmas, Spruce s.n. (NY).

This species appears close to Lepidopilum cuspidans Mitt. and L. brevipes Mitt., but differs by the seta that is over twice the length as found in the two above mentioned species, and by the calyptrae that are densely hairy and plicate. The clasping lateral leaves are a distinctive feature of L. chloroneuron.

8. *Lepidopilum cuspidans* Mitten, J. Linn. Soc., Bot.

12: 378. 1869. Type. Ecuador. Canelos, Spruce 757 (lectotype, NY; isoelectotype, NY).

Plants rather small, greenish-yellow to golden-yellow, glossy, ramicolous. Primary stems short creeping; secondary stems ascending to suberect, few branched, often attenuate; in cross-section outer cortical cells in 2-3 rows, cells small, thick-walled, rusty-red, inner cortical cells several, thin-walled, hyaline. Leaves crowded, smooth to somewhat crispate; lateral leaves erect-spreading to wide-spreading, asymmetric, short ovate-lanceolate to somewhat oblong-lanceolate, 1.7-2.2 mm long, 0.5-0.8 mm wide, often long acuminate; margins plane to occasionally recurved at base, serrate, often sharply so, 1/3-1/2 lamina length; costae short, diverging, 1/4-1/3 lamina length,

often rather weak; median cells linear-fusiform, 88-130 um long, 6-10 um wide, basal cells oblong-rectangular; median leaves erect to appressed, symmetric, ovate-lanceolate to oblong-lanceolate, 1.5-2.0 mm long, 0.5-0.7 mm wide, acuminate. Dioicous. Perichaetial leaves lanceolate-subulate, 0.7-1.2 mm long. Setae short, erect to curved, (1.5)2.5-3.5 mm long, spinose, often densely so; capsules erect to suberect, ovoid-short cylindrial, 0.7-1.2 mm long; exothecial cells oblong-rectangular, very thick-walled; opercula conic-short rostrate, ca. 0.8 mm long; exostome to 445 um long, endostome to 530 um long. Spores 13-16 um in diameter, lightly papillose. Calyptrae mitrate-short campanulate, 0.7-1.0 mm long, plicate, with several to many hairs, laciniate at base.

Etymology. Cuspidans, from the Latin, *cuspis* (point); in likely reference to the leaf apices.

Distribution. Colombia and Ecuador. In mid montane forests, on branches of shrubs and treelets.

Specimen examined. COLOMBIA. Cundinamarca: Sibate to El Penon, 29 Oct 1917, Rusby & Pennell s.n. (NY).

Lepidopilum cuspidans, like L. brevipes Mitt. is a rather small species but differs basically by the differences in the calyptra and seta; see discussion under L. brevipes. Given the variation presently accepted in L. brevipes, particularly with the gametophyte, the differences between the two species is not particularly impressive. However at this time I prefer to retain L. cuspidans.

9. Lepidopilum brevipes Mitten, J. Linn. Soc., Bot.

12: 376. 1869. Type. Peru. Andes Peruviana, Tabalosos, Spruce s.n. (holotype, NY). Fig. 27.

Lepidopilum acutum Mitten, J. Linn. Soc., Bot. 12:

379. 1869, syn. nov. Type. Ecuador. Canelos, Spruce s.n. (holotype, NY).

Lepidopilum anceps Mitten, J. Linn. Soc., Bot. 12:

378. 1869, syn. nov. Type. Ecuador. Canelos, Spruce s.n. (lectotype, NY). Syntype. Ecuador. Chimborazo, Spruce s.n. (NY).

Lepidopilum antillarum Mitten, J. Linn. Soc., Bot.

12: 377. 1869, syn. nov. Type. St. Vincent. Guilding s.n. (lectotype, NY). Syntypes: St. Vincent. Parker s.n. (NY); Barbados, Parker

s.n. (NY).

Lepidopilum calvum Mitten, J. Linn. Soc., Bot. 12:

377. 1869, syn. nov. Type. Peru. In monte
Guayrapurina, Spruce s.n. (holotype, NY).

Lepidopilum gracile Mitten, J. Linn. Soc., Bot. 12:

377. 1869, syn. nov. Type. Ecuador. Andes
Quitenses, ad pedem montis Abitagua, Spruce 778
(holotype, NY; isotype, H-BR).

Lepidopilum nudum Mitten, J. Linn. Soc., Bot. 12:

376. 1869, syn. nov. Type. Ecuador. Andes
Quitenses, Chimborazo, Spruce s.n. (holotype,
NY).

Lepidopilum subfuscum Mitten, J. Linn. Soc., Bot.

12: 376. 1869, syn. nov. Type. Brazil.
Moretes near Paranagua, 100 ped, Weir 77
(lectotype, NY; isoelectotype, H-BR).

Lepidopilum decaisnei Beschereille, Mém. Soc. Sci.

Nat. Cherbourg 16: 228. 1872. Type. Mexico.
Cordoba, Salle s.n. (isotypes, L, NY).

Lepidopilum nanothecium C. Mueller, Hedwigia 39:

270. 1900, syn. nov. Type. Brazil. Santa
Catarina: Brazil. Santa Catharina: Blumenau,
R. Bugarbach, May 1888, Ule 306 (lectotype, H-
BR). Syntype, Brazil. Santa Catarina:
Blumenau, R. Riberão, 1888, Ule 305 (H-BR).

Lectotype choosen on the basis of the abundance of material with sporophytes.

Lepidopilum laxirete C. Mueller, Hedwigia 39: 271.

1900, syn. nov. Type. Brazil. Santa

Catarina: Nova Venezia, Jul 1891, Ule 1172

(lectotype, H-BR). Syntype. Brazil. Santa

Catarina: Tubarão, Sep 1889, Ule 773 (NY).

Lepidopilum buchtienii Brotherus in Herzog,

Biblioth. Bot. 87: 172. 1916, nom. nud. Based

on: Bolivia. Autahuacana, Espirito Santo, 750

m, Jun 1909, Buchtien (B, H-BR, NY).

Lepidopilum subgracile Brotherus, Rev. Bryol. 47:

38. 1920, syn. nov. Type. Ecuador. Azuay:

Gualaquiza, in silva, prope San José, 1300 m,

Jul 1909, Allioni s.n. (holotype, H-BR).

Plants small, rather delicate and slender, glossy green to yellowish-green or golden-yellow, ramicolous, corticolous or saxicolous. Primary stems short- to long-creeping; secondary stems ascending or erect, rather rigidly so, to 10 cm long, several branched; hyalodermis well developed, outer cortical cells small, thick-walled, in 2-3 rows, inner cortical cells large, hyaline, several. Leaves crowded to more commonly somewhat distant with stem often exposed, crispate or

flexuose; lateral leaves erect-spreading to spreading and often recurved, asymmetric, short to long ovate-lanceolate, or short to long oblong-lanceolate, (1.4)1.9-2.7(3.0) mm long, (0.4)0.7-1.0 mm wide, short to more often long-acuminate; margins plane to recurved below, elimbate, serrate in distal 1/4-1/3; costae gradually diverging, 1/4-1/2 lamina length, weak to rather strong; median cells narrowly to broadly fusiform, (78)88-133 μ m long, 8-17 μ m wide, mostly thin-walled, basal cells oblong-rectangular or oblong-fusiform, somewhat lax; median leaves erect to appressed, ovate- to oblong-lanceolate, 1.4-2.3 mm long, 0.5-0.9 mm wide, rather abruptly long acuminate, margins serrate in distal 1/4, costae ca. 1/3 lamina length. Autoicous and possibly dioicous. Perigonial leaves short to somewhat long broadly oblong-lanceolate, 0.4-0.6 mm long, concave, broadly short-acuminate. Perichaetial leaves ovate-lanceolate, 0.7-0.9 mm long, acuminate. Setae short, 1.7-2.2(3) mm long, straight to flexuous, rusty-red or yellowish-orange, papillose throughout, papillae short to slightly elongate; capsules erect to suberect, urn ovoid to short-cylindrical, 0.8-1.2 mm long; exothecial cells short to rather long oblong-rectangular, thick-walled; opercula conic-short rostrate, 0.5-0.8 mm long;

exostome to 440 μ m long, endostome to 480 μ m long.
Spores ca. 14 μ m in diameter, lightly papillose,
Calyptrae short mitrate-campanulate, 0.8-1.1 mm long,
naked or occasionally with a few scattered hairs, weakly
plicate.

Etymology. *Brevipes*, from the Latin, *brevi-*
(short), *-pes* (foot); in reference to the short seta.

Distribution (Fig. 10). From Mexico and the Lesser
Antilles south to Colombia, and on the eastern range of
the Andes and upper Amazon from Ecuador south to Peru,
Bolivia, and Brazil, with an apparent disjunction to
southeast Brazil. In tropical to montane forests, from
100-2400 m; most commonly found on tree branches and
trunks, occasionally on rocks.

Specimen citations. MEXICO. Veracruz: Xico, 1908,
Barnes & Land s.n. (NY); Cañada de Texolo, 3 km SW de
Xico, 1250 m, 14 Aug 1980, Juárez G. & Hernández L.
1561 (MO).

GUATEMALA. Quezaltenango: Along Quebrada San
Geronimo, Finca Pirineos, lower S-facing slopes of
Volcán Santa María, between Santa Maria de Jesús and
Calahuache, 1300-2000 m, 1-2 Jan 1940, Steyermark

33441a (F). Suchitepéquez: Near Pueblo Nuevo, ca. 750 m, 1 Mar 1939, Standley 66872a, 66914 (F).

COSTA RICA. Alajuela: Los Angeles, San Ramón, 20 Nov 1923, Brenes 3950 (NY); 21.8 km de San Ramón, orilla del río La Balsa, 1100-1160 m, 9 Jan 1980, Morales et al. 1063 (FLAS). Limón: La Asunción, Río Banano, 5 Apr 1935, Gutierrez 212a (F, NY). Puntarenas: Monteverde, 10 Jun 1966, James 18 (US); SE of Wilfords Tract, 8 Jan 1972, James s.n. (US). San José: Alto de la Palma, via San José-La Hondura, 1500 m, 3 Feb 1979, Griffin & Morales A47 (FLAS).

PANAMA. Goyona, Seeman s.n. (NY). Canal Zone: Cana, Darien, 3000 ft, 17 Apr-8 Jun 1908, Williams 1057 (F, NY).

COLOMBIA. Andes Bogotenses, s. loc., Weir s.n. (NY). Antioquia: Municipio de Campamento, 6.6-14.6 km de Campamento en carretera a Las Brisas, 1430-1830 m, 2 Aug 1986, Churchill et al. 15026, 15034, 15036, 15038, 15048 (HUA, NY); Municipio de Medellín: Ca. 25 km NO de Medellín carretera a Boqueron, 2400-2600 m, 28 Jun 1986, Churchill et al. 13976 (NY); Municipio de Salgar, ca. 12 km O de Salgar, Hacienda la Regada, Quebrada Liboriana, 2100 m, 16 Jan 1980, Churchill et al. 15813, 15825 (HUA, NY).

ECUADOR. Napo: Ca. 6.7 km S of Tena on road to

Puyo, 600 m, 22 Jul 1985, Churchill & Sastre 13654 (NY).

PERU. San Martín: Rioja, between Moyobamba & Chachapoyas km 409, 1100 m, 29 Aug 1982, Frahm et al. 100 (B, NY).

BRAZIL. Minas Gerais: Fazenda Bom Destino, 21 Mar 1924, Bandeira 292 (H-BR, NY). Rondonia: 3 km E of Main Mibrasa Mining Camp, Alto Condeias, 200 m, 16 May 1982, Fife et al. 4169 (INPA, NY). Santa Catarina: São Jose, Serra da Boa Vista, 1000 m, 7 Sep 1960, Reitz & Klein 9890 (US); Blumenau, Ule 74 (H-BR), 7 Oct 1876, Schenek 4894 (H-BR). São Paulo: Rio Mambu, Conceição de Itanhaem, 100 m, 30 Jun 1901, Schiffner 539 (H-BR); "Brasso grande", Itapecirica, 1000 m, 16 Jun 1901, Schiffner 1255 (H-BR).

Lepidopilum brevipes is rather variable in leaf shape from ovate-lanceolate to oblong-lanceolate, and laminal cells from narrowly to broadly fusiform. This variation can often be found on an individual or between individual collections. Much of this variation accounts for several names given to this species. The calyptra is almost always lacking ornamentation, but occasionally a few multicellular hairs can be observed as well as aborted archegonia. The curvature of the

seta, used by Mitten (1869), I believe is of little value. I have observed populations in Colombia where the plants occur as epiphytes on trunks and branches of shrubs or treelets in which the gametophyte is perpendicular to the substrate and the sporophytes are directed downward at a slight angle, with the seta curved or straight. Likewise the sexuality, autoicous vs. dioicous, may be found in this species though typically plants are autoicous.

This species appears most closely related to L. cuspidans Mitt. Both species are rather small with a similar habit and short seta, but that species exhibits a more or less short spinose seta and a calyptra that is plicate, distinctly hairy and rather deeply laciniate at the base. Lepidopilum chloroneuron (Tayl.) Hampe is likewise similar and possibly closely related, it differs from both by the longer seta (7-9 mm long). Some sterile forms of L. brevipes may be confused with L. scabrisetum (Schwaegr.) Steere, but that species generally has longer leaves and leaf apices short acuminate; when fertile L. scabrisetum exhibits a longer seta (4-9 mm) and a calyptra that is hairy.

10. *Lepidopilum verrucipes* Cardot in Renauld & Cardot
in Grandidier, Hist. Phys. Madagascar 39: 416.
1915. Type. Madagascar. Maroantsetra, 1902,
Mathieu s.n. (holotype, PC). Fig. 28.

Plants small, glossy green, ramicolous. Primary stems creeping; secondary stems ascending, to 14 mm long. Leaves slightly crispate, complanate; lateral leaves spreading, oblong to oblong-short lanceolate, slightly falcate, 1.4-1.6 mm long, 0.3-0.4 mm wide, short and abruptly acuminate; margins somewhat recurved below, serrate in distal 1/3; costae diverging, 1/3-1/2 lamina length; median cells broadly fusiform to hexagonal, 70-105 μ m long, 11-20 μ m wide, somewhat lax below, distally somewhat thick-walled, basal cells oblong-fusiform; median leaves erect, oblong-lanceolate, 0.7-1.0 mm long, gradually acuminate. Autoicous? Perichaetial leaves ovate-acuminate, 0.5-0.6 mm long. Setae short, 3.2 mm long, rusty-red, short-spinose distally, lower half roughened or papillose; capsule erect; urn ovoid-short cylindrical, 0.8 mm long.

Etymology. *Verrucipes*, from the Latin, *verruca* (=

wart or swelling), pes (=foot); in reference to the rough seta.

Distribution (Fig. 8). Known only from the type in Madagascar. Cardot's protologue states that the plants occur on branches of shrubs.

The only collection is the type, and is only represented by a secondary stem with a single sporophyte. Thus little is known about the general morphology of this species. The plant does appear to differ from the other species of Lepidopilum occurring in Madagascar by the smaller size of the gametophyte and sporophyte, and on leaf shape.

Lepidopilum verrucipes exhibits the typical exostome morphology found in the genus. Cardot further stated that the calyptra is naked or nearly so, and with a laciniate base.

11. Lepidopilum grevilleanum Mitten, J. Linn. Soc., Bot. 12: 381. 1869. Hookeria grevilleana Taylor, London J. Bot. 5: 60. 1846, hom. illeg.
Lepidopilum grevillei Kindberg, Enum. Bryin. Exot. 22. 1888, nom. illeg. Type. Ecuador.

Esmeraldos, 2000 ft, 29 Nov 1829, Greville s.n.

(holotype, E; isotypes, BM, NY).

Fig. 29.

Lepidopilum pulcherrimum Steere, Brittonia 34: 438.

1982, syn. nov. Type. Ecuador, Los Rios, Hacienda

Clementina, virgin forest, Samama, 750 m, 24 Mar

1947, Harling 2157 (holotype, NY).

Plants glossy green to rufous-golden, robust, forming mats. Primary stems creeping; secondary stems spreading, 4-5 cm long, branches few; in cross-section with hyalodermis. Secondary stem lateral leaves crowded, complanate, strongly undulate, erect-spreading to spreading wet or dry, asymmetric, narrowly lanceolate to oblong-lanceolate, curved to somewhat sigmoid, 4.5-5(5.5) mm long, 1.2-1.5 mm wide, gradually acuminate; margins plane, elimbate, serrate in distal 1/3-1/2; costae ca. 1/2 lamina length, closed or set apart, gradually diverging; median cells linear to linear-fusiform, 110-135 μ m long, 25-29 μ m wide, lower and basal cells rectangular to broadly fusiform, porose; dorsal leaves oblong-lanceolate, 3.5-4 mm long, acuminate, serrate in distal 1/3, costae ca. 1/2 lamina length, separate or closed at base, gradually diverging. Gemmae present in leaf axils, cylindrical,

hyaline, ca. 135 μ m long, observed on damaged distal branches. Dioicous. Perichaetial leaves ovate to short-lanceolate, short to long acuminate, costa absent to weakly double. Setae elongate, 22-28 mm long, reddish-orange, with low and spinose (170 μ m long) papillae; capsules erect, ovoid-cylindrical, 1.5-2.2 mm long; exothecial cells irregularly short rectangular; stomata several at base, sunken; annulus indistinct, 2-3 cells high, mostly short rectangular (oblate); operculum conic-rostrate, 1.2-1.5 mm long. Calyptrae mitrate-campanulate, ca. 4 mm long, plicate, pilose, lacerate at base.

Etymology. Grevilleanum, named in honor of Robert K. Greville (1794-1866).

Distribution (Fig. 11). Presently known only from the type localities along the coastal regions of Ecuador, at elevations from 750-925 m. In humid premontane to possibly low montane forests, on branches and trunks of shrubs or treelets.

Mitten (1869) included Mueller's L. affine, named in 1848, as a synonym of L. grevilleanum (Tayl.) Mitt., however as noted by Florschütz-de Waard (1986) these

are two very different plants! In aspect, the leaves of L. affine C. Muell. resemble a small version of L. grevilleanum, particularly the somewhat undulate forms with acuminate apices that characterizes part of the variation in that species. The lateral leaves in L. affine are generally 1.8-2.5 mm long, 0.5-1.0 mm wide, and in L. grevilleanum they are 4.5-5.5 mm long, 1.2-1.5 mm wide. Possibly because of the confusion surrounding the status of L. grevilleanum, Steere (1982) described L. pulcherrimum as new. Without a doubt this taxon is, as noted by Steere, a handsome and beautiful moss, without equal among Lepidopilum species. This species should be expected in the premontane coastal forests in southern Colombia.

12. Lepidopilum affine C. Mueller, Linnaea 21: 192.

1848. Type. Suriname, ad trunco arborum prope Paramaribo, Juno 1844, Kegel 741 (isotype, H-BR).

Figs. 30-31.

Lepidopilum pacimonense Spruce, Cat. Musc. Amaz.

And. 11. 1867, nom. nud. Based on: Brazil. Rio Negro, Spruce 746 (NY).

Lepidopilum undulatum Hampe & Lorentz, Bot. Zeit.

- 26: 815. 1868, hom. illeg. Type. Ecuador.
Timbara, 3500-4000', Krause s.n. (syntype, NY).
- Lepidopilum pumilum Mitten, J. Linn. Soc., Bot. 12:
381. 1869. Type. Peru. Huallaga River, Spruce
780 (lectotype, NY; isolectotype, BM).
- Lepidopilum mittenii C. Mueller, Linnaea 38: 607.
1874, syn. nov. Type. Ecuador. Pastasa, Spruce
750 (holotype, NY; isotype, BM).
- Lepidopilum obtusulum C. Mueller, Linnaea 38: 606.
1874, syn. nov. Type. Brazil. São Gabriel,
Spruce 748 (holotype, NY; isotype, BM).
- Lepidopilum subobtusulum Brotherus, Hedwigia 45:
281. 1906, syn. nov. Lepidopilum spathulatum
Brotherus, Hedwigia 45: 281. 1906, nom. nud. in
syn. Type. Brazil. Acre: Rio Juruá, Juruá Miry,
Ule 298 (holotype, H-BR; isotypes, BM).
- Lepidopilum ambiguum Brotherus, Hedwigia 45: 282.
1906, syn. nov. Type. Peru. Rio Huallaga, Cerro
de Escalero, 1200 m, an Baumstammen, 1903, Ule
2387 (lectotype, H-BR).
- Lepidopilum allionii Brotherus, Rev. Bryol. 47: 39.
1920, syn. nov. Type. Ecuador. Prov. Morona
Santiago: Gualaquiza, ad ramos arborum
secus rivum Tres Cruces frequenter, 900-1000 m, 17
Oct 1910, Allioni 625 (lectotype, H-BR).

Syntypes. Ecuador. Morona Santiago: Gualaquiza, in ramusculis arborum silvae, Jul 1909, Allioni 8285 (H-BR); ad truncos ramulosque arborum in silva Guayusa, 20 Aug 1909, Allioni 8330 (H-BR); ad ramulos in silva montis Sapotilla, 800 m, 19 Jan 1910, Allioni 8482 (H-BR); prope fl. Rio Salado, 800 m, Jan 1909, Allioni 8284 (H-BR); ad truncos ramosque secus rivum S. Francisco, 950 m, 18 Sep 1910, Allioni 577 (H-BR). The lectotype was chosen on the basis of abundant material with sporophytes.

Lepidopilum antisanense Bartram, Rev. Bryol.

Lichénol. 33: 11. 1964, syn. nov. Ecuador.

Cerro Antisana, 8 km SE of Tena, ca. 1500 ft, 25 Sep 1960, Grubb 2925 (isotype, US).

Plants mostly medium sized, glossy pale to dark green to yellowish-green, corticolous. Primary stems creeping, leaves mostly eroded. Secondary stems commonly spreading, often perpendicular to substrate, occasionally ascending, to 2.5 cm or more long, few- to several-branched; leaves complanate, crowded, occasionally crisped when dry, smooth to undulate, apex often pinched, lateral leaves erect-spreading to spreading, ovate-oblong to oblong-lingulate, (1.4)1.8-

2.5(3) mm long, 0.5-1.0 mm wide, obtuse (rarely truncate), apiculate or shortly and sometimes sharply acute, to short acuminate; margins plane, elimbate, serrate in distal $1/3-1/2(2/3)$, serration often sharp and composed of two adjoining cells; costae weak to strong, mostly set apart, $1/3-1/2$ lamina length, gradually diverging; median cells linear to long-fusiform, 80-155 μm long, 12-14 μm wide, apical cells rhomboidal, marginal cells narrow but not notably differentiated, basal cells long rectangular or hexagonal; median leaves ovate to ovate-oblong or -lingulate, 1.9-2.2 mm long, 0.8-1.0 mm wide, acute, costa weak, separate, $1/4-1/3$ lamina length, diverging. Dioicous. Perichaetial leaves with ovate base, abruptly narrowly lanceolate above, ca. 1.25 mm long, often with teeth perpendicular to recurved, costa absent. Setae long, often rather slender, 6-12 mm long, reddish-orange, papillose throughout, papillae both low-projecting and elongate and perpendicular, 60-115 μm long, blunt; capsules erect, urn ovoid, 1-1.4 mm long; exothecial cells oblong to rectangular, thick-walled; operculum conic-rostrate, ca. 1.2-1.4 mm long; exostome to 1.15 mm long, endostome to 1.30 mm long. Spores ca. 20 μm in diameter, lightly papillose. Calyptrae mitrate-campanulate, 1.8-3 mm long, plicate,

with few hairs, often deeply laciniate at base.

Etymology. Affine from the Latin, affinis, referring to relationship; in reference to the similiarity between L. affinis and L. scabrisetum (Schwaegr.) Steere suggested by Mueller.

Distribution (Fig. 11). From Costa Rica east to Trinidad and Surinam, and south along the Cordillera and upper Amazonia in Colombia, Ecuador, Peru and Brazil, including the Rio Negro. On lianas and branches and trunks of trees, at elevations from near sea level to 1100 m in humid lowland to premontane forests.

Representative specimens examined. COSTA RICA.
Puntarenas: Penn. de Osa, ca. 7 km NW of Rincon, 12 Aug 1968, Koch 5050 (NY, US).

COLOMBIA. Meta: La Macarena, Cano Guepyita, 27 Dec 1950, Schultes & Cabrera 11165 (FH, NY).

VENEZUELA. Trujillo: 15 km al sur de La Puerta, in mediaciones del Salto La Nevera, 1800 m, 3 Sep 1966, Steyermark & Rabe 97187, 97190 (US).

TRINIDAD. Sin. loc., Purdie s.n. (NY).

SURINAM. Nickerie: Area of Kabalebo Dam project,

camp rd. km 212, 0-50 m, 20 Nov 1981, Florschutz-de Waard & Zielman 5673 (U). Nassau: 12 Mar 1949, Lanjouw & Lindeman 2647 (U). Sara Creek, 15 Nov 1950, Florschutz-de Waard & Florschutz 259 (U).

ECUADOR. Bombonasa, Spruce 749 (BM, NY). Canelos, Spruce 751 (BM, NY). Napo: Anangu along Río Napo, ca. 75 km E of Puerto Francisco de Orellana, 245-325 m, 29 Jul-4 Aug 1985, Churchill & Sastre 13786, 13831 (NY).

PERU. Andes Peruviana, Spruce 742 (BM). Loreto: above Pongo de Manseriche, above mouth of Rio Santiago, 400 m, 2 Dec 1931, Mexia 6205-a (BM, FH, MO, NY, US). San Martín: Tarapoto, Spruce 747 (NY); Rioja, Moyobamba-Chachapoyas km 409, 1100 m, 29 Aug 1982, Frahm et al. 106 (B), 121 (B, NY, U), 141 (B, NY, U), 314 (B).

I have taken a rather broad view of this taxon in the present treatment. Given the extremes in leaf variation, cf. types of L. obtusulum or L. pumilum with L. mittenii, I could recognize two or more species. However after examining the various collections under a host of names (see list of synonyms), the possibility of separating two or more taxa consistently became nearly impossible. The oblong-lingulate leaves vary in length and width (or their ratio of length:width), with

surface texture (smooth to undulate), in distal marginal serration (dentate to sharply serrate), and particularly in the shape of leaf apices. The apex is most notable when comparisons are made between the types of L. mittenii and L. allionii (rather sharply acute to short acuminate) with L. obtusulum or L. pumilum (obtuse to nearly truncate) but these extremes in shape are readily bridged by intermediate forms including the type of L. affine. At present I prefer to recognize L. affine as a rather polymorphic species in terms of leaf variation. Possibly with further collecting, particularly in the Amazonian region of Colombia, Ecuador, Peru and upper river regions in Brazil a better understanding will be provided for the apparent variation.

Mitten (1869) unfortunately confused Taylor's L. grevilleanum with this species, possibly because of similar description of shape and undulate texture of the leaves. However that species differs in several respects including the robust habit and much longer leaves (4.5-5.5). Welch (1976) only recognized L. pumilum, citing the distribution as Costa Rica, Ecuador and Peru. Florschütz-de Waard (1986) described L. affine for the Surinam flora recording the distribution from Trinidad and Peru. Finally, in the Peruvian transect study, Menzel (Schultze-Motel & Menzel, 1987) correctly considered L. pumilum a synonym of L. affine.

LONGIFOLIUM GROUP

13. *Lepidopilum longifolium* Hampe, Ann. Sci. Nat. Bot. sér. 5, 4: 365. 1865. Type. Colombia. Tequendama, Escaleros 2500 m, Lindig s.n. (lectotype, BM). Lectotype chosen based on presence of sporophytes, though the gametophytes are apparently terminal branches and thus not particularly typical of the species.

Figs. 32-33.

Lepidopilum robustum Mitten, J. Linn. Soc., Bot. 12: 386. 1869, syn nov. Type. Colombia. Pacho, Weir 134 (lectotype, NY). Syntype. Ecuador. Tungurahua, Spruce s.n. (NY). Lectotype chosen based abundant material with sporophytes and Mitten illustration.

Lepidopilum integerrimum Mitten, J. Linn. Soc., Bot. 12: 382. 1869, syn. nov. Type. Ecuador. Monte Tungurahua, Spruce s.n. (lectotype, NY). Syntypes. Ecuador. Chimborazo, Spruce 752 (NY); Lligua, Spruce 754 (NY); monte Tungurahua, rivulum Vascum (Baccun), Spruce 755 (NY).

Lepidopilum cladorrhizans Bescherelle, J. Bot. (Morot) 8: 63. 1894. Type. Guadeloupe.

Marie 43 (holotype, BM).

Lepidopilum herzogii Brotherus in Herzog, Biblioth.

Bot. 87: 135. 1916, syn. nov. Type. Bolivia.

Tocorani, 2800 m, Jul 1911, Herzog 4097

(holotype, JE; isotype, L).

Plants medium to rather robust in size, glossy light yellowish-green to dark green or golden-brown, ramicolous, corticolous or lignicolous, often forming dense tufts or mats. Primary stems short creeping; secondary stems short to long, spreading or erect, to 5 cm long, few branched; in cross-section hyalodermis well developed, outer cortical cells in 2-3 layers, rusty-red or orange. Secondary stem leaves densely crowded, radially foliose and erect to complanate, when erect often imbricate to subulaceous, appressed to erect, when complanate erect-spreading, symmetric to slightly asymmetric, rarely strongly asymmetric, crispate or flexuose, oblong-lanceolate, 3-4 mm long, 0.8-1.0 mm wide, often concave, gradually to abruptly short- or long-acuminate, often distinctly subauriculate; margins usually recurved, elimbate, entire or serrulate to serrate in distal 1/4-1/3; costae mostly closed, 1/4-1/3(1/2) lamina length, weak to strong, gradually diverging to parallel; median

cells linear to fusiform (rarely hexagonal), (78)90-125 um long, 9-11 um wide, rather thick-walled, smooth to slightly porose, basal cells short to long rectangular or oblong, rather lax; median leaves similar, more symmetric, oblong-lanceolate. Propagula present in leaf axils on distal branches, short to long cylindrical, to 0.5 mm long, smooth or lightly papillose. Autoicous (dioicous?). Perigonial leaves short ovate-lanceolate, ca. 1 mm long, concave. Perichaetia lateral, leaves long lanceolate or lanceolate-subulate, 1.2-1.7 mm long, long acuminate. Setae elongate, (2)7-14 mm long, somewhat slender to rather stout, strongly spinose, spines to 165 um long, rarely only papillose, dark rusty-red; capsules erect to suberect, urn ovoid-cylindrical, 1.0-1.7 mm long, mouth flared when deoperculate; opercula long rostrate; exostome to 700 um long, endostome to 850 um long. Spores 16-20 um in diameter, distinctly papillose. Calyptrae mitrate-campanulate, (2)2.5-3 mm long, plicate, with several to many hairs.

Etymology. Longifolium, from the Latin, longi- (long), and folium (leaf); in reference to the length of the leaves.

Distribution (Fig. 12 A). Mexico and probably elsewhere in Central America, widespread in the Caribbean (Cuba, Dominican Republic, Haiti, Jamaica, Puerto Rico, Guadeloupe), western Venezuela and Colombia south to Bolivia. In low to high montane forests, from 900 to 3700 m; epiphytic on branches and trunks of shrubs and treelets, on lianas, occasionally on logs.

Specimens examined. MEXICO. Veracruz: Orizaba, Jan 1892, Smith s.n. (NY).

CUBA. Oriente: Sierra Maestra, near La Gran Piedra, 1100 m, 10 Nov 1917, Ekman 8802 (BM, NY); Pico Turquino, Turquino ridge, Jul 1922, Ekman 11231 (NY); La Gran Piedra, summit of peak, 1200 m, 6 Apr 1982, Buck 7757 (HAC, NY). Santa Clara: Trinidad Mountains, Arroyo Cimarron, 470 m, 1-12 Mar 1910, Britton 5117 (NY).

JAMACIA. Moody's Gap, 10 Sep 1908, Britton 909 (NY). Portland: Hardwar Gap, Blue Mountains, ca. 20 mi N of Kingston, ca. 4000 ft, 2 Feb 1980, Steere J-68 (NY); near Hardwar Gap, 4000 ft, 15 Apr 1903, Underwood 2268 (NY).

HAITI. Sud'est: Massif de la Selle, 5 km E of Seguin on road to Mare Rouge, 1780 m, 22 Nov 1982, Buck

9502 (NY).

DOMINICAN REPUBLIC. Independencia: Near crest of Sierra de Neiba, along carretera Internacional, 1700-2000 m, Jul 1967, Norris et al. 6039b (NY). La Estrelleta: Sierra de Neiba, 15 km N of Angel Feliz, 5500 ft, 22 Mar 1981, Buck 4787 (NY). La Vega: 4.7 km S de la calle principal de Constanza y 8 km al O en el camino al Pinar Parejo, 6150 ft, 27 Apr 1982, Zanoni et al. 20188 (NY). Pedernales: 6 km N of Los Arroyos, 5200 ft, 6 May 1982, Buck 8302 (NY). Peravia: La Nevera, 19 km S of Valle Nuevo, 6700 ft, 1 May 1982, Buck 8151 (NY). Santiago: Pico Diego de Ocampo, 1170 m, 17 May 1976, Judd 1536 (NY).

PUERTO RICO. Monte Torrecilla, 900-1100 m, 20 Mar 1915, Britton 5693a (NY). Caribbean National Forest, Toro Negro Division, along Hwy 143, 3.5 km E of Hwy 139, 27 Feb 1981, Buck 3746 (NY).

GUADELOUPE. S. loc., Marie 151 (NY). Sanite Rose, Apr 1899, Duss 1340a (H-BR, NY). Vallie de St. Louis, 1906, Duss 70 (NY).

COLOMBIA. Antioquia: Municipio de Andes, ca. 2.7 km SO de Santa Rita, 1790 m, 20 Jul 1986, Churchill et al. 14559 (HUA, NY); Municipio de Jardín, en Ventanas, 8-10 km S de Jardín, 2900 m, 4 Oct 1987, Churchill & Marulanda 15744 (HUA, NY); Municipio de Medellín, ca.

25 km NO de Medellín, Boqueron, 2400-2600 m, 28 Jun 1986, Churchill et al. 13941, 13973 (HUA, NY); Municipio de Sonsón, de Sonsón hacia Los Medios, ca. 6 km O de Sonson, 2420 m, 8 Jul 1987, Churchill et al. 15522 (HUA, NY); Municipio de Urrao, ca. 58 km S de Urrao hacia Betulia, antes del descenso al valle del río Pabon, 2270 m, 28 Jun 1985, Churchill et al. 13240, 13249 (HUA, NY), abajo de Páramo de Frontino, ca. 3400 m, 1 Jul 1985, Churchill et al. 13432 (HUA, NY). Cundinamarca: Páramo de Chisaca, Santa Rosa, Bodegas de Sumapas, Ladera Oriental del valle del río Colorados, 3460 m, 20 Aug 1976, van der Hammen & Jaramillo M. 4271 (FLAS); Usaquen, 3050 m, 20 May 1972, Cleef 3921 (FLAS); Páramo de Cruz Verde, Alto de La Viga, 3620 m, 11 Apr 1972, J. & P. Florschütz 2777 (FLAS). Huila: Municipio de La Plata, vereda Candelaria, 2300 m, 29 Sep 1984, Aguirre et al. 6337 (FLAS). Risaralda: Municipio de Santa Rosa de Cabal, camino real entre Termas y el Volcan Otun, "El Magarital", 2500 m, 18 Jul 1980, van Reenen 1985 (FLAS). Santander: Filo de la Jequera, arriba de la Laguna La Jequera, Páramo entre Valle del río Susa y Coromoro, 3730 m, 29 Nov 1967, van der Hammen & Jaramillo M. 1842 (FLAS).

VENEZUELA. Merida: Rangel, Sierra de Santo Domingo, paramo de Mucubaji, around Laguna Negra, 3400 m, Jul-

Aug 1972, Griffin et al. 1252 (FLAS).

ECUADOR. Agoyan, Spruce s.n. (NY). Chimborazo,
Spruce s.n. (NY). Pauatanga, Spruce s.n. (NY).

Pichincha: Rio El Cinto, S slope of Volcán de
Pichincha, below Lloa, ca. 9000 ft, 2 Nov 1983, Steere
26995 (NY).

The lectotype choosen here and the syntype cited by Hampe (Pacho, 2200 m, Lindig) differ in some respects. The latter exhibits the more robust nature of this species, with the leaves broader and apex smooth, thus in keeping with Mitten's L. robustum, whereas the lectotype appears to be a terminal branch with the leaves narrower and serrulate at the apex. Also the lectotype has slightly shorter setae and smaller capsules.

This species is rather variable in habit and leaf shape. The complanate form is rather common in the Caribbean area and characteristically exhibits widespreading leaves that are narrow and slightly asymmetric. Furthermore some collections exhibit sporophytes in which the seta is relatively short (ca. 2.2 mm long) and not strongly spinose. The erect form is more common in the Andes and often is quite robust, with the plants often subjulaceous, with broader leaves

with the apices often recurved. However both forms can be found throughout the range of L. longifolium, and both exhibit the generally symmetric leaf shape with the margins generally entire or slightly serrulate, and recurved.

Lepidopilum amplirete (Sull.) Mitt. is somewhat similar but generally occurs on calcareous rock, and the leaves are plane to recurved on one side.

Lepidopilum integrifolium Broth. in Urban is also similar, and possibly related. This species differs in having smaller leaves (2.0-2.7 mm long), and a smooth seta.

14. Lepidopilum integrifolium Brotherus in Urban, Symb.

Antill. 3: 427. 1903. Type. Martinique. Morne-Rouge, 1901, Duss 372 (lectotype, H-BR). Syntype. Guadeloupe. Bois des Bains-Jaunes, Aug 1901, Duss 222 (H-BR, NY).

Fig. 34.

Plants somewhat small, rather delicate, glossy olive-green, corticolous, ramicolous or lignicolous. Primary stems short creeping, rhizoids inconspicuous; secondary stems erect, to 3 cm tall, few-branched; in cross-section hyalodermis well differentiated, outer

cortical cells in 1-2 layers, thick-walled, rusty-red, inner cortical cells enlarged, hyaline. Secondary stem and branch leaves similar, latter somewhat smaller, lateral and median leaves with no apparent differentiation, crowded, symmetrical, erect to somewhat erect-spreading, oblong-lanceolate, 2.0-2.7 mm long, 0.5-0.8 mm wide, short acuminate, weakly auriculate; margins recurved throughout except at apex, apex serrulate or entire; costae closed at base, $(1/3)1/2-2/3$ lamina length, parallel; median cells oblong-hexagonal, 100-150 μ m long, 14-20 μ m wide, basal cells oblong-rectangular or fusiform, insertion cells often golden-yellow or -brown. Propagula produced in leaf axils, short to somewhat long cylindrical, to 0.3 mm long. Autoicous. Perigonial leaves lanceolate, to 1.25 mm long, acuminate, costae absent. Perichaetial leaves ovate-lanceolate. Setae elongate, 5.5-9.5 mm long, smooth, rusty-red; capsules erect to suberect, urn ovoid-short cylindrical, 1.2-1.5 mm long; exothecial cells oblong-short rectangular; opercula conic-rostrate, 0.5-0.7 mm long. Calyptrae mitrate, 1.1 mm long, slightly plicate, naked or slightly scabrous distally.

Etymology. *Integrifolium*, from the Latin, *integri-*

(entire), folia (leaf); in reference to the leaves.

Distribution (Fig. 12) Windward Islands (Martinique and St. Vincent) and Leeward Islands (Guadeloupe and Dominica) south to Venezuela, at elevations to ca. 1100 m. In forests, on tree trunks and branches, also on decaying logs.

Specimens examined. DOMINICA. Laudat, 30 Jul 1892, Elliott 480 (BM), Luzon Flats, 21 Mar 1896, Elliott 2140 a.1 (BM).

ST. VINCENT. S. loc. & col. (BM).

VENEZUELA. Bolivar: Alo largo del camino entre km 119 y 123 al sur de El Dorado, 1030-1100 m, 11 Jan 1964, Steyermark & Dunsterville 92970 (NY).

This is a distinctive species with strongly recurved leaf margins for nearly the entire leaf length and smooth setae that should separate it from possibly related species such as L. amplirete (Sull.) Mitt. and L. longifolium Hampe. Only the latter species is also known from the Windward Islands.

15. *Lepidopilum amplirete* (Sullivant) Mitten, J. Linn.

Soc., Bot. 12: 382. 1869. Cylindrothecium
amplirete Sullivant, Proc. Amer. Acad. Arts Sci.
 5: 284. 1861. Entodon ampliretis (Sullivant)
 Jaeger, Ber. St. Gall. Naturw. Ges. 1876-77: 292.
 1878. Type. Cuba. Rocky ledges in woods, Wright
72 (holotype, FH?; isotypes, BM, G, H-BR, L, NY).

Fig. 35.

Plants rather large, glossy green to yellowish-green, saxicolous, corticolous, or ramicolous, forming dense to somewhat loose mats. Primary stems creeping; secondary stems spreading, rarely ascending, to 5 cm long; in cross-section hyalodermis well developed, epidermis enlarged, outer cortical cells smaller and thick-walled, inner cortex cells enlarged, hyaline and thin-walled. Leaves usually densely foliate, complanate, smooth, rarely crispate; lateral leaves spreading, asymmetric, oblong-lingulate to oblong-lanceolate, 2.5-3.0 mm long, 0.70-0.85 mm wide, rounded short-acuminate or cuspidate, base slightly auriculate, at least on one side; margins plane or occasionally recurved on one side, elimbate (cells becoming linear gradually toward margin), serrate in distal 1/3-1/2, sharply so toward apex; costae set apart, gradually diverging, 1/4-1/3 lamina length, usually weak or

appearing absent; median cells fusiform to long-hexagonal, 82-114 μ m long, 12-17 μ m wide, thick-walled, upper cells toward apex distinctively hexagonal and very thick-walled, marginal cells linear, basal cells long-rectangular or hexagonal; median leaves appressed, $\pm$ symmetric, oblong-lanceolate, 2.0-2.3 mm long, 0.7-1.0 mm wide, gradually short-acuminate, slightly auriculate at base, serrate in distal 1/3, costae set apart, 1/4-1/3 lamina length, weak, median and upper cells fusiform. Propagula generally present, long cylindrical, to 0.7 mm long. Dioicous. Perichaetia lateral, leaves broadly ovate-lanceolate, long acuminate, costae absent, median cells linear. Sporophytes not known.

Etymology. Amplirete, from the Latin, ampli- (= increase), -rete (= a net, network); in reference to the lamina cell pattern.

Distribution (Fig. 12 B). West Indies (Cuba, Jamaica, Haiti, Dominican Republic, and Puerto Rico). In humid forests at elevations from 500-1070 m, most often encountered on limestone rock, occasionally on tree trunks, branches and exposed roots, or on decaying logs.

Specimens examined. CUBA. Santa Clara: Trinidad Mountains, Trinitario, Rio Negro, 550 m, 1-12 Mar 1910, Britton 5198 (NY).

JAMAICA. Union Hill, 7 Apr 1908, Britton 798 (NY). Trelawny: Just N of Wilson's Run, 18°16'N, 77°40'W, 500 m, 18 Apr 1981, Crosby 13880 (NY).

HAITI. Massif de la Hotte, S of Morne Formon, 975 m, 1 Jun 1984, Skean 1218 (NY). Plaisance to Marmelade, ca. 3000 ft, 25 Aug 1903, Nash 842 (F, NY, US). Vicinity of Marmelade, ca. 800 m, 20 Dec 1925, Leonard 8385 (BM, FH, NY, US).

DOMINICAN REPUBLIC. Pedernales: Las Abejas, ca. 40 km N along road from Cabo Rojo from junction of road from Oviedo to Pedernales, 18°09'N, 71°36'W, 3900 ft, 13 Mar 1981, Buck 4299, 4305, 4362 (NY), Reese 14952 (NY).

PUERTO RICO. Arecibo to Utuado, 14 Mar 1906, Britton 330, 349a (NY). 8.2 mi S of Utuado, 3.7 mi N of Adjuntas, 27 Feb 1981, Reese 14519 (NY). Caribbean National Forest, Luquillo Division, trail to El Toro, 25 Feb 1981, Buck 3639 (NY).

This species is somewhat similar to L. affine, especially the the short acuminate forms of that

species, however L. amplirete is more robust, with larger leaves and distinctive hexagonal, thick-walled upper cells. However, in the West Indies this species appears to have affinity with, and will most likely be confused with L. longifolium Hampe. Both exhibit a similar leaf shape, but L. longifolium has generally recurved margins, and a narrow and gradually acuminate apex, whereas L. amplirete has plane margins or is recurved on one side, and a leaf apex that is broadly and short acuminate-cuspidate.

16. *Lepidopilum erectiusculum* (Taylor) Mitten, J. Linn.

Soc., Bot. 12: 372. 1872. Hookeria erectiuscula

Taylor, London J. Bot. 5: 60. 1846. Type.

Ecuador. Forest of Esmeraldos, 6000 ft, 1827,

Jameson s.n. (holotype, FH; isotypes, BM, E, FH).

Fig. 36.

Plants medium to rather large, glossy green to yellowish-green, ramicolous. Primary stems creeping, densely tomentose, secondary stems ascending to erect, compressed or flattened, to 5.5 cm long, distal branches occasionally subulaceous and rather long attenuate; stem in cross-section with hyalodermis,

epidermis small, thin-walled, outer cortex in 2-3 rows of small thick-walled rusty-red cells, inner cortex of large thick-walled cells. Leaves distant, stem readily observed except on some attenuate branches, flexuose, erect-spreading to erect, lateral and median leaves little differentiated, concave and somewhat plicate, oblong-lanceolate, laterals narrowly so, (2.8)3-4 mm long, (0.8)1.0-1.4 mm wide, gradually to rather abruptly acuminate; margins plane or more often somewhat recurved, elimbate, serrate in distal 1/3, rather sharply so at times; costae closed at base, parallel to slightly diverging, 1/3-1/2 lamina length; median cells fusiform to somewhat linear, 85-142 μ m long, 11-14 μ m wide, somewhat thick-walled, porose or not. Autoicous? Perichaetial leaves ovate-subulate, 1.2-1.8 mm long, serrate distally. Setae elongate, 15-20 mm long, rusty-red or reddish-orange, papillose-low spinose distally, papillose below; capsules erect to suberect, urn ovoid-short, cylindrical, (1.5)2.0-2.5 mm long; opercula conic-rostrate, 1.4-1.6 mm long. Spores 17-20 μ m in diameter, appearing smooth. Calyptrae mitrate-campanulate, 2.5-3.5 mm long, plicate, somewhat densely hairy, base laciniate.

Etymology. *Erectiusculum*, from the Latin, *erectiusculus* (= somewhat erect); in probable reference to the habit of the secondary stems or possibly to the urn.

Distribution (Fig. 12 A). From Ecuador to possibly northernmost Chile. Apparently in premontane to low montane forest, to at least 1900 m; on shrub or treelet branches.

Specimens examined. ECUADOR. Pastaza: Monte de Canelos, 3000 ft, Spruce 734 (BM, E, H-BR, NY).

PERU. San Martín: Rioja, between Chachapoyas-Moyobamba km 387, 1900 m, 31 Aug 1982, Frahm et al. 610, 621, 665 (B).

CHILE. Sachapata?, Lechler (NY).

Although Mitten (1869) placed this species in the section Peromilla Spruce ex Mitten based on leaves 10-ranked, this species appears closely related to Lepidopilum longifolium Hampe, at least phenetically, by both gametophytic and sporophytic characters. Leaf shape in particular is similar to L. longifolium but in that species the distal margins are smooth or indistinctly serrulate, whereas in L. erectiusculum

the margins are serrate, and often sharply so. Also, lower secondary stems in L. erectiusculum often have crowded leaves similar to those more typically found in L. longifolium. In addition to the serrate margins, L. erectiusculum exhibits features differing from L. longifolium that include the densely tomentose primary stems, occasionally producing early or later branches that are subulaceously attenuate and leaves that are distantly spaced.

Though distinctive, this species is poorly represented by collections and thus not well characterized. I have been unable to locate the exact locality for the Chilean specimen collected by Lechler. Given that the species has been collected on both sides of the Andes in Ecuador, the species is likely to be found in Colombia.

17. **Lepidopilum aurifolium** Mitten, J. Linn. Soc., Bot. 12: 371. 1869. Type. Ecuador. Quito, Jameson s.n. (lectotype, NY). Syntype. Ecuador. Llalla, Spruce 764 (NY). Lectotype choice based on presence of mature sporophytes (2) and Mitten illustration which depicts the peristome.

Fig. 37.

Plants small, glossy golden-yellow, ramicolous, forming small tufts. Primary stems short creeping, secondary stems erect, to 3 cm tall; in cross-section hyalodermis not well differentiated, epidermal cells somewhat thick-walled, rusty-red, outer cortical cells thick-walled in 1-2 rows, rusty-red, inner cortical cells few, thin-walled, hyaline. Leaves crowded, erect to slightly erect-spreading wet or dry, no distinct differentiation between lateral and median leaves, symmetric, narrowly lanceolate-oblong, 1.5-1.8 mm long, 0.3-0.4 mm wide, plicate, somewhat long-acuminate and channeled distally, base slightly auriculate; margins recurved except near apex, entire below, distally serrulate to serrate; costae closed at base, ca. 4/5 lamina length, parallel, terminating at back with a short spine; median cells linear to long-fusiform, 38-48 μ m long, 4-6 μ m wide, basal cells oblong to fusiform-rectangular. Autoicous? Perichaetial leaves ovate-lanceolate. Setae elongate, (6)8-12 mm long, rusty-red, twisted, papillose in distal 2/3 (or more), papillae low, not particularly distinct; capsules suberect, ovoid-cylindrical, ca. 1.5 mm long; operculum conic-rostrate, ca. 1.5 mm long. Calyptrae mitrate-campanulate, 1.8-2.1 mm long,

plicate, laciniate at base.

Etymology. Aurifolium, from the Latin, auri- (= golden yellow), folia (leaf); in reference to the color of the leafy plant.

Distribution (Fig. 12 B). Known only from the type localities cited above from Ecuador. Probably from premontane to montane forest, on treelets or shrubs.

Mitten (1869) placed L. aurifolium in his section Helicoblepharum based on the arrangement of the leaves in a series 10 per rotation, lamina cells often with papillae projecting at cell angles and exostome teeth slender and outer and inner cell plates equal in thickness. Another feature of Helicoblepharum is that the plants are prostrate, which L. aurifolium is not and rather the secondary stems are erect. The arrangement of the leaves (in a series of 10) and the twisted setae (both right and left on the same seta) does not fit particularly well in Lepidopilum, but at this time I prefer to retain L. aurifolium in Lepidopilum.

18. *Lepidopilum caviusculum* Mitten, J. Linn. Soc.,
Bot. 12: 383. 1869. Type. Ecuador. Monte de
Canelos, Spruce s.n. (lectotype, NY;
isolectotype, NY). Fig. 38.

Plants small to medium-sized, glossy golden-green, ramicolous. Primary stems short-creeping, secondary stems ascending to erect, to 2.5 cm long, few-branched; hyalodermis well developed, outer cortical cells in 2-3 rows, small, thick-walled, rusty-red, inner cortical cells numerous, large, hyaline. Leaves flexuose, concave, lateral leaves erect-spreading, mostly narrowly ovate-oblong, 2.2-2.7 mm long, 0.7-1.0 mm wide, apiculate to short and broadly acuminate, subauriculate; margins recurved, 1/2 of lamina length, elimbate, serrulate in distal 1/4; costae set apart, gradually diverging, 1/3-1/2 lamina length; median cells fusiform to rhomboidal, 78-104 μ m long, 11-17 μ m wide, thick-walled, basal cells oblong-rectangular; median leaves appressed or erect, broadly ovate-oblong, 2.2-2.4 mm long, 1.0-1.2 mm wide. Propagula in leaf axils, cylindrical, to 0.55 mm long. Dioicous? Perichaetial leaves ovate-subulate, to 1.6 mm long, long-acuminate. Setae elongate, 9-16 mm long, rusty-red, papillose and short spinose throughout; capsules

ovoid-cylindrical, 1.5-1.7 mm long; opercula conic-rostrate, 1.5-1.7 mm long. Calyptrae mitrate-campanulate, 2.6-2.9 mm long, plicate, sparsely hairy.

Etymology. *Caviusculum*, from the Latin, *Cavus* (concave), and *culum* (diminutive); in reference to the leaves.

Distribution (Fig. 12 B). Known only from the type in Ecuador. Probably occurring in low montane forests, on branches.

Distinctive features include the rather broadly ovate-oblong concave leaves with a distinctly recurved margin.

19. *Lepidopilum frondosum* Mitten, J. Linn. Soc., Bot. 12: 381. 1869. Type. Colombia. S. loc., Purdie s.n. (holotype, NY). Fig. 39.

Plants medium sized, glossy green to yellowish-green, possibly ramicolous. Primary stems creeping; secondary stems erect-spreading; hyalodermis present, outer cortical cells small, thick-walled, rusty-red, in 3-4 rows, inner cortical cells large, thin-walled,

hyaline. Leaves crispate or flexuose, crowded; lateral leaves erect-spreading, oblong to oblong-lanceolate or ligulate, 2.0-2.8 mm long, 0.6-0.8 mm wide, short acuminate, often twisted or pinched at apex; margins indistinctly limbate with linear cells between marginal serration and inner lamina cells, serrate in distal $1/3-1/2$, teeth rather large and blunt, composed of two adjoining cells, often appearing hyaline; costae diverging, $1/2-3/4$ lamina length; median cells hexagonal to fusiform, 100-157 μm long, 14-20 μm wide, basal cells oblong-rectangular to oblong-fusiform; median leaves appressed, ovate-short oblong, 2.0-2.2 mm long, 0.8-1.1 mm wide, short-acuminate to apiculate, often twisted. Dioicous? Perichaetial leaves ovate-subulate, to 1.6 mm long. Setae elongate, 7.5-8.5 mm long, rusty-red, spinose throughout; capsules erect to suberect, ovoid-cylindrical, 1.4-1.6 mm long; opercula conic-rostrate, to 1.0 mm long. Calyptrae mitrate-campanulate, 1.6-1.9 mm long, plicate, base laciniate, hairy to nearly naked.

Etymology. Frondosum, from the Latin, frondosus (=leafy, full of leaves); in reference to the densely foliate plant.

Distribution. Known only from the type from Colombia. Probably from a premontane to montane area, likely occurring on branches of shrubs or treelets.

The distinctive marginal serration readily separates this species from any other species likely to be found at least in Colombia. Mitten (1869) suggested that the habit of this species was similar to L. affine C. Muell., but that species typically forms mats, whereas L. frondosum is erect, and also the serration is quite different.

20. *Lepidopilum brevifolium* Mitten, J. Linn. Soc., Bot. 12: 385. 1869. Type. Ecuador. Mont de Canelos, Spruce 784 (lectotype, NY; isotype, E). Syntype. Ecuador. Montis Abitagua, Spruce 785 (E, NY). Choice of lectotype based abundant plant material with sporophytes and Mitten illustration.

Fig. 40.

Plants small, golden- or yellowish-green, glossy, ramicolous, forming mats. Primary stems creeping; secondary stems spreading, branches irregularly pinnate, few, in cross-section hyalodermis present,

epidermal cells thin-walled and larger than outer cortical cells, outer cortical cells small and thick-walled, 2-3 rows, rusty-red, inner cortical cells hyaline, very enlarged and few. Leaves crowded, crispate to smooth, erect to erect-spreading wet or dry, little differentiation between lateral and median leaves, both ovate-oblong, 1.2-1.5 mm long, 0.5-0.6 mm wide, mostly symmetrical, short acuminate-apiculate; margins plane to slightly recurved below, elimbate, entire to inconspicuously serrulate; costae set apart at base, gradually diverging, 1/3-1/2 lamina length; median and upper cells long-fusiform to more commonly linear, 77-94 μ m long, 8-12 μ m wide, smooth, basal cells rather lax, oblong. Dioicous? Perigonial leaves ovate, 0.7-0.9 mm long, short-acuminate, costae absent. Perichaetial leaves ovate-lanceolate, 0.6-0.8 mm long, acuminate, costae absent. Setae elongate, 12.5-14.0 mm long, papillose and spinose, spines to 100 μ m long. Capsules erect to suberect, ovoid-cylindrical, 1.5-1.8 mm long; exothecial cells oblong-rectangular, 42-64 μ m long; operculum conic rostrate, 1.2-1.4 mm long. Spores lightly papillose, 14-17 μ m in diameter. Calyptrae mitrate-campanulate, with few to no hairs, base laciniate.

Etymology. *Brevifolium*, from the Latin, *brevi-* (short) and *-folia* (leaf); in reference to the short leaves of this species.

Distribution (Fig. 11). Known only from Ecuador. In premontane to low montane forests, on branches of shrubs and treelets.

Specimen examined. ECUADOR. Napo-Pastaza: Mera, Mangayacu, 1160 m, 10 Nov 1958, Harling 3184 p.p. (NY).

This is a distinctive species, not readily confused with any other species of Lepidopilum. The relatively small plants with short ovate-oblong symmetrical leaves are diagnostic.

POLYTRICHOIDES GROUP

21. *Lepidopilum permarginatum* Williams, Bryologist 28:
60. 1925. Type. Colombia. Dept. El Valle:
Cordoba, forest along Río Calima, 80-100 m, 9 Oct
1922, Killip 11794 (holotype, NY; isotypes, FH,
US).

Fig. 41.

Plants medium sized, corticolous or ramicolous.
Primary stems creeping, secondary stems erect; in
cross-section both primary and secondary stems with
enlarged epidermal cells, outer cortex of 3-4 small
thick-walled cells, inner cortex of larger hyaline
cells. Leaves flexuose and somewhat plicate,
lateral and median leaves not strongly differentiated,
laterals somewhat more flexuose, loosely erect-
spreading wet or dry, ovate- or oblong-lanceolate, 4.0-
5.2 mm long, 1.5-2.0 mm wide, acuminate, often abruptly
so and generally twisted; margins plane, limbate,
border 8-15 rows of linear porose cells, serrate to
spinose in upper half, border continuing into apex;
costa double, strong, somewhat projecting from lamina
surface on back, at base closed or slightly set apart,
(1/2)2/3-3/4 lamina length, diverging and distally

parallel or converging; median and distal cells between costae rhomboidal to hexagonal, 33-45 μ m long, 15-25 μ m wide, cells between costae and border on lower 2/3 of lamina and within costae in lower 1/2 long rectangular to somewhat linear. Dioicous. Perichaetia lateral. Setae elongate, 11-14 mm long, both papillose and spinose for full length, reddish-orange; capsules erect, urn ovoid, ca. 1.1-1.2 mm long; opercula conic-short rostrate, ca. 1.0-1.2 mm. Calyptrae mitrate-campanulate, ca. 3 mm long, laciniate at base, naked or with a few hairs or old archegonia.

Etymology. Permarginatum, from the Latin per- (= along), marginatus (= enclosed with a border); in reference to the bordered margin consisting of several rows of linear cells.

Distribution (Fig. 13 A). From Nicaragua south to Pacific Colombia. In lowland wet tropical to premontane forests, from 80 to 1190 m, on tree trunks and branches.

Specimens examined. NICARAGUA. Rivas: Isle de Ometepe, Baluge, vertiente norte del volcan Madera, 1190 m, 15 Aug 1984, Granzow de la Cerda & Moreno 1685

(DUKE, NY).

COLOMBIA. Choco: Corcovada region, upper Río San Jaun ridge along Yeracui Valley, 200-275 m, 24-25 Apr 1939, Killip 35325 (US). Valle: Buenaventura, 0-10 m, 5-10 Oct 1922, Killip 11767 (FH, NY).

Lepidopilum permarginatum appears to be rather rare (or rarely collected), but should at least be expected in the Choco forests that extend into Panama and northern Ecuador. Gametophytically L. permarginatum is very similar to L. inflexum Mitt.; see comments under the latter for differences.

22. Lepidopilum stillicidiorum Mitten, J. Linn. Soc., Bot. 12: 373. 1869. Type. Ecuador. Mont de Canelos, in stillicidies, Spruce 735 (holotype, NY). Fig. 42.

Lepidopilum wallisii C. Mueller, Flora 58: 549.

1875, syn. nov. Type. Colombia. Prov. (Dept.)

Antioquia, cerro prope Frontino, 8000 ped.

altum, 1874, Wallis s.n. (isotypes, BM, NY).

Lepidopilum crispum Herzog, Hedwigia 67: 266. 1927,

syn nov. Type. Bolivia. Polopolo bei,

Coroico, N. Yungas, ca. 1300 m, x.1912,

Buchtien s.n. (holotype, JE).

Lepidopilum carneum Bartram, Contr. U. S. Natl.

Herb. 26: 103, f. 33. 1928, syn. nov. Type.

Costa Rica. Prov. Cartago, La Estrella, on
tree, 26, 27 Mar 1924, Standley 39202

(holotype, US).

Plants glossy dark-green or golden-yellow, rather large, occasionally somewhat wiry in appearance, saxicolous or ?corticolous. Primary stems short and creeping, leaves mostly eroded; secondary stems prostrate or ascending, few branched, to 10 cm long, distal branches becoming attenuate; in cross-section epidermis equal to or somewhat smaller than outer cortical cells, outer cortical cells thick-walled, rusty red, inner cortical cells large and hyaline. Secondary stem leaves densely foliate or somewhat distant, erect-spreading dry or wet, contorted or not, if contorted then distal lamina tortuose when dry, less so when wet, lateral leaves oblong-lanceolate to oblong-lingulate, asymmetric, (3.5)4-5 mm long, 1.40-1.75 mm wide, short acuminate to more often acute, often rather bluntly so, base with lamina folded; margins plane, bordered from near apex to base, entire

below, serrate in distal $1/2-1/4$; costae $2/3(3/4)$ lamina length, gradually diverging, generally separate at base; median and upper central cells hexagonal, 65-115 μm long, 35-43 μm wide, smooth, lower and basal cells oblong to long-rectangular, somewhat lax, border of 2-3(4) rows of linear cells; median leaves ovate to ovate-lanceolate, 3-4 mm long, 1.2-1.7 mm wide, + symmetrical, short acuminate; attenuate plants with secondary stem and branch lateral leaves 3.2-4.0 mm long, 0.8-1.2 mm wide, gradually and rather broadly acuminate, often bluntly so, costae ca. $2/3$ lamina length, closed or set apart, diverging to somewhat parallel, often appearing quite strong, median and upper central cells broadly hexagonal, appearing somewhat lax, 110-144 μm long, basal and lower cells short to long rectangular, 85-170 μm long, lax and porose; median leaves ovate to ovate-short lanceolate, 1.8-2.5 mm long, 1.0-1.2 mm wide, acuminate, margin distally serrate, costae $2/3$ lamina length, diverging to + parallel, separate at base, median and upper central cells hexagonal, 100-115 μm long, limbate cells in 3-4 rows. Dioicous? Perichaetial outer leaves ovate-lanceolate, 0.9-1.1 mm long, to 0.4 mm wide, acuminate, costae absent. Setae short, ca. 3.5 mm long, low papillose throughout; capsules ca. 1 mm long.

Calyptrae mitrate, short campanulate, ca. 1.5 mm long, hairy.

Etymology. Stillicidiorum, from the Latin, stillicidium (dripping or dropping moisture); in reference to the habitat of the plant.

Distribution (Fig. 13 B). In streams, on rocks or soil banks associated with seeps in premontane to high montane regions from 800-2500 m. From Costa Rica and Colombia, south to Ecuador and Bolivia.

Specimens examined. COSTA RICA. Cartago: Finca La Palmira, ca. 12 km NW of Turrialba, 1800 m, 18 Jan 1972, Maas 797 (U).

COLOMBIA. Antioquia: Municipio de Medellín, Corregimiento de San Antonia de Prado, ca. 10 km de San Antonia, ca. 06°10'N, 75°35'O, 4 Jul 1986, Churchill et al. 14050 (HUA, NY), Medellín, en el Alto de El Boqueron, 2500 m, Jan 1952, Uribe U. 2276 (F); Municipio de Salgar, ca. 12 km O de Salgar, Hacienda la Regada, ca. 05°59'N, 76°00'O, en quebrada Liboriana, 16 Jan 1988, Churchill et al. 15820 (HUA, NY); Santander: Between Piedecuesta and Las Vegas, 2000-2500 m, 19-24 Dec 1926, Killip & Smith 15565 (NY).

ECUADOR. Pichincha: Ca. 18 km NW of San Miguel de los Bancos, ENDESA reserve, 00°05'N, 78°55'W, 800 m, 27-29 Dec 1983, Buck 10470A (NY).

This taxon is not well represented by collections and thus poorly characterized in terms of general morphology and ecology. I have included L. wallisii as a synonym based mostly on the similarity of the lateral leaves and given the general variation exhibited in aquatic Lepidopilum species. Although the type of L. carneum Bartr. records the habit of this plant as on trees, my field observations in Colombia, and other collections cited above, suggest that the common habitat is on wet or seepy soil banks (probably thinly covering rocks) or on rocks in streams usually associated with cool, moist montane forests.

23. Lepidopilum inflexum Mitten, J. Linn. Soc., Bot.

12: 375. 1869. Type. Ecuador. Monte Abitagua, Spruce 727 (lectotype, NY; isolectotype, NY). Syntypes, Ecuador. Canelos, Spruce 726 (NY); Abitagua, Spruce 728 (NY). Selection of type based on plants with sporophyte (only one) and Mitten illustration. Fig. 43.

Lepidopilum aubertii Thériot, Rev. Bryol. Lichénol.

10: 15. 1937, syn. nov. Type. Colombia.

Depto. de Valle, Rio Yurumangui, 1933, Rue 133
(holotype, PC).

Lepidopilum perlaxum Thériot, Rev. Bryol. Lichénol.

10: 16. 1937, syn. nov. Type. Colombia.

Depto. de Valle, Rio Yurumangui, 1933, Rue 132
(holotype, PC).

Plants medium sized, primary stems short creeping, secondary stems ascending or erect, to 6 cm long; stem cross-section with well developed hyalodermis, outer cortical cells in 4-6 layers, very thick-walled, rusty-red, inner cortical cells larger, hyaline. Secondary stem leaves generally distant, radially foliate, median and lateral leaves not readily differentiated, not complanate, crispate and contorted when dry, often so when wet, ovate-oblong, 2.2-2.6(3.7) mm long, 0.8-1.2 mm wide, rounded distally to abruptly short to somewhat long acuminate; margins plane, strongly limbate, serrate in distal 1/2-2/3; costa usually set apart, 2/3 lamina length, strong to weak, slightly diverging, subparallel, distally costae often juxtapositioned to limbate margin, costae often with terminal projecting

spine or tooth on lamina back; upper median cells rhomboidal or rarely broadly fusiform, 44-55(67) μ m long, 13-20 μ m wide, porose, basal cells irregularly short to long rectangular, porose, insertion cells often golden-yellow or orange. Autoicus? Setae short, 1.8-2.8 mm long, ornamented with low projecting papillae, reddish-orange; capsules erect, oblong-short cylindrical, 0.8-1.2 mm long; operculum conic-short rostrate, 1-1.2 mm long. Calyptrae mitrate, smooth, appearing roughened distally.

Etymology. Inflexum, from the Latin inflexus (= bent inwards); in reference to inwardly curved leaves.

Distribution (Fig. 13 B). From Colombia south to Ecuador. Probably from lowland to possibly premontane forests; possibly associated with aquatic habitats or epiphytic. Known only from the types.

Both L. aubertii and L. perlaxum readily appear to be the same taxon; both types differ in minor features from L. inflexum, particularly the upper cell shape of stem leaves. Lepidopilum aubertii and L. perlaxum exhibit cells that are rhombic whereas in L. inflexum the cells are more elongate, i.e., rhomboidal to

broadly fusiform. However, this is somewhat variable in the very limited material examined. Furthermore, in the branch leaves of all three types the cell pattern is similar. Thérriot's (1937) description of the sporophyte of L. aubertii appears to match that of the Mitten's taxon, however no sporophytes have been described for L. perlaxum. Lepidopilum inflexum appears to be closely related to L. permarginatum, but differs by a narrower border and shorter setae. Given the amount of material available this taxon is not well characterized or is anything known about the ecology.

24. Lepidoplum tortifolium Mitten, J. Linn. Soc., Bot.

12: 374. 1869. Type. Ecuador, Bombonasa, Spruce 783 (lectotype, NY; isoelectotype, NY). My choice of the type is based on abundant material with sporophytes, and an accompanying Mitten illustration. Fig. 44.

Hookeria riparia Mitten, J. Linn. Soc., Bot.

12: 345. 1869. Cyclodictyon riparium (Mitten) Kuntze, Revis. Gen. Pl. 2: 835. 1891. Type. Ecuador. Andes Quitenses, Bombonasa, Spruce 783 (holotype, NY).

Lepidopilum crispifolium Bartram, Rev. Bryol.

Lichénol. 33: 11. 1964, syn. nov. Type.

Ecuador. Shingupino rain forest between Río Napo and Tena, 8 km SE of Tena, ca. 1500 ft., 1960, Grubb et al. 2947 (isotypes, BM, US).

Plants medium sized, pale to dark green or yellowish-green, generally saxicolous, rarely corticolous. Secondary stems few branched, to 3 cm long; in cross-section hyalodermis generally distinct, at least formed on one side, epidermal cells larger than outer cortical cells. Leaves crowded to distant, crispate and tortuose; lateral leaves erect-spreading when wet, oblong to oblong-obovate, occasionally orbicular-obovate, (1.5)2-2.5 mm long, 0.6-0.9 mm wide, obtuse or rounded, apiculate or abruptly short acuminate, often pinched at the apex; margins plane, limbate with 2-5 rows of linear cells, entire below, serrate in distal 1/4-1/3; costa set apart or closed, ca. 1/2-2/3 lamina length, gradually diverging; median cells rhomboidal to more commonly broadly hexagonal, 40-85(110) um long, 28-55 um wide, + thick-walled, marginal cells linear, often extending into acumen and to leaf base, usually distinct from inner basal cells, lower and basal cells short to long rectangular, +

porose; lateral leaves smaller, broadly ovate to ovate-short lanceolate. Setae long, 8-12 mm long, reddish-orange, papillose throughout, papillae blunt and short; urn ovoid to short cylindrical, ca. 1.5 mm long; operculum short rostrate, ca. 1.5 mm long. Calyptrae mitrate-campanulate, 2.2-2.5 mm long, with few hairs, base laciniate.

Etymology. Tortifolium, from the Latin tortilis (= twisted), and folia (= leaf), in reference to leaf habit, most noticable in a dry condition.

Distribution (Fig. 13 B). From scattered localities in the West Indies (Dominican Republic, Jamaica and Puerto Rico), and from southern Mexico south to Peru and upper Amazonian Brazil. Wet lowland to premontane forests, most common on rocks in streams or associated with seeps and waterfalls, rarely on decaying logs.

Specimens examined. MEXICO. Oaxaca: Side of mountain above Valle Nacional, 13 May 1963, Robinson 10025 (US).

GUATEMALA. Izabal: Between Virginia and Lago Izabal, Montana del Mico, 50-500 m, 5 Apr 1940, Steyermark 38819 (F); Cerro San Gil, 300-900 m, 25 Dec

1941, Steyermark 41866 (F).

COSTA RICA. Heredia: Finca La Selva, in quebrada El Salto, 3 Mar 1980, Hammel 7962 (MO).

JAMAICA. Moody's Gap, 10 Sep 1908, Britton 909 (NY). St. Andrew: Below Morce's Gap, ca. 1 mile NE of Clydesdale, 18°05'N, 76°40'W, 4500-4700 ft, 17 Aug 1966, Crosby 3590B (MO). St. Thomas: Ca. Corn Puss Gap, ca. 4 miles N of Bath, 18°00'N, 76°21'W, 2100 ft, 29 Jul 1966, Crosby 3307 (MO).

DOMINICAN REPUBLIC. La Vega: 42 km E of Constanza, 7 km W of Carraterra Duarte, Casabito Falls, 19°01'N, 70°33'W, 3000 ft, 4 Apr 1981, Buck 5344 (NY), Reese 15802 (NY).

PUERTO RICO. Alto de la Bandera, near Adjuntas, 14 Mar 1913, Britton & Marble 2204 (NY).

COLOMBIA. Antioquia: 6.6-14.6 km de Campamento, en carretera a Las Brisas, 1430-1830 m, 2 Aug 1986, Churchill et al. 15042 (HUA, NY). Putumayo: ca. 40 km NW of Puerto Asis, ca. 1000 ft, 28-29 Jul 1963, King & Guevara C-1037 (US). Santander: Bucaramanga, 5000 ft, Weir 147 (NY). Valle: La Elsa hacia El Danubio, ca. 03°30'N, 76°45'O, 520-700 m, 24 Jun 1987, Churchill et al. 15250 (CUVC, HUA, NY).

ECUADOR. Esmeraldas: Parroquia Concepcion, Playa Rica, 105 m, 10 Dec 1936, Mexia 8426a (B, BM, F, NY).

PERU. San Martín: Lamas, Yurimaguas-Tarapoto km 107, 700 m, 15 Sep 1982, Frahm et al. 1389, 1606 (B), 500 m, 16 Sep 1982, Frahm et al. 1629 (B).

BRAZIL. Amazonas: Slopes and summit of Serra Curicuriari, from Igarape Arabu of the Rio Curicuriari, 00°20'S, 66°50'W, ca. 450 m, 9-12 Jul 1979, Buck 2506 (INPA, NY). Acre: Serra da Moa, Rio Moa, 6 km above school, 25 Apr 1971, Prance 12460 (NY).

Lepidopilum tortifolium Mitt. is most likely to be confused with another aquatic species, L. stillicidiorum Mitt., but that species is more robust with elongate leaves often 4-5 mm long and with corresponding longer median lamina cells (65-115 μ m). Furthermore the attenuate forms of L. stillicidiorum have leaves that are smaller but in shape are ovate-lanceolate with a broadly and gradually acuminate apex.

25. Lepidopilum arcuatum Mitten, J. Linn. Soc., Bot.

12: 375. 1869. Type. Ecuador. Bombonasa, Spruce 733 (holotype, NY). Fig. 45.

Lepidopilum erubescens C. Mueller, Flora 58: 547.

1875, syn. nov. Type. Colombia. Antioquia:

Frontino, 8000 ft, 1874, Wallis s.n. (isotype,
H-BR).

Plants glossy green, rather large, ramicolous.
Primary stems creeping; secondary stems ascending and erect, to 6 cm long, branches few; hyalodermis well developed, outer cortical cells in 2-3 layers, rusty-red, inner cortical cells large, hyaline, numerous. Leaves crowded, strongly complanate, flexuose or crispate when dry, lateral leaves spreading, narrowly oblong-lanceolate to oblanceolate or obovate, strongly asymmetric, 3-3.5 mm long, 0.6-0.9 mm wide, short- to long-acuminate; margins plane to somewhat erect above, limbate, border often quite strong, serrate in distal $1/4-1/3$, occasionally nearly entire or bluntly serrate; costae not particularly strong, ca. $2/3$ lamina length, often set apart at base, gradually diverging; upper and median cells short- to long-hexagonal, often somewhat irregularly so, 75-100 μ m long, 27-31 μ m wide, porose, marginal cells linear, in 2-3 rows, basal cells long-rectangular, oblong, or hexagonal, porose; median leaves appressed or erect, generally symmetric, ovate, abruptly long-acuminate, often distally channeled, distally serrulate or entire, costae $2/3-3/4$ lamina length, gradually diverging, upper and median cells

hexagonal to broadly fusiform, 75-95 μm long, 22-27 μm wide, porose. Autoicous. Perigonia distributed along upper stem and branch with perichaetia, leaves ovate-short lanceolate, 1-1.2 mm long, acuminate, costae absent, antherida many. Perichaetial leaves ovate lanceolate, 2.7-3.5 mm long, acuminate, costae absent. Setae short, 1.3-1.8 mm long, densely papillose throughout, papillae low, rounded, reddish-orange; capsules erect, urn ovoid, becoming flared when deoperculate, 1.0-1.3 mm long; exothecial cells oblong to rectangular, evenly thick-walled; stomata appearing sunken; annulus cells in 2-3 rows, obliquely short rectangular or quadrate-rounded; opercula conic-short-rostrate, to 1 mm long; exostome to 610 μm long, papillose, endostome to 710 μm long, papillose. Spores 13-15 μm in diameter, lightly papillose. Calyptrae mitrate-short campanulate, 3.5-3.8 mm long, smooth, pilose, base lacerated.

Etymology. Arcuatum, from the Latin arcutus (curved like a bow); in likely reference to the lateral leaf shape.

Distribution (Fig. 13 A). From Colombia south to Ecuador. In premontane to montane forest, to 2430 m,

on tree or shrub branches.

Specimen examined. ECUADOR. Bombonasa, Spruce 374
(NY).

This taxon is poorly characterized owing to so few collections. I have included Mueller's L. erubescens based on the similiarity of the leaf shape. Unfortunately the type of L. erubescens is represented by only 2 leaves (H-BR)! Thus, the placement of this collection should be considered tenuous at best, however Mueller's description of the sporophyte notes that the setae are short.

26. *Lepidopilum diaphanum* (Swartz ex Hedwig) Mitten, J.

Linn. Soc., Bot. 12: 382. 1869. Fig. 46.

Hypnum diaphanum Swartz ex Hedwig, Spec. Musc. 243,
pl. 61, f. 1-6. 1801. Pterygophyllum
diaphanum (Swartz ex Hedwig) Bridel, Mant.
Musc. 150. 1819; Hookeria diaphana (Swartz ex
Hedwig) Hooker & Greville, Edinburgh J. Sci. 2:
227. 1825. Type. Jamaica, Swartz s.n.
(holotype, G; isotypes BM, NY, H-BR).

Lepidopilum tenuifolium Mitten, J. Linn. Soc., Bot.

12: 382. 1869, syn. nov. Type. Ecuador.

Chimborazo, Spruce s.n. (holotype, NY).

Lepidopilum brachyphyllum Brotherus in Herzog,

Biblioth. Bot. 87: 136. 1916, syn. nov. Type.

Bolivia. Espirito Santo, 1600 m, Jun 1911,

Herzog 2724 (holotype, H-BR; isotypes, JE, L,

NY).

Lepidopilum apollinairei Brotherus & Paris in

Paris, Rev. Bryol. 33: 104. 1906, syn. nov.

Type. Colombia. La Vega, Jun 1905, Apollinaire

s.n. (holotype, H-BR; isotypes, L, NY).

Lepidopilum huallagense Brotherus, Hedwigia 45: 282.

1906, syn. nov. Type. Peru. Río Huallaga,

Cerro de Escalero, 1100 m, Jan 1903, Ule 2383

(lectotype, H-BR; isoelectotype, L). Syntype.

Peru. Río Huallaga, Cerro de Escalero, 1100 m,

Jan 1903, Ule 2382 (H-BR). My choice of the

type is based on abundance of material and

a duplicate collection.

Plants medium sized, rather lax in appearance,
glossy and metallic pale to olive green, occasionally
rufous, corticolous or saxicolous. Primary stems
creeping; secondary stems rather lax, spreading to

ascending, to 12 cm long; in cross-section stem often flattened, hyalodermis with 2-3 layers of outer cortical cells, + thick-walled, rusty-red. Secondary stem leaves complanate, loosely crowded to somewhat distant, flexuose or not; lateral leaves loosely erect-spreading or spreading, weakly to strongly asymmetric, shape variable, ovate-short oblong, obovate to ovate-short lanceolate, 2.2-3.0 mm long, 1.0-1.3 mm wide, very short to long acuminate, usually abruptly so; margins plane, folded below, limbate, smooth to inconspicuously serrulate or serrate in distal $1/5-1/3$; costae weak to somewhat strong, closed or set apart, $(1/3)1/2-2/3$ lamina length, gradually diverging; median and upper cells large, hexagonal to broadly fusiform, 130-150 μm long, 30-55 μm wide, marginal cells linear in 1-3 rows, basal cells short to long oblong or irregularly rectangular, insertion cells often golden-brown; median leaves erect to appressed, nearly symmetric, broadly ovate to ovate-oblong, occasionally nearly orbicular, ca. 2 mm long, 1.2 mm wide, very short to long acuminate, margins smooth to serrate in distal $1/5-1/4$, costae set apart, ca. $1/2$ lamina length, gradually diverging, median and upper cells hexagonal, marginal cells linear in 1-3 rows. Propagula occasionally present, long cylindric, long cylindric,

septate, to 0.8 mm long. Dioicous. Sporophytes unknown.

Etymology. Diaphanum, from the Latin, diaphanius (colorless, or nearly transparent); in reference to the color of the leaves.

Distribution (Fig. 13 A). From Jamaica and Guatemala south to Venezuela and Colombia to Peru and Bolivia. In low to mid montane forests, from near sea level to 1700 m; on wet rocks (often associated with water falls), soil, leaf litter and base of tree trunks.

Specimens examined. GUATEMALA. Baja Verapaz: Near Jicaro, 4300 ft, 21 Feb 1945, Sharp 2700 (US). Zacapa: Along Rillito del Volcan de Monos, 1150-2100 m, 10 Jan 1942, Steyermark 42374 (F).

COSTA RICA. Cartago: Reserva Forestal Tapanti, vertiente oriental del Río Macho, 1340-1600 m, 3-4 Jul 1977, Griffin et al. 209 (B, F, FLAS, NY, U).

JAMAICA. Vicinity of Cinchona, Morce's Gap, 2-10 Sep 1905, Britton 154 (NY). Dollwood, 31 Aug 1906, Nichols 107a, 168 (NY).

VENEZUELA. Amazonas: Cerro de la Neblina, Rio Yatua, 140-1700 m, 28 Dec 1957, Maguire et al. 42543a

(NY).

COLOMBIA. Cundinamarca: La Vega de Bogota, May 1905,
Apollinaire s.n. (US).

The areolation of these plants is of a lax nature that suggests an association with a very humid or aquatic environment. The species, as described here, is quite variable in leaf shape (Fig. 46), possibly because of the often wet habitats, but the laxness of the plants, the border of linear cells in 1-3 rows and the very large cells are distinctive and should separate it from other Lepidopilum species.

27. Lepidopilum curvifolium Mitten, J. Linn. Soc., Bot.

12: 374. 1869. Type. Ecuador. Bombonasa, Spruce 724 (lectotype, NY; isoelectotypes, H-BR, NY, US).

Two collections exist at NY of Spruce 724, the one I selected contains abundant material, is attached to a branch, and has an associated Mitten illustration. Fig. 47.

Lepidopilum gertrudis Herzog, Biblioth. Bot. 87:

137. 1916, syn. nov. Type. Bolivia.

An Baumen im Bergwald des Rio Tocorani, ca.

2200 m, Jul 1911, Herzog 4020 (holotype, JE;

isotypes, L, NY).

Plants glossy light- to dark-green, medium to somewhat robust, ramicolous. Primary stems short creeping, secondary stems erect or ascending, 4-10 cm long, few-branched; in cross-section hyalodermis well developed, outer cortical cells in 5-6 layers. Secondary stem leaves crowded to somewhat distant, loosely complanate, erect-spreading wet or dry, crispate, oblong to obovate, (2.6)3.5-5.0 mm long, (1)1.5-2 mm wide, short acuminate, apex often pinched; margins entire below, serrate in distal 1/2-2/3 of lamina, limbate but often indistinct; costae closed to set apart, 1/3-1/2 lamina length, gradually diverging; upper median cells rhomboidal to hexagonal, (44)55-78 μ m long, 15-24 μ m wide, somewhat thick-walled, smooth to porose, basal cells long hexagonal, rectangular or oblong, porose; median leaves ovate to ovate-oblong, to 2-3 mm long, 1.2-2 mm wide, short to somewhat long acuminate, costae 1/3-1/2 lamina length. Propagula in leaf axils, sometimes extending along one or both fork of costa, mostly on secondary stem branches and on damaged shoots, long cylindrical, to 0.6 mm long. Dioicous. Perigonal leaves oblong-lanceolate, to 1.2 mm long, broadly acuminate. Perichaetial leaves

ovate-subulate, to 2 mm long, long-acuminate or subulate, distally with a few sharp serrations, costae absent. Setae somewhat elongate, straight or curved, 4.5-6(8) mm long, reddish-orange, papillose throughout except at very base, papillae low and also short spinose, rounded, to 45 μ m long; capsules erect, ovoid, 1.5-1.8 mm long; exothecial cells short- to long-rectangular or oblong, thick-walled; stomata few at urn base, sunken; operculum conic long rostrate, ca. 1.2 mm long. Spores 14-17 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, 1.4-1.8 mm long, pilose, laciniate at base.

Etymology. *Curvifolium*, from the Latin, *curvi-* (curved) and *folia* (leaf); in reference to leaf shape.

Distribution. (Fig. 14). From Ecuador south to Peru and Bolivia on the eastern slopes of the Andes. In lowland to montane forest, at 245-2200 m, on branches of shrubs and trees.

Specimens examined. ECUADOR. Morona-Santiago: Mision Bomboiza, 03°29'S, 78°34'W, ca. 800 m, 23 Apr 1973, Holm-Nielsen et al. 4174 (US). Napo: Anangu, south shore of Rio Napo, ca. 00°32'S, 76°23'W, 245-325

m, 29 Jul-4 Aug, 1985, Churchill & Sastre 13800, 13819 (NY).

PERU. Cuzco: Rio Pachiri meeting with Rio Tintiniquiato, 1500 m, 6 Dec 1930, Bues s.n. (F). San Martín: Rioja, between Moyobamba-Chachapoyas km 409, 1100 m, 29 Aug 1982, Frahm et al. 119, 315, 344 (B), km 397, 1500 m, 30 Aug 1982, Frahm et al. 185, 466 (B, U); Lamas, between Yurimaguas-Tarapoto, km 107, 700 m, 15 Sep 1982, Frahm et al. 1365, 2051 (B).

BOLIVIA. Autahuacaua, Espirito Santo, 750 m, Jun 1909, Buchtien s.n. (B, H-BR).

The higher elevational plants tend to be more robust gametophytically, and exhibit propagula that extend along one or both costae as in the type described by Herzog as L. gertrudis and illustrated in his figure 60 (Herzog, 1916). The BRYOTROP project represented by the above collections by Frahm et al. are a remarkable series of collections that allowed a good assessment of the higher elevational forms.

In aspect this species resembles L. polytrichoides, but the ovate-lanceolate leaves, the gradually long-acuminate apex, and short setae readily separate that species from L. curvifolium. Likewise L. curvifolium exhibits rather distinctive perichaetial leaves that are

ovate-subulate or linear and are easily observed in the perichaetial buds or on the mature perigynia. The lowland forms are small and somewhat less densely foliate, thus they may be confused with L. surinamense, but that species exhibits usually dense rhizoids on the primary and occasionally secondary stem bases, smaller leaves, often with a twisted apex, inconspicuous perichaetial leaves and a sporophyte with a short seta.

28. Lepidopilum polytrichoides (Hedwig) Bridel,

Bryol. Univ. 2: 269. 1827. Hypnum polytrichoides

Hedwig, Spec. Musc. 244, Tab. 61, f. 7, 8. 1801.

Type. Jamaica, Swartz s.n. (isotypes, BM, H-BR,

NY).

Fig. 48.

Pilotrichum biductulosum P. Beauvois, Prodr. 82.

1805. Lepidopilum biductulosum (P. Beauv.)

Wijk & Margadant, Taxon 10: 24. 1961. Type. S.

loc., s. coll. (G).

Campylotrichum acuminatum Sikora, Beitr. Natur-

Heilwissenschaft 1(2): 283. 1836. Type. Nova

Holland (probably Trinidad), Sieber s.n.

(holotype, FH). See Buck & Churchill, 1989.

Lepidopilum excelsum C. Mueller, Flora 58: 547.

1874, syn. nov. Type. Colombia. Antioquia,
Frontino, 8000', Wallis s.n. (isotypes, BM, H-
BR).

Lepidopilum polytrichoides Hedwig var. pellucens
Bescherelle, Ann. Sci. Nat. Bot. sér. 6, 3:
231. 1876. Type. Guadeloupe, L'Herminier s.n.
(isotype, NY).

Lepidopilum subpolytrichoides C. Mueller, Linnaea
42: 495. 1879, syn. nov. Type. Venezuela.
1855, Fendler s.n. (isotypes, BM, FH, H-BR,
NY).

Lepidopilum platyphyllum Renauld & Cardot, Bull.
Soc. Roy. Bot. Belgique 32(1): 192. 1894, syn.
nov. Type. Costa Rica. La vallee du Río Tuis,
bassin du Reventazon, 600 m, Pittier 5656
(holotype, PC; isotypes, G, H-BR, US).

Lepidopilum polytrichoides Hedwig var. costa-ricense
Renauld & Cardot, Bull. Soc. Roy. Bot.
Belgique 32(1): 192. 1894. Type. Costa Rica.
Buenos Aires, Pittier 5654 (lectotype, G;
isotypes H-BR, NY, PC). Syntype. Costa
Rica. Forets du Río Naranjo, 200-250 m, Pittier
5655 (NY).

Lepidopilum mnioides C. Mueller, Flora 83: 337.
1897, syn. nov. Type. Venezuela. Tovar, 3000

ft, Goebel s.n. (isotype, H-BR).

Plants large, often robust, glossy light- to dark-green, rarely rufous, ramicolous or corticolous, rarely epiphyllous or saxicolous. Primary stem prostrate and creeping, occasionally indistinct; rhizoids beneath, rusty-red; leaves often eroded from stem, scale-like, ovate-triangular, acuminate, costa double, parallel, widely separated; in cross-section stem epidermis larger than inner adjoining cortex cells, outer cortical cells in 2-5 rows of small and thick-walled cells, inner cortical cells larger and thin-walled, central strand absent. Secondary stems erect or ascending, solitary or moderately to sparsely branched, to 12 cm or longer, terminal branches rarely flagelliform or attenuate, in cross-section similar to primary stems; leaves usually distant, crispate when dry, wide-spreading when wet; lateral leaves ovate-lanceolate to ovate-oblong, asymmetric, 5.5-8 mm long, 2-3 mm wide, short to long acuminate, occasionally twisted, base folded $1/3$ - $1/2$ of leaf length; margins plane, limbate, border weak to strongly distinct, serrate to spinose in upper $1/2$ - $3/4$; costae closed at base, $1/2$ - $2/3$ lamina length, diverging; median cells rhomboidal to hexagonal, somewhat thick-walled, 75-120

um long, 28-34 um wide, basal cells long rectangular, marginally with 1-4(5) rows of linear cells, occasionally border indistinct; median leaves broadly ovate-short lanceolate, generally symmetrical, 5-5.5 mm long, 2-2.2 mm wide, short to long acuminate, margin plane, limbate, with 2-5 rows of linear cells, serrate in upper half, serrulate below to near base, costa divergent, often slightly separated. Autoicous or synoicous. Perigonial leaves ovate-lanceolate, costa absent; paraphyses numerous, long cylindrical. Perichaetial leaves ovate-subulate, costa absent. Setae short, 2-3(3.8) mm long, often stout, reddish-orange, papillose usually in distal half but occasionally to near base, papillae low and rounded or somewhat projecting, below appearing low or absent; capsules erect, urn ovoid- or oblong-cylindrical, 1.2-1.6 mm long; exothecial cells long rectangular, thick-walled, 55-85 um long, cells at urn mouth short oblate rectangular, thick-walled, dark golden-red in 2-4 rows; annulus of a few short-quadrate cells, reddish-orange; opercula short rostrate, ca. 0.9-1.2 mm long; exostome to 840 um long, endostome to 860 um long, keeled, yellowish-white, cilia absent. Spores spherical, 15-17 um in diameter, appearing smooth. Calyptrae mitrate-campanulate, ca. 1.8 mm long, smooth or occasionally

plicate, with few to many multi-cellular hairs,
laciniate at base.

Etymology. Polytrichoides, from the moss genus Polytrichum, in likely reference to the Polytrichum-like robustness of this species.

Distribution (Fig. 14). From southern Mexico south through Panama, widespread in the West Indies, and in South America from the Guianas to Colombia south to Peru on the eastern ranges, and on the upper regions of Brazilian Amazonia. Plants are commonly epiphytic, on branches, trunks and buttresses, exposed roots and occasionally on rocks in humid tropical to low or mid montane forests at elevations from 50-1800 m.

Representative specimens examined. MEXICO. s. loc. Ruiz & Pavon s.n. (NY). Chiapas: 3 km E of Francisco Madero, NE of Cintalapa, 1250 m, 4 Oct 1974, Breedlove 38080 (MO). Oaxaca: Oaxaca?, Galiotti s.n. (BM).

GUATEMALA. Alta Verapaz: Cubilguitz, 350 m, Oct 1906, Turckheim 6914 (BM, H-BR), 6915 (H-BR, NY); Cerro Chinaja, between Finca Yalpemech & Chinaja, 150-700 m, 1-2 Apr 1942, Steyermark 45548a (F). Huehuetenango: Between Ixcán & Rio Ixcán, Sierra de los Cuchumatanes,

150-200 m, 23 Jul 1942, Steyermark 49368 (F). Izabal:
Along Rio Bonita, 30-150 m, 21 Dec 1941, Steyermark
41736 (F).

BELIZE. British Honduras-Guatemala border survey,
camp 32B, 2600 ft, 26 Feb 1934, Schipp 8-855 (MO, NY).
Toledo: Maya Mts., Gabriel Camp-Edwards Central Camp,
25 Mar 1977, Boutin & Schlosser 5152 (MO).

HONDURAS. Atlantida: Lancetilla Valle, near Tela,
20-600 m, 6 Dec-20 Mar 1928, Standley 53220 (F, US).
Copan: Quebrada Mojanales, 16 May 1919, Blake 7481B
(NY, US).

NICARAGUA. Gracias a Dios, Cabo, 1 May 1923,
Schramm s.n. (NY, US). Zelaya: Mt. Liveco, near Siuna,
6 Jan 1970, Seymour 3073 (MO).

COSTA RICA. Cartago: Chetaria, 700 m, 20 Dec 1928,
Valerio 218 (US); Reserva Forestal de Tapanti, 1500 m,
Aug 1973, Griffin 282 (FLAS). Guanacaste: Near
Tilaran, 750 m, Standley & Valerio 44691 (H-BR).
Heredia: Ca. 12 km by rd. 113 from San Rafael, 1850 m,
2 May 1975, Crosby 10935 (U). Limon: W of bridge over
Río Toro Amarillo, W of Guapiles, 20 Feb 1966,
Crosby 3673 (H). Puntarenas: 6 km S of San Vito, 1250
m, 1 Aug 1968, Koch 4966 (NY).

PANAMA. Cocle: N of El Valle de Anton, base of
Cerro Pilon, 1000 m, 28 Mar 1969, Crosby 4419 (MO).

Colon: Ca. 7 km SW of Portobelo, Río Guanche near sea,
3 Jun 1975, Crosby 10782 (MO). Panama: Cana, Williams
1056 (F, NY); below Su-Lin Motel, Cerro Campana, 1000
m, 25 Mar 1969, Crosby 4362 (B, F, FLAS, MO, NY, U,
US). Veraguas: 5.4 km NW of Santa Fe, 580 m, 18 May
1975, Crosby 10240 (MO).

CUBA. Oriente: top of El Yunque, 17-18 Dec 1914,
Ekman 3947 (BM, NY); Mt. Baracoa, Underwood & Earle 652
(NY); Yunque de Baracoa, 2 Jun 1860, Wright 162 (NY).

JAMAICA. Portland: Gorge of Stony River below jct
of the Macungo River, 3 Mar 1970, Proctor 31254 (MO);
foothills of John Crow Mts., E of Seamen's Valley, 200-
425 m, Feb 1920, Maxon & Killip 217 (BM, F, NY, US).
St. Andrew: Hardwar Gap, 3800 ft, Griffin & Steere 36
(B, FLAS). St. Thomas: House Hill, 600 m, Maxon 3496
(B, BM, F, H, MO, NY, US); vicinity of Corn Puss Gap,
ca. 4 miles N of Bath, 2100 ft, 9 Apr 1969, Crosby &
Crosby 4588 (MO, NY, U). Trelawny: Cockpit Country,
just N of Wilson's Run, 500 m, 18 Apr 1981, Buck 5891
(NY).

HAITI. Riviere Glace, la Hotte, 4-7 Aug 1945,
Holdridge 3091 (FH).

DOMINICAN REPUBLIC. Barahona: Ca. 1 km NW of Pae
Mingo, 1000 m, 28 Dec 1982, Zanoni et al. 25070-I (U).
El Seibo: 16 km S of Miches on rd. to El Seibo, 1400

ft, 28 Mar 1981, Buck 5026 (NY, U). La Vega: Loma Campana, 1036 m, 2 Jan 1948, Allard 18328 (US).

PUERTO RICO. Caribbean Natl. Forest, Luquillo Div., S of Mameyes at 8.2 km marker, 14 Apr 1969, Crosby & Crosby 4657 (FLAS, MO, NY, U); along Rio Juan Diego, Sierra de Luquillo, Steere 5438 (MO); Arroyo de Los Corchos, between Adjuntas & Jajuya, 800-900 m, 13 Mar 1915, Britton 5342 (NY).

GUADELOUPE. s.loc., 1867, L'Herminier s.n. (BM, NY); s. loc., Nov 1900, Duss 595 (NY).

DOMINICA. Roseau, 1914, Noel 16 (BM, NY); Larier Claire River, 30 May 1896, Elliott 2342 (BM); Trafalgar Falls trail, 1500 ft, 13 Jul 1968, Griffin s.n. (FLAS).

MARTINIQUE. Fontaine Didier, 1868, Husnot 156 (B, BM, FH, H-BR, NY); W of Hopital de Colson, 600 m, 19 Apr 1969, Crosby & Crosby 4762a (MO).

ST. LUCIA. Upper slopes of Morne Gimie, 2000-3100 ft, 16-17 Feb 1936, Box s.n. (BM).

ST. VINCENT. Richmond Valley, 26 Jan 1892, Elliott 173 (BM).

GRENADA. Grand Etang forest, 6 Jan 1906, Broadway 7868 (NY).

COLOMBIA. Antioquia: 2 km NNE of Barroblano, 280-310 m, 31 Jul 1986, Churchill et al. 14950 (HUA, NY). Choco: Truando, Dec 1857, Schott 1 (F); Negria, along

Rio San Juan, 50 m, 17 Apr 1939, Killip 35013 (US).

Cordoba: Río Sinu, Bolivar, 1918, Pennell 4790 (NY).

Magdalena: Sierra Nevada de Santa Marta Natl. Pk., Río Buritaca, Griffin et al. 1141(F, FLAS, U).

VENEZUELA. Aragua: La Cumbre Natl. Pk., 1100 m, Alston 5854 (US); Henri Pittier National Park, 800 m, 21 Jul 1977, Owens 26 (FLAS). Amazonas: Río Yatua, Cerro de la Neblina, 650-900 m, 21 Dec 1953, Maguire et al. 36828 (MO, NY). Carabobo: s. loc., Funck & Schlim 615 (NY); Rio San Gian, 700-900 m, Steyermark & Steyermark 95278 (US). Yaracuy: Montana de Maria Lionza, Quebrada Quibayo, 250-1000 m, 14 Mar 1981, Steyermark et al. 125087-a (FLAS). Zulia: Sierra de Perija, W of Dakuma, 1000 m, 22 Sep 1947, Jangoux 10213 (US); San Jose de los Altos, 1600-1800 m, 7-24 Jul 1975, Griffin 235 (FLAS).

TRINIDAD. St. George: Heights of Aripo, 9 Mar 1922, Broadway 7124 (F, MO, NY); S slope of Cerro del Aripo, 1900 ft., 5 Jul 1965, Crosby 2206 (MO).

SURINAM. Sipaliwini, Oelemari, 25 km downstream from airstrip, 23 Mar 1963, Boer 1042 (FLAS, U).

FRENCH GUIANA. Sin loc., Lepieur s.n. (NY). Cayenne: Cayenne, Walker s.n. (BM). Saint-Laurent du Maroni: Saul, Monts La Fumee, 200-400 m, 19 Nov 1982, Boom & Mori 2486 (NY); Saul, near Bateau, 200-300 m, Mar 1985,

Aptroot 15407 (U).

ECUADOR. Azuay: Gualaquiza, 20 Jun 1909, Allioni 8311 (H-BR). Morona Santiago: Santiago River, Kerr 27247 (US). Napo: Anangu, along Río Napo, ca. 75 km E of Puerto Francisco de Orellana, 245-325 m, 29 Jul-4 Aug 1985, Churchill & Sastre 13744 (NY); Hotel Jaguar, Río Napo, ca. 50 km below Puerto Misahualli, 400 m, 11 Jan 1981, Steere E-95 (NY). Pastaza: Southern border of Río Napo, 2 km W of Yuraipa, 440 m, 24 Jun 1968, Holm-Nielsen & Jeppesen 944 (MO, U, US). Los Rios: Hacienda Clementina, 500 m, 20 Feb 1947, Harling 2135 (NY).

PERU. S.loc. Spruce 718 (NY). Huanuco: Monzon, 200-600 m, 1903, Weberbauer 3676 (H-BR). Junin: Satipo, Aug 1940, Ridoutt 11803 (FLAS, US). Loreto: Pongo de Cainarachi, Sep 1902, Ule 2371 (FH, H-BR). San Martín: Yurimaguas-Tarapoto km 107, 700 m, 15 Sep 1982, Frahm et al. 1608, 2072 (B); Campana, Spruce s.n. (NY).

BRAZIL. Acre: Río Moa, 8 km above Cachoeira Grande, 27 Apr 1971, Prance et al. 12551 (INPA, NY). Amazonas: Serra Curicuriari, 450 m, 9-12 Jul 1979, Buck 2472 (INPA, NY).

Although most populations of L. polytrichoides exhibit little variation, there are a number of forms

that have drawn the attention of bryologists leading them to describe these as new species, however the variation discussed below can often be found throughout the range of the species.

In the following discussion all taxa exhibited identical sporophytic features: Lepidopilum excelsum exhibits an abruptly long hair point that is somewhat unusual but is not particularly uncommon in other collections examined; L. subpolytrichoides was originally described as being dioicous, but examination of type material (BM!, FH!) showed that the plants are both autoicous and synoicous; L. platyphyllum is a more robust form with the apex somewhat rounded (at least in some of the type material examined) but this is not atypical, I can find no fundamental reason to recognize this taxon as did Welch (1976).

Lepidopilum polytrichoides is not likely to be confused with any other species except possibly L. surinamense which has a similar sporophyte but the leaves are oblong-obovate, and L. curvifolium Mitt. which has ovate-oblong to obovate leaves and a seta that is elongate (4-8 mm) and densely papillose or short spinose.

I have not seen the collection cited by Crum and Anderson (1981) from Florida (at Yale Univ.); however, they question the presence of this species in the U.S.

29. Lepidopilum surinamense C. Mueller, Linnaea 21:

193. 1848. Hookeria surinamensis (C. Mueller) C.
Mueller, Syn. Musc. 2: 207. 1851. Type.
Surinam. Mariepaston, Kegel 1406 (isotype, H-BR).

Fig. 49.

Lepidopilum flexifolia C. Mueller, Syn. Musc. 2:

206. 1851. Type. Trinidad. Monte Tocuche,
Cruger s.n. (isotype, NY).

Lepidopilum subflexifolium C. Mueller, Linnaea 38:

605. 1874, syn. nov. Type. Brazil. Parana-miri
dos Ramos, Spruce 719 (lectotype, NY;
isolectotypes, BM, H-BR, NY).

Lepidopilum aurescens C. Mueller, Linnaea 42: 435.

1879, syn. nov. Type. Argentina. Chaco: Rio
Seco - San Andres, subtropica, Lorentz s.n.
(isotypes, H-BR, NY).

Lepidopilum leptoloma Brotherus, Hedwigia 45: 281.

1906, syn. nov. Type. Brazil. Amazonas: Rio
Madeira, Marmellos, ad ramulos arborum, Mar
1902, Ule 265 (lectotype, H-BR; isolectotypes,
BM, H-BR, NY).

Lepidopilum rotundifolium Bartram, Bryologist. 54:

239. 1952. Type. Costa Rica. General, 800 m,

22 Aug 1934, Alfaro 160 (isotype, NY).

Lepidopilum steyermarkii Bartram, Fieldiana Bot. 28:

6. 1951, syn. nov. Type. Venezuela. Merida:
Between Hacienda Agua Blanca above La Azulita
and Rio Capaz, 975 m, 26 Apr 1944, Steyermark
56138 (isotype, US).

Plants medium-sized, glossy light to dark green or yellowish-green, corticolous, ramicolous, lignicolous or rarely epiphyllous. Primary stems creeping, usually covered by dense tomentum; secondary stems ascending or erect, to 6 cm tall, often solitary or few branched, loosely complanate; hyalodermis present, outer cortex cells small, thick-walled, rusty-red in 4-5 rows, inner cortex cells large, hyaline, numerous. Leaves somewhat crowded below, becoming distant above, crispate or flexuose, erect-spreading when dry, usually spreading when wet, lateral and median leaves not strongly differentiated; lateral leaves ovate-oblong, narrowly-oblong to obovate, (2.5)2.8-3.2 mm long, 1.5-1.8 mm wide, asymmetric, abruptly short acuminate to rounded-apiculate, apex pinched, often twisted; margins plane, weakly to distinctly limbate, border of 1-2 rows of linear cells, serrate in distal 2/3-3/4, distally often sharply serrate, below often serrulate; costae closed

to set apart, diverging, $1/3-1/2$ lamina length; median cells rhomboidal to hexagonal, often thick-walled and porose, 62-100 μm long, 17-34 μm wide, basal cells rectangular to oblong, insertion cells golden-yellow; median leaves ovate-oblong, mostly symmetric, 2.5-2.8 mm long, 1.25-1.5 mm wide, bluntly short acuminate, costa mostly joined, otherwise similar to lateral leaves. Propagula in leaf axils, long cylindrical. Dioicous. Perichaetial leaves oblong-lanceolate, 1.8 mm long, acuminate, margins distally serrate, costae absent. Setae short, 2.5-3.0 mm long, smooth or distally roughened, reddish-orange; capsules erect to suberect, ovoid-cylindrical, 2.5-3.0 mm long (usually equal to or shorter than setae); exothecial cells mostly short rectangular, thick-walled; opercula rostrate, ca. 1-1.2 mm long; exostome to 550 μm long, often fragile and absent, endostome to 700 μm long. Spores 14-17 μm in diameter, lightly papillose. Calyptrae shortly mitrate-campanulate, ca. 1.5 mm long, plicate, sparsely hairy.

Etymology. Surinamense, in reference to the country, Surinam.

Distribution (Fig. 15). From Cuba, St. Vincent and

Nicaragua south to Peru and northern Argentina, widespread in Amazonia and along coastal Brazil. In wet lowland forest from 10 to 975 m; on lianas, branches of treelets and shrubs, tree trunks and exposed roots, rarely found on decaying logs or epiphyllous.

Representative specimens examined. NICARAGUA.

Zelaya: Ca. 6.3 km S of bridge at Colonia Yolania, on rd. to Colonia, 200-300 m, 29-31 Oct 1977, Stevens 4892, 4893, 4895 (MO).

COSTA RICA. Río Bamamo, 470 m, 9 Nov 1934, Alfaro 67c (F).

PANAMA. Panama: Canal Zone, Barro Colorado Island, Jan-Feb 1938, Willis s.n. (F, FH).

CUBA. Sierra Maestra, Río Oro, ca. 30 km S of Bayamo, 350-400 m, 17 Aug 1951, Webster 963 (FLAS).

ST. VINCENT. Bonhome Valley, 1500 ft., 1892, Elliott 58c (BM).

COLOMBIA. Antioquia: 2 km NNE of Barroblanco, 280-310 m, 31 Jul 1986, Churchill et al. 14947 (HUA, NY); Rio Ampurrumiado, 200 m, 11 Oct 1947, Gutierrez & Barkley 17C098b (F). Choco: Truando, Dec 1857, Schott 2, 12 (F). Vaupes: Río Apaporis, vicinity of Jerijerimo, Mar 1951, Schultes 11754 (FH, FLAS, NY).

VENEZUELA. Amazonas: Dept. Río Negro, along Río Mawarinuma, beyond Canon Grande, 140 m, Feb-Mar 1984, Buck 11267 (NY, VEN).

TRINIDAD. Ortorie River, Guayaguayare Rd., 25 Mar 1921, Britton 2558 (NY); Blanchisseuse Rd., 8th mile, 1350 m, 6 Nov 1938, Alston 8963a (BM).

GUYANA. Mazaruni-Potaro: Akaio Landing, River Cuyuni, 1929, Richards 826 (BM, NY); Essequibo River, Moraballi Creek, near Bartica, 1929, Richards 84 (BM).

SURINAM. Coronie: W of mouth of Coppename River, 10 Mar 1954, Lindeman 5616 (U). Nickerie: Area of Kabalebo Dam project, near camp rd. km 212, 0-50 m, 20 Feb 1981, Florschutz-de Waard & Zielman 5682 (U).

FRENCH GUIANA. Cayenne: S slope of Mont Grand Matoury, 10 km SW of Cayenne, 0-200 m, Mar 1985, Gradstein 5860 (U); Montagne de Kaw, 250 m, 13 Jun 1979, Cremers 5805 (FLAS). Saint Laurent du Maroni: Haut Tampoc, Crique Alice, Orstom 4768 (U); 1 Apr 1977, Cremers 4768 (FLAS); Marouini, 10 Sep 1977, Cremers 5154b (FLAS).

ECUADOR. Chimborazo: Chimborazo, Spruce s.n. (NY). Esmeraldas: 2-4 km SE of San Lorenzo, 10 km, 7-17 Aug 1983, Boom 2633 (NY). Napo: Anangu, Río Napo, ca. 75 km E of Puerto Francisco de Orellana, 245-325 m, 29 Jul-4 Aug 1985, Churchill & Sastre-De Jesus 13809 (NY);

confluence of Quiwad and Tiwaeno Rivers, 28 Apr 1981, Davis & Yost 1050 (NY). Pichincha: 18 km NW of San Miguel de los Bancos, ENDESA reserve, 800 m, 27-29 Dec 1983, Buck 10547 (NY).

PERU. Loreto: Balsapuerto, lower Río Huallaga, 150-350 m, 28-30 Aug 1929, Killip & Smith 28463 (NY).

BRAZIL. Amazonas: Rio Madeira, Marmellos, Mar 1902, Ule 265 (BM); N from Sao Gabriel da Cachoeira to Cucui, just N of Igarape Ia-Mirim, near Jerusalem, 17 Jul 1979, Buck 2586 (INPA, NY); along Igarape Santa Luzia, just off Rio Uatuma, 16 Aug 1979, Buck 2853 (INPA, NY); Marari, Rio Jurua, Oct 1900, Ule 2240 (H-BR). Bahia: 8 km W of Itanagra on rd. to Subauma, 50 m, 27 May 1981, Boom & Mori 968 (NY). Para: Serra do Cachimbo, cataracts on Rio Curua, 887 km N of Cuiaba on BR 163, 350-500 m, 2-8 May 1983, Reese 16583 (INPA, NY); Serra Maze, 1208-1229 km N of Cuiaba, along RB 163, 100-200 m, Reese 16829 (INPA, NY); Macau airstrip, upstream on Rio Maicuru, 800 ft, Strudwick & Sobel 3433 (NY). Rondonia: Alto Condeias, 3 km E of Main Mibrasa Mine Camp, 200 m, 15 May 1982, Fife et al. 4143 (INPA, NY). Sao Paulo: Rio Mambu, Conceicao de Itanhaen, 100 m, Jun 1901, Schiffner 1431 (H).

This species is widespread in the neotropics and

thus has been given a wealth of names over the years by various bryologists. In most of South America this taxon is not likely to be confused with any other species, however in coastal region of northern South America this species overlaps with another closely related species, L. cubense. Lepidopilum cubense is rather widespread in the Caribbean and also known for the Guianas, Colombia, and Central America; given further field work in Colombia and Venezuela both are likely to be found. Differences between these species have been discussed under L. cubense.

30. Lepidopilum cubense (Sullivant) Mitten, J. Linn.

Soc., Bot. 12: 384. 1869. Hookeria cubensis
Sullivant, Proc. Amer. Acad. Arts Sci. 5: 285.
1861. Type. Cuba. Wright 85 p.p. (isotypes, BM,
FH, G, L, NY). See discussion section.

Figs. 50-51.

Lepidopilum phyllorhizum Mitten, J. Linn. Soc., Bot.

12: 385. 1869. Lepidopilum phyllorrhizans
Mitten ex Paris, Ind. Bryol. ed. 2, 3: 141.
1905, nom. inval. err pro L. phyllorhizum
Mitten. Type. Cuba. Wright 85 p.p.

(holotype, NY). Syn. fide Richards, Misc. Inf.

Kew 1934: 331. 1934. See discussion section.

Lepidopilum semilaeve Mitten, J. Linn. Soc., Bot.

12: 385. 1869, syn. nov. Type. Panama.

Charges, Sinclair s.n. (lectotype, NY). Choice of type based on number of plants with sporophytes and Mitten illustration.

Syntype. Ecuador, Quito, Jameson s.n. (NY).

Lepidopilum contiguum Renauld & Cardot, Bull. Soc.

Roy. Bot. Belg. 32(1): 193. 1894, syn. nov.

Type. Costa Rica. Río Naranjo, (1893, Gonduzapu) "Pittier 5657" (holotype, PC; isotype, NY).

Lepidopilum apiculatum Bartram, J. Washington Acad.

Sci. 24: 477, fig. 3. 1934, syn. nov. Type.

Costa Rica. Prov. Limon: Banano River, 80 m,

Gutierrez s.n. (isotype, US).

Lepidopilum skutchii Bartram, Bryologist 54: 239.

1952, syn. nov. Type. Costa Rica. Vicinity

of El General, 800-1000 m, Skutch 2530

(isotype, US).

Plants somewhat small, dull to glossy green to yellowish-green or golden-yellow, ramicolous or corticolous, forming small, loose tufts. Primary stems creeping, rhizoids few and inconspicuous; secondary

stems erect, to 2.5 cm long, few branched, branching often toward the base and appearing clustered; hyalodermis distinct, epidermal cells thin-walled, outer cortical cells in 2-4 rows, small, very thick-walled, reddish-orange, inner cortical cells larger, hyaline. Leaves mostly crowded to somewhat distant distally on branches, crispate or contorted when dry, erect-spreading when wet, lateral and median leaves not strongly differentiated, the latter somewhat smaller. Lateral leaves oval-oblong, oblong to oblong-lanceolate or oblong-obovate, symmetrical, 1.4-2.6 mm long, 0.4-1.2 mm wide, short acuminate to acute-apiculate, often pinched or twisted; margins plane to slightly recurved below, elimbate or weakly limbate, serrate in distal $1/4-1/3(1/2)$, rarely serrulate or entire, distal most teeth occasionally bifid; costae closed at base or slightly set apart, gradually diverging to somewhat parallel, $1/3-1/2$ lamina length; median and upper cells rhomboidal, fusiform or oblong-hexagonal, 40-70 μm long, 11-17 μm wide, thick-walled, occasionally somewhat lax, slightly porose, basal cells oblong-rectangular, usually porose, insertion cells yellow or golden-yellow; median leaves 0.4-1.2 mm long, short acuminate-apiculate. Propagula often on leaf apices, and occasionally along distal margins, short-cylindrical, often abundant. Dioicous. Perichaetial

leaves ovate-lanceolate, narrowly acuminate, costae absent. Setae elongate, (4)5-13 mm long, rusty-red, smooth below, papillose on distal 1/2; capsules erect to suberect, ovoid-cylindrical, 1.3-2.0 mm long; opercula conic-rostrate, 1.0-1.2 mm long. Spores 17-23 μ m in diameter, lightly papillose. Calyptrae mitrate-campanulate, 2.0-2.6 mm long, plicate, hairy.

Etymology. Cubense, in reference to the island of Cuba.

Distribution (Fig. 15). Cuba and Jamaica south to French Guiana, and from Guatemala to Panama and Colombia south to Ecuador. In lowland wet tropical to mid montane forests, from 80-1200 m; on branches and trunks of shrubs and treelets.

Specimens examined. GUATEMALA. Sacatepequez: Near Lake Lajas, ca. 1200 m, 28 Nov 1938, Standley 58125 (F).

COSTA RICA. Alajuela: San Ramon, 31 Jan 1936, Brenes s.n. (F). San Jose: Vicinity of El General, 850 m, Dec 1936, Skutch 3023 (F, FH, NY, US).

PANAMA. Cana, 2200 ft, 20 Apr 1908, Williams 1054 (F, NY). Above Penonome, at Bismark, 19 Mar 1908,

Williams 1065 (F, NY).

CUBA. Sierra de Camoa, Havana, 27 Jun 1911, Leon 2693 (NY); Sierra de Anafe, Havana, 19 Aug 1911, Leon 1828 (NY).

JAMAICA. Trelawny: Vicinity of Windsor Cave, 140 m, 21 Apr 1981, Buck 5923, Crosby 13922, 13927 (NY).

PUERTO RICO. Caribbean Natl. Forest, Luquillo Division, trail to El Toro, 25 Feb 1981, Buck 3639 (NY).

COLOMBIA. Cauca: Municipio de Guapi, Parque Nacional Natural Isla Gorgona, Gorgonilla, cerca al Faro, 100 m, 14 Sep 1987, Rudas Ll. & Aguirre C. 286, 298 (FLAS).

SURINAM. Van Asch van Wijek Mts., Ebbatop, 15 Nov 1951, J. & P. Florschutz 1480 (U); Kabaleo, 19 May 1951, J. & P. Florschutz 2205 (U).

FRENCH GUIANA. Confluence of I'Itany (Haut Maroni) and Marouini Rivers, 14 Jan 1977, Cremers 5128 (U).

The type collection by Wright, no. 85, represents a mixture of at least 2 and possibly 3 species. It is apparent from Mitten (1869), and the type collection with illustration (NY), that he erroneously considered the original description of L. cubense to be a plant with ovate leaves and an abruptly acuminate apex

(=Lepidopilidium portoricense (C. Muell.) Crum & Steere). The other element Mitten (1869) described as a new species, L. phyllorhizum which he illustrated with the characteristic propagula at the leaf apex. Richards (1934) addressed this problem and was the first to point out that L. phyllorhizum is an obligate synonym of L. cubense.

I had originally considered L. cubense and L. semilaeve Mitt. as two distinct and closely related species but several intermediate forms have been observed. It is possible that two subspecies could be recognized based on the following: L. cubense with leaves mostly 1.4-2.0 mm long, 0.4-0.6 mm wide, and seta 6-13 mm long, and distributed in the Caribbean and the Guianas; L. semilaeve with leaves 2.0-2.6 long, 0.7-1.2 mm wide, and seta 4-5(6) mm long, and distributed in Central America south along the Andes. Plants from Colombia overlap completely, furthermore the above features abut. Possibly more collecting in the costal and high elevations of the northern Andes will provide further evidence in resolving or establishing the taxonomic level that could be assigned to these two forms. At present, I prefer not to recognize these forms at the subspecies or species level.

Lepidopilum cubense appears close to L. surinamense C. Muell. in respect to the gametophyte, but differs significantly sporophytically. The setae of L. cubense is elongate, usually 5-13 mm, with short capsules, 1.3-2.0 mm, whereas the seta of L. surinamense is shorter, 2.5-3.0 mm, with longer capsules, 2.5-3.0 mm. Gametophytically, the separation of these two species is more problematic. However in L. surinamense the primary stems are often conspicuously covered by dense rhizoids, and the secondary stem leaves, at least the lower ones, are larger, 2.8-3.2 mm long, 1.25-1.40 mm wide, whereas in L. cubense the primary stem rhizoids are usually inconspicuous, and the secondary stem leaves smaller, 2.0-2.6 mm long, 0.6-1.2 mm wide.

Bartram's L. apiculatum differs mainly in that the distal margin is entire to slightly serrulate. The inclusion of L. contiguum Ren. & Card. as a synonym is based on the above separation of the gametophytic features - the type material lacked sporophytes.

I have not noted elsewhere in Lepidopilum the presence of propagula at the leaf apex. In the small growth forms of L. cubense with propagula one is reminded of a Streptopogon or a member of the Calymperaceae in the aspect of the plant. Propagula on the leaf apices appear to be diagnostic for L. cubense although they not found in all collections.

DOUBTFUL NAMES & EXCLUDED TAXA

No attempt has been made to list all taxa that have been described as Lepidopilum and later transferred to other genera. This can be found in Index Muscorum (Wijk et al., 1964 & 1969). Nomina nuda listed below are those, in part, for which no material was available to assign to recognized taxa in the present treatment.

Lepidopilum aureo-purpureum C. Mueller in Ule, Hedwigia

38: 38. 1899, nom. nud.

Lepidopilum brachychaete C. Mueller in Paris, Ind.

Bryol. 720. 1897, nom. nud.

Lepidopilum daltoniaceum Fleischer, Hedwigia 63: 216.

1922, nom. nud. (Hookeria daltoniacea C. Mueller,

1922, nom. nud.).

Lepidopilum dubyanum Fleischer, Hedwigia 63: 215.

1922, nom. nud. (Hookeria dubyana C. Mueller ex

Fleischer, 1922, nom. nud.).

Lepidopilum flaccidissimum Bescherelle in Kindberg,

Enum. Bryin. Exot. 100. 1891, nom. nud.

= Crossomitrium orbiculatum C. Mueller, based on

collection at G from Guadeloupe. There is a very

small amount of material for determination but while

the plant is sterile the gametophytic features best match those described for C. orbiculatum.

Lepidopilum humblotii Renault & Cardot, Bull. Soc. Roy.

Bot. Belgique 33(2): 128. 1895, syn. nov.

= Leucomium strumosum (Hornsch.) Mitten

Type. Grande Comore, Humblot s.n. (holotype, PC).

The gametophytic plants exhibit all the features discussed by Allen (1987) for this pantropical species.

Lepidopilum latius Fleischer, Hedwigia 63: 216. 1922,

nom. nud. (Hookeria latior Geheeb & Hampe ex Fleischer, 1922, nom. nud.).

Lepidopilum leiopus C. Mueller in Paris, Ind. Bryol.

726, 1898, nom. nud.

Lepidopilum longicuspis C. Mueller, Hedwigia 38: 59.

1899, nom. nud. = ? Hookeria longicuspis C.

Mueller, = ? Lepidopilidium nitens (Hornsch.)

Brotherus, cf. Brotherus, Denkschr. Ak. Wiss. Wien. Math. Nat. Kl. 83: 328. 1926.

Lepidopilum novae-guineae Bartram, Britton 13: 373.

1961. = Chaetomitrium novae-guineanum (Bartram)

Churchill comb. nov.

Type. New Guinea. Wewak-Angoram Area, Sepik Dist., near Nagipem Village, Prince Alexander Ranges, Maprik-But track, 28 Jul 1959, Robbins 1990

(isotype, L).

Lepidopilum mariei Bescherelle in Kindberg, Enum.

Bryin. Exot. 100. 1891, nom. nud.

= Lepidopilidium portoricense (C. Mueller) Crum & Steere, based on a collection at G. This collection is sterile but all the gametophytic features match those in L. portoricense.

Lepidopilum muricatum C. Mueller in Paris, Ind.

Bryol. 723. 1897, nom. nud.

Lepidopilum orizabense Schimper in Hampe, Vid. Medd.

Naturh. For. Kjoebenh. ser. 3, 6: 155. 1875, nom. nud.

Lepidopilum phialothecium C. Mueller in Polakowsky,

Verh. Bot. Ver. Brandenburg 19: 69. 1878, nom. nud. (Hookeria phialothecia C. Mueller, 1877, nom. nud.).

Lepidopilum rugulosum C. Mueller in Kindberg, Enum.

Bryin. Exot. 100. 1891, nom. nud.

Lepidopilum schistostega Spruce, Cat. Musc. Amaz. And.

11. 1867, nom. nud.

Lepidopilum sikorae C. Mueller ex Flesicher, Hedwigia

63: 216. 1922, nom. nud. = Lepidopilidium sikorae Fleischer, nom. nud.

Lepidopilum subalpinum Spruce, Cat. Musc. Amaz. And.

12: 1867, nom. nud.

Lepidopilum subenerve Bridel var. integrifolium Bridel,
 Bryol. Univ. 2: 268. 1827. Type. Brazil. Rio de
 Janeiro: Estrella, Raddi. Type not seen. This is
 likely not a synonym of L. subenerve Bridel (= L.
scabrisetum) since that species is presently not
 found in southern Brazil; more likely it is
L. subsubulatum Geh. & Hampe, but until the type
 type is located the name cannot be referred to any
 other species.

Lepidopilum virens Cardot, Bull. Herb. Boissier ser.
 2, 5: 312, pl. 2f, f. 20-31. 1905.

= Tetrastichium virens (Cardot) Churchill

Type. Azores, San Miguel, 1898, Carreiro 703
 (holotype, PC!; isotype, MO!). See Churchill
 (1989).

The following types could not be located. I have
 not attempted to assign any of these names to those
 recognized in this treatment for the present time.

Lepidopilum convallium (Bridel) Mitten, J. Linn. Soc.,

Bot. 12: 377. 1869. Pterygophyllum convallium

Bridel, Bryol. Univ. 2: 354. 1827.

Lepidopilum curvirameum (C. Mueller) Paris, Ind.

Bryol. Suppl. 223. 1900. Hookeria curviramea

C. Mueller, Naov. Giorn. Bot. Ital. n. ser. 4:

132. 1897.

Lepidopilum falcatum C. Mueller, Linnaea 38: 648.

1874.

Lepidopilum glaziovii Hampe, Vid. Medd. Naturh. For.

Kjoebenh. ser. 4, 1: 122. 1879.

Lepidopilum krauseanum C. Mueller, Linnaea 38: 608.

1874.

Lepidopilum leiomitrium C. Mueller, Linnaea 42: 495.

1879.

Lepidopilum maculatum C. Mueller, Flora 58: 546. 1875.

Lepidopilum mniaceum C. Mueller, Flora 58: 546. 1875.

Lepidopilum pergracile C. Mueller, Flora 58: 548.

1875.

FIGURES

Fig. 1. Gametophytic features of Lepidopilum. A. Stem cross-section of L. brevipes. B. Stem cross-section of L. stillicidiorum. C. Axillary hair of L. longifolium. (A. Weir 77; B. Churchill et al. 15820; C. Griffin et al. 1252).

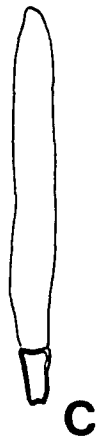
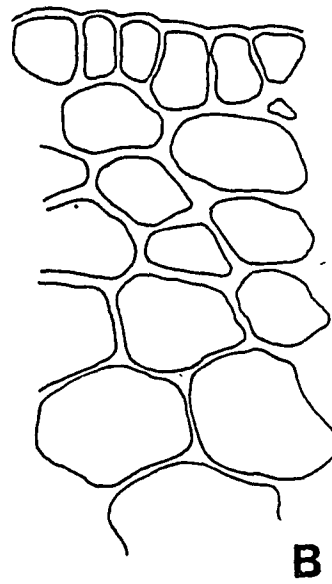
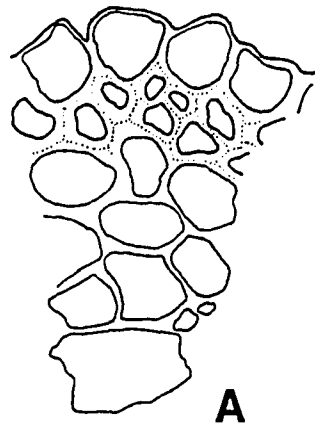


Fig. 2. Gametophytic features of Lepidopilum; developmental sequence, from earliest (left) to later (right) juvenile leaves. A. L. polytrichoides. B. L. tortifolium. (A. Churchill & Sastre 13744; B. Churchill et al. 15250).

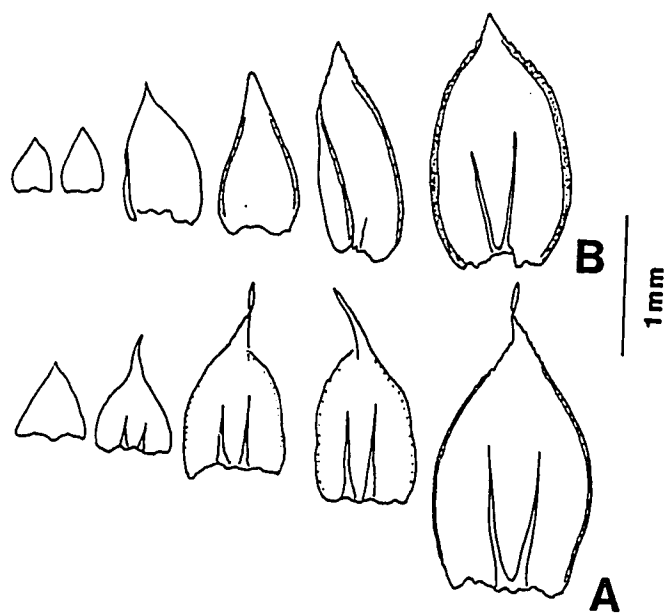


Fig. 3. Gametophytic features of Lepidopilum;
reproductive asexual structures. A. Propagulum of
L.integrifolium. B. Deciduous branch and leaves of L.
scabrisetum. (A. Steyermark 92970; B. Steere 4882).

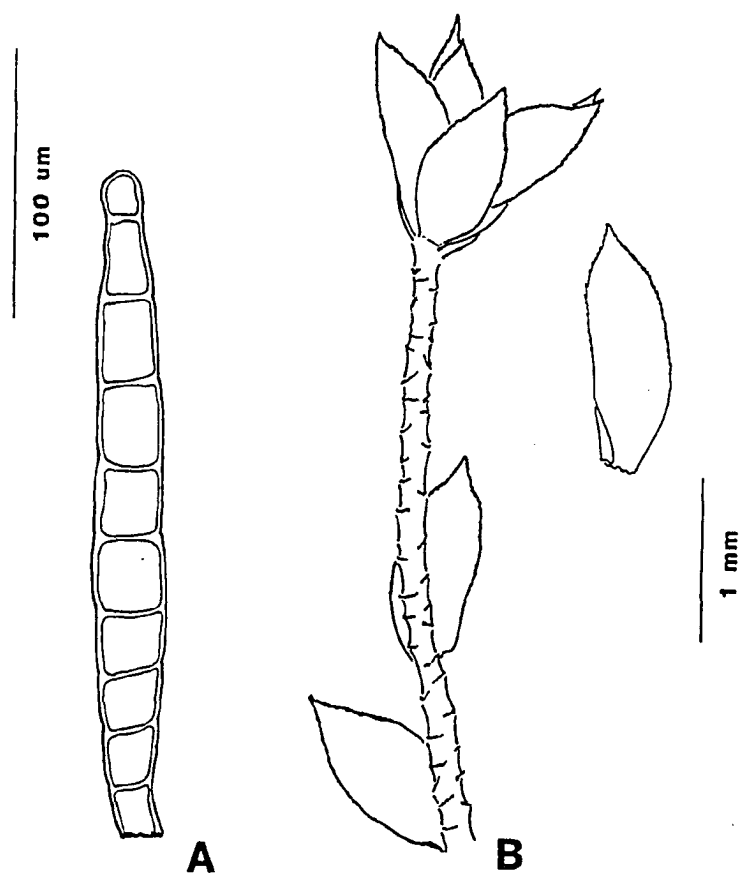


Fig. 4. Gametophytic features of Lepidopilum; calyptra morphology and anatomy. A. Calyptra of L. cubense. B. Calyptra of L. brevipes. C. Calyptra anatomy of L. longifolium; note multicellular hairs that are modified paraphyses (arrows). D. Early development of a paraphysis of L. polytrichoides. (A. Skutch 2530; B. Churchill et al. 13976; C. Churchill et al. 13941; D. Griffin et al. 1225).

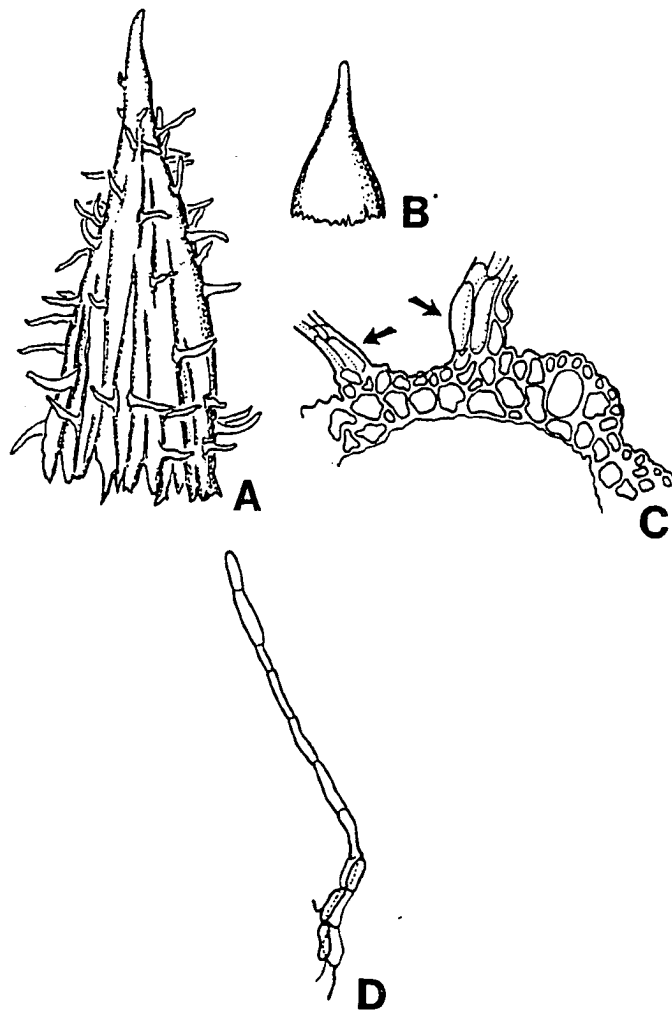


Fig. 5. Sporophytic features of Lepidopilum;
illustrating variation of seta, urn and operculum. A.
L. surinamense. B. L. brevipes. C. L. longifolium.
D. L. integrifolium. (A. Spruce 719; B. Churchill et
al. 13976; C. Churchill et al. 13432; D. Steyermark
92970).

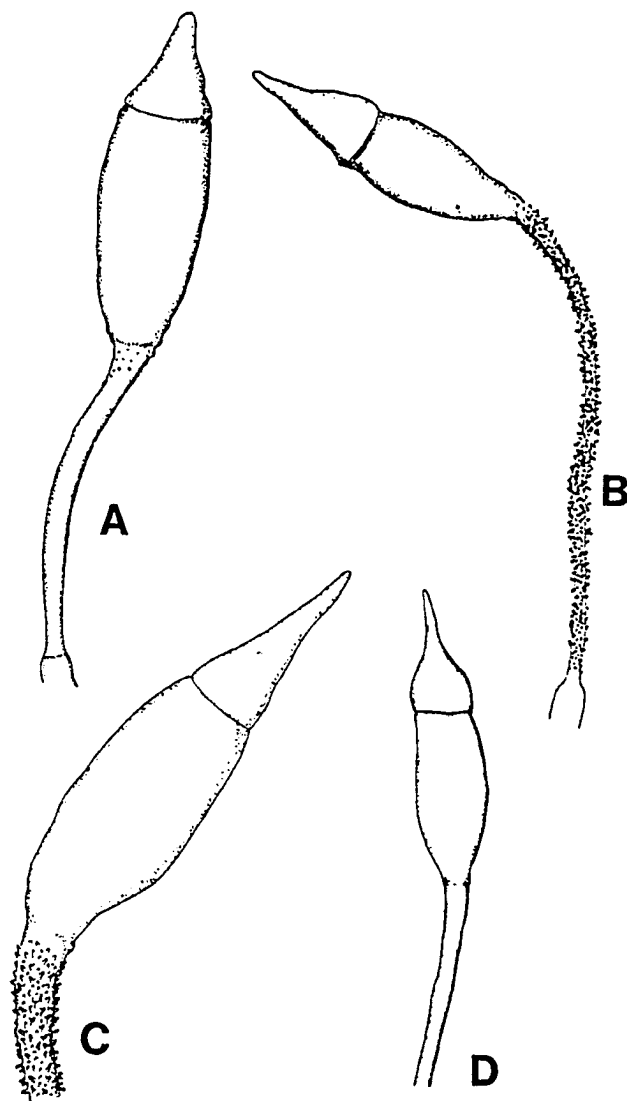


Fig. 6. Sporophytic features of Lepidopilum;
morphology and anatomy of seta and capsule. A. Seta
cross-section of L. longifolium. B. Seta cross-section
of L. polytrichoides. C. Stomatal guard cells, stomata
immersed or sunken; L. longifolium (left), L.
pallidonitens (right). D. Annulus region (arrow) and
exothecial cells of L. cuspidans. E. Side view of
exostome of L. cubense; note that the outer plate
(upper) is thicker than inner plate (lower, arrow). F.
Front view of exostome at mid region of L. longifolium;
note hyaline border. G. Front view of endostome near
base of L. longifolium. (A. Churchill et al. 13941; B.
Griffin et al. 1225; C. left - Weir 134, right -
Germain s.n.; D. Spruce 757; E. Sinclair s.n.; F & G.
Underwood 2268).

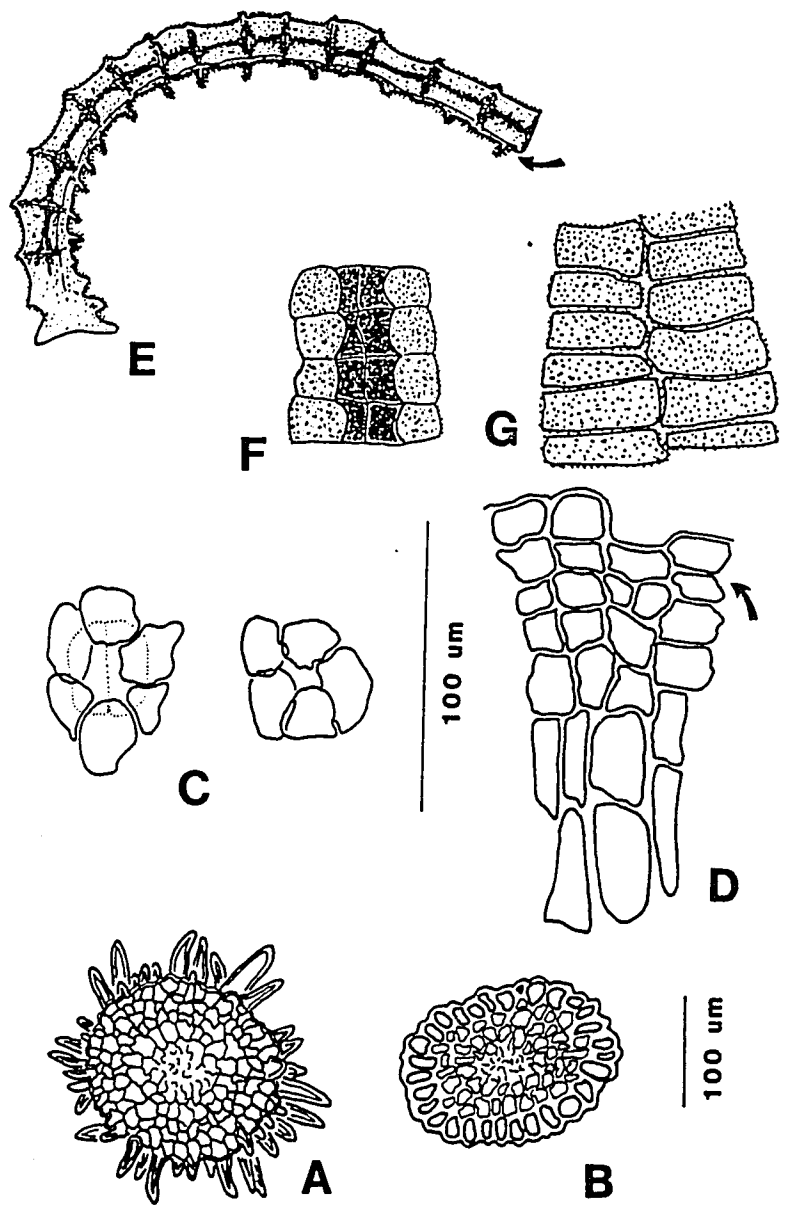


Fig. 7. Distribution of Lepidopilum in the
neotropics. Lepidopilum muelleri (dots).

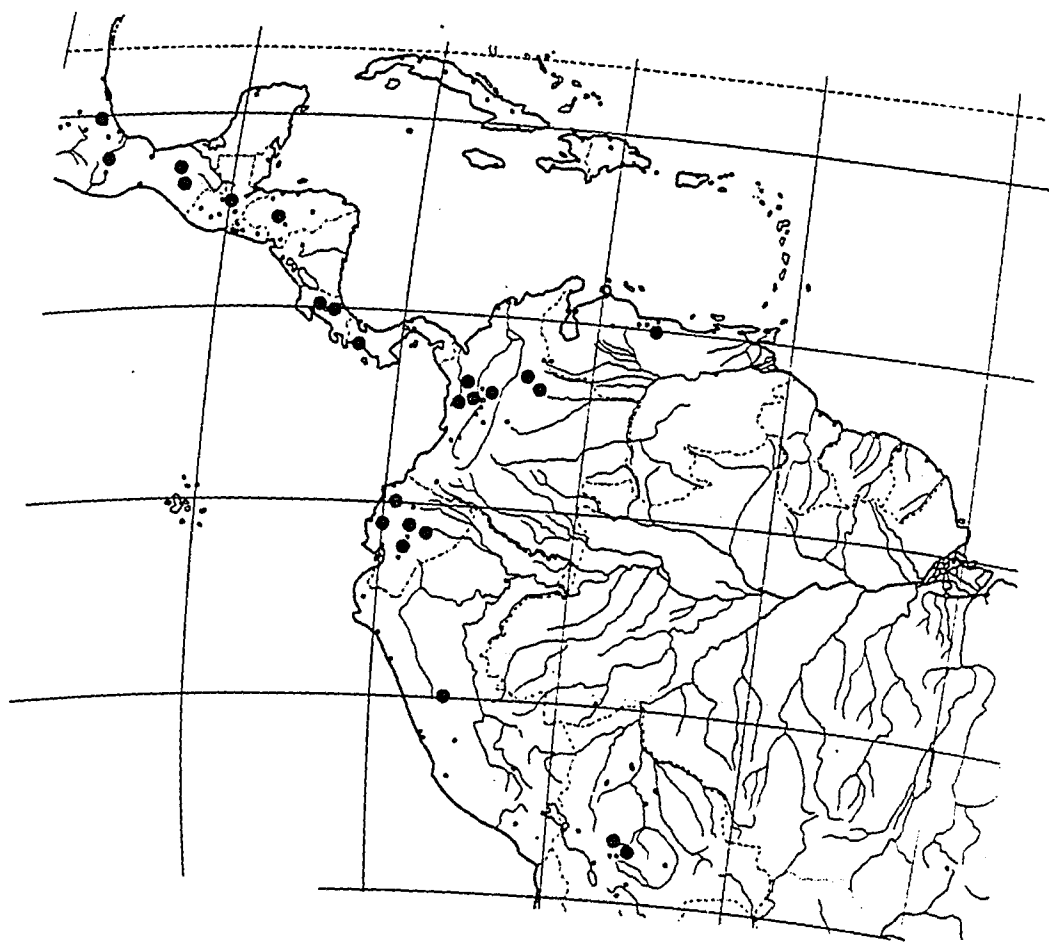


Fig. 8. Distribution of Lepidopilum in the
paleotropics. Lepidopilum lastii (dots), L.
verrucipes (triangle).

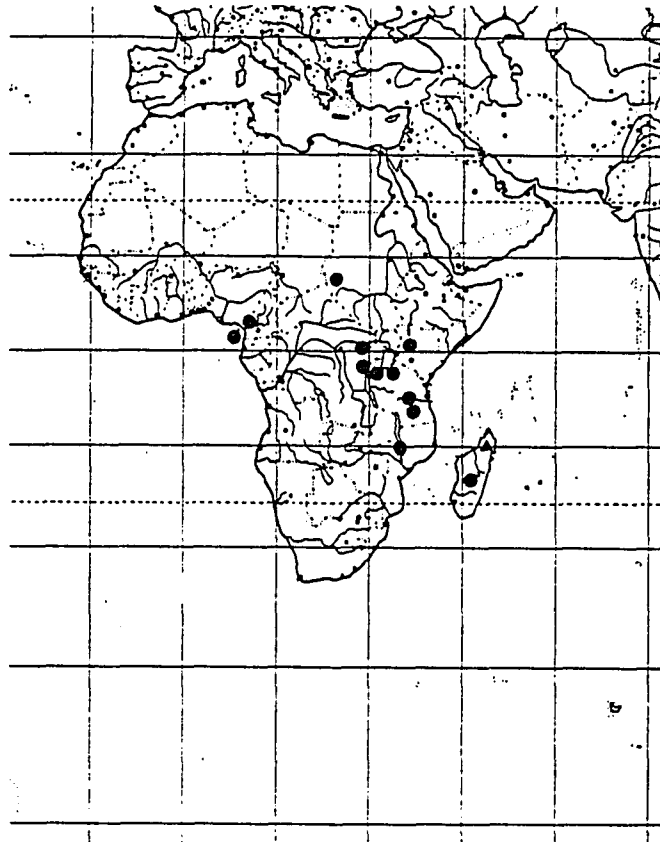


Fig. 9. Distribution of Lepidopilum in the neotropics. Lepidopilum scabrisetum (dots), L. apophysatum (triangles).

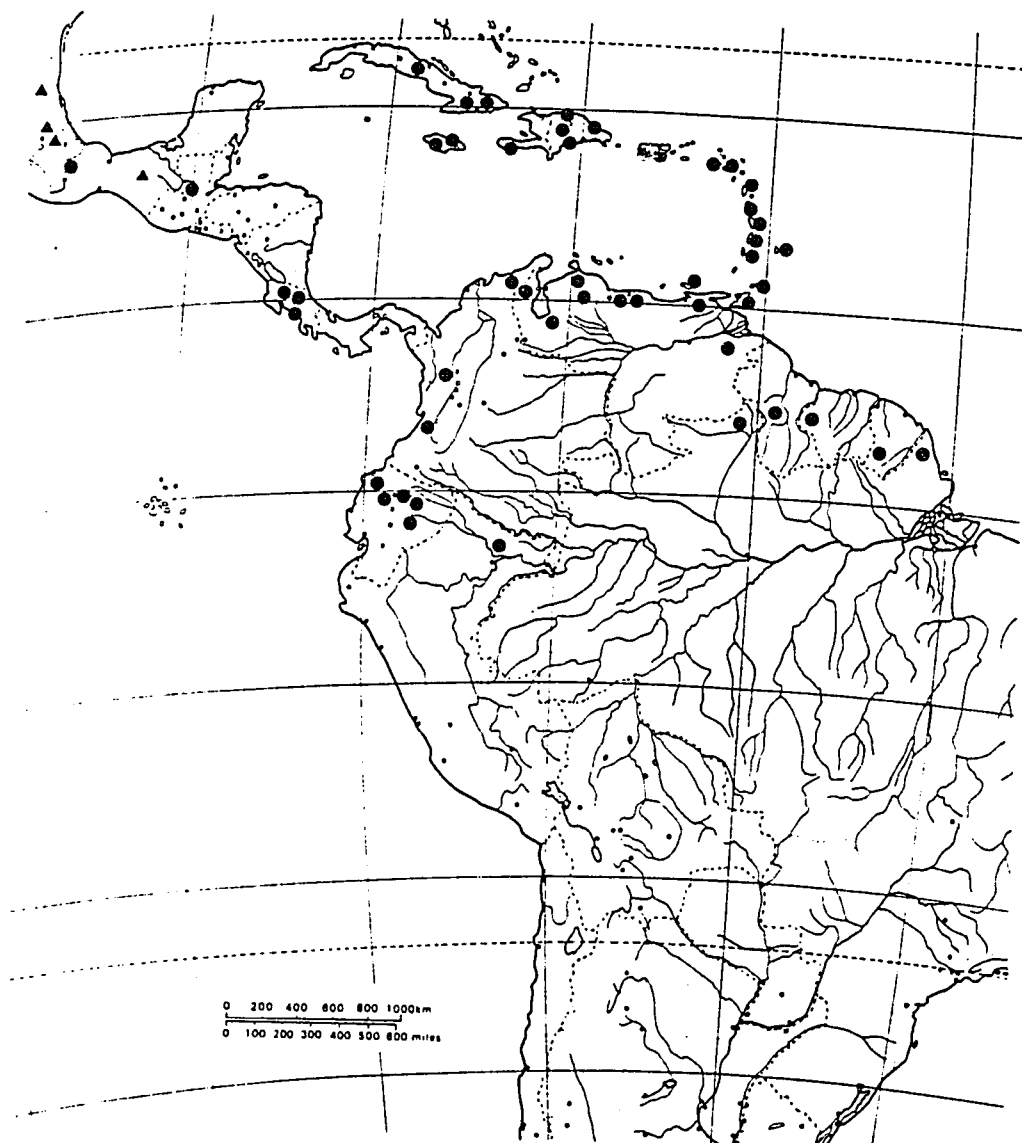


Fig. 10. Distribution of Lepidopilum in the neotropics. Lepidopilum brevipes (dots), L. chloroneuron (triangles).



Fig. 11. Distribution of Lepidopilum in the neotropics. Lepidopilum affine (dots), L. brevifolium (triangles), L. grevilleanum (squares).

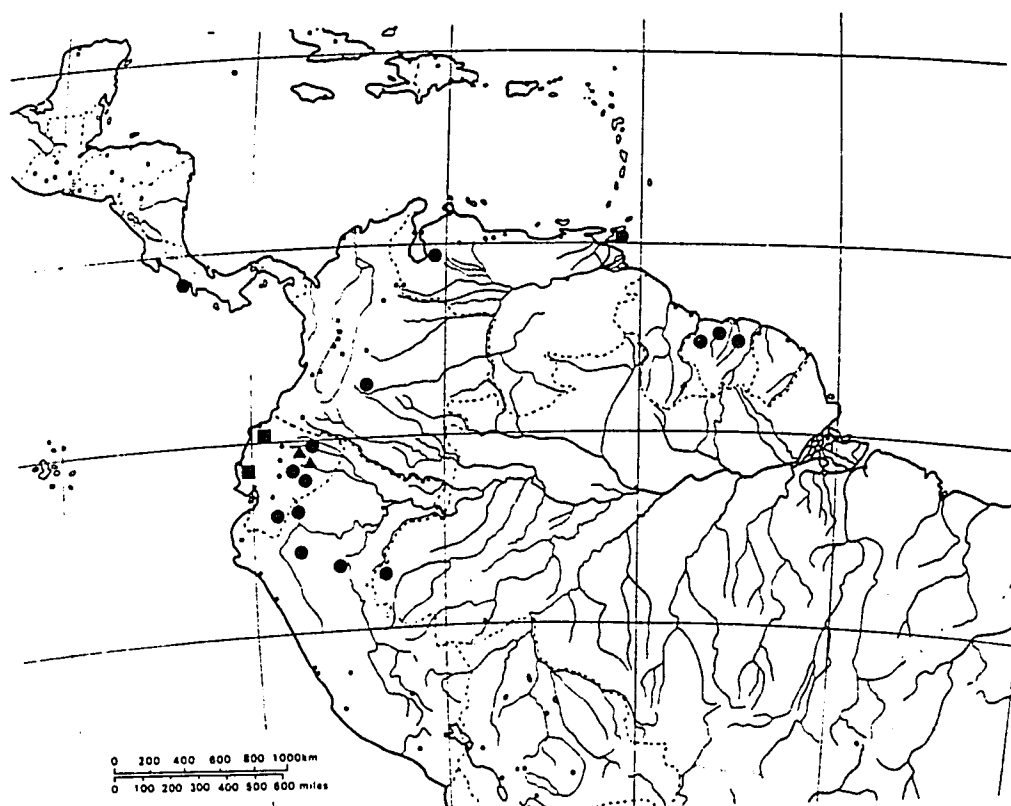


Fig. 12. Distribution of Lepidopilum in the neotropics. A. Lepidopilum longifolium (dots), L. erectiusculum (squares). B. Lepidopilum amplirete (dots), L. integrifolium (diamonds), L. aurifolium (triangles), L. caviusculum (square).

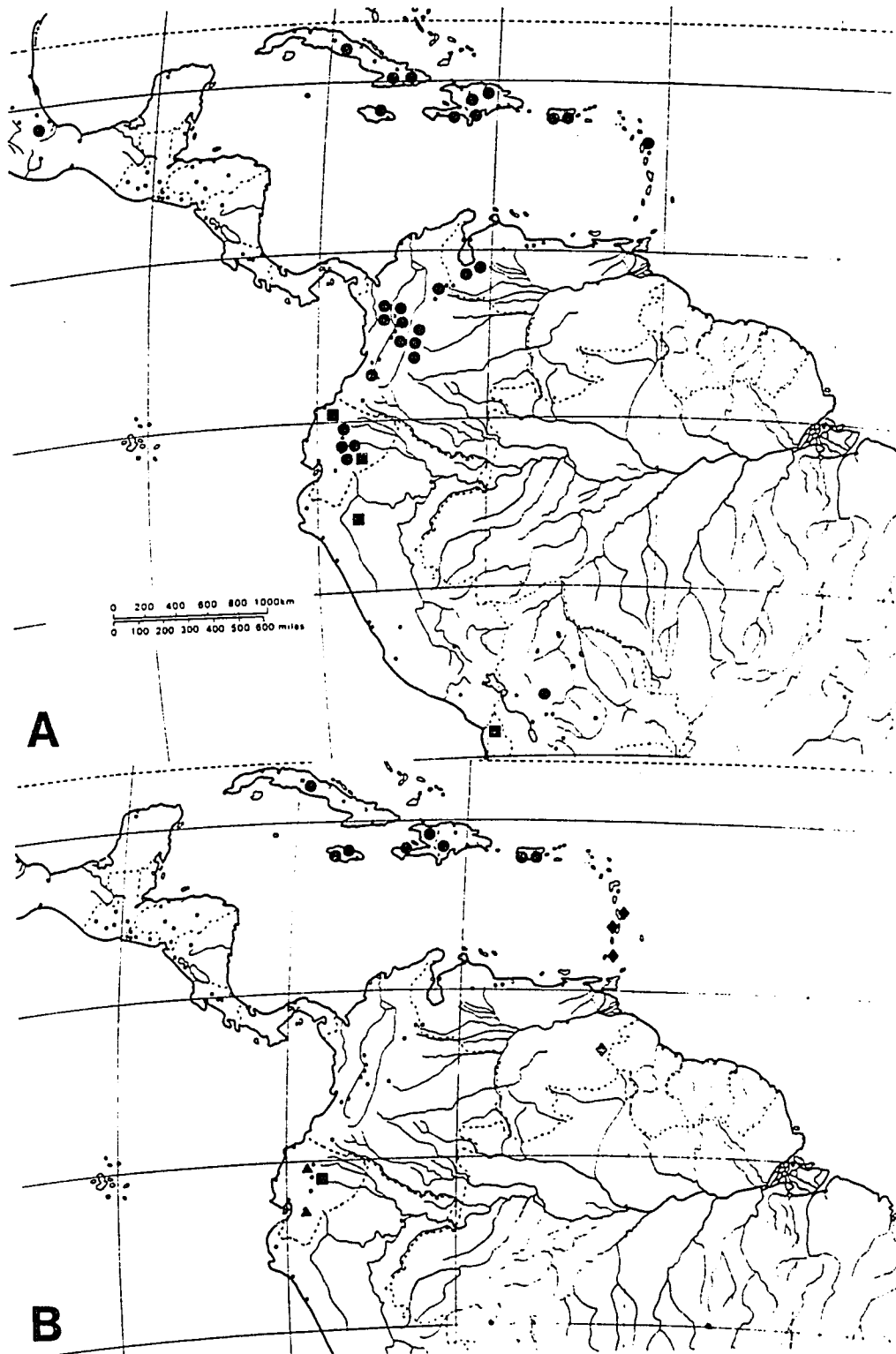


Fig. 13. Distribution of Lepidopilum in the neotropics. A. Lepidopilum diaphanum (dots), L. arcuatum (triangles), L. permarginatum (squares). B. Lepidopilum tortifolium (dots), L. stillicidiorum (squares), L. inflexum (triangles).

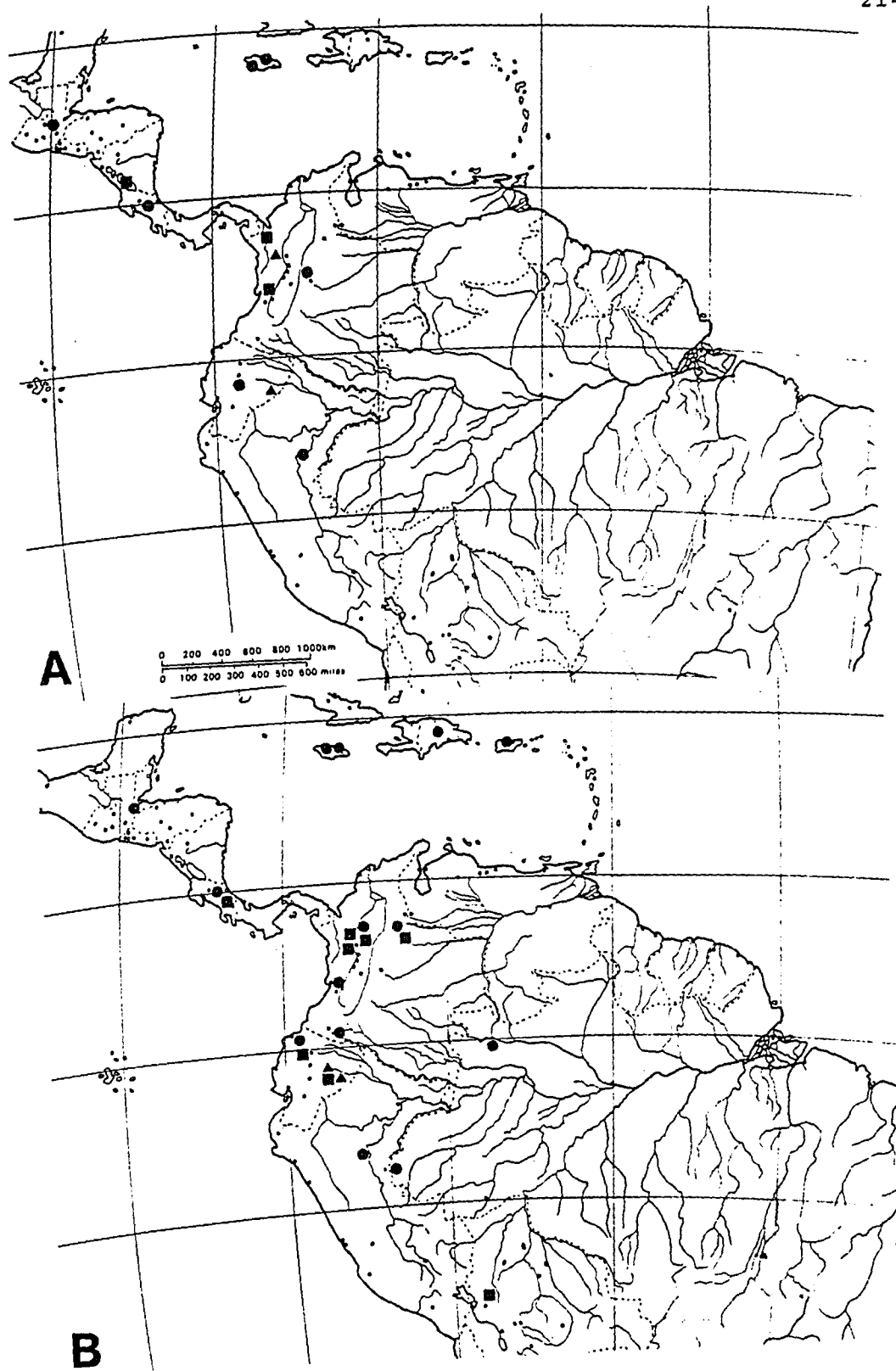


Fig. 14. Distribution of Lepidopilum in the neotropics. Lepidopilum polytrichoides (dots), L. curvifolium (squares).

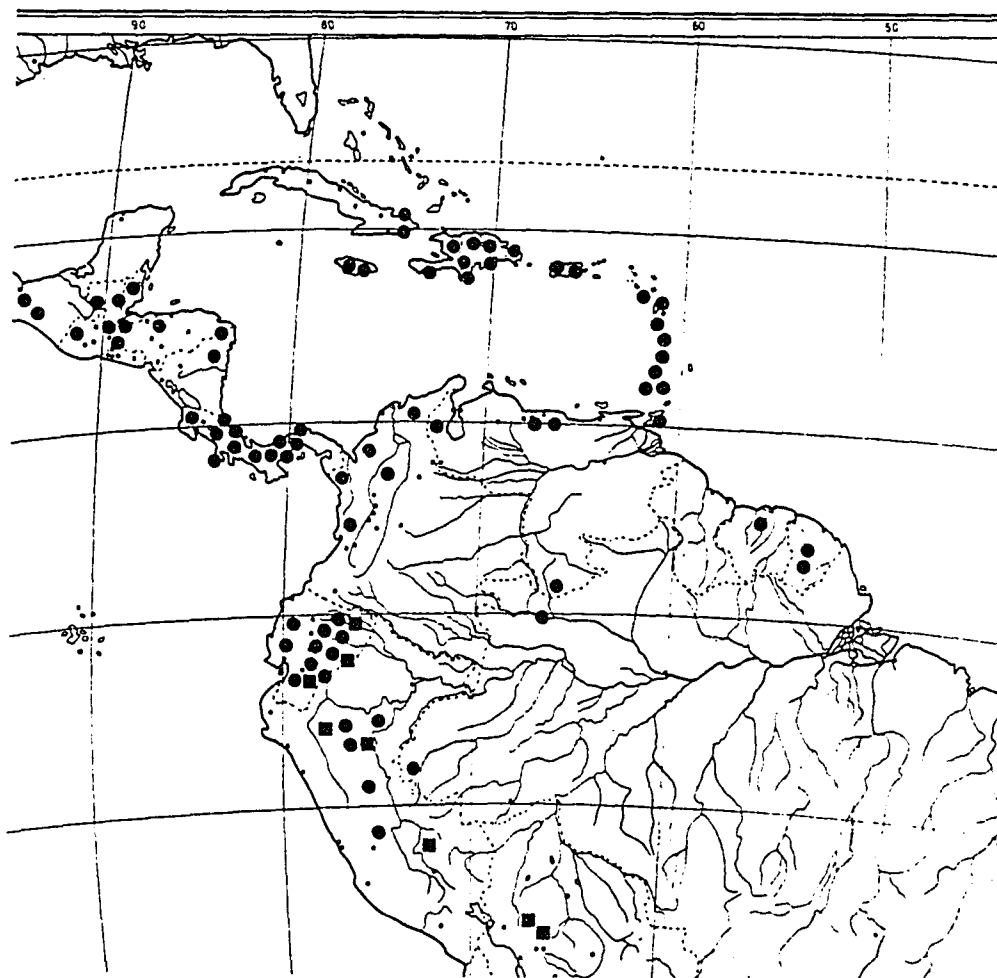


Fig. 15. Distribution of Lepidopilum in the neotropics. Lepidopilum surinamense (dots), L. cubense (triangles).

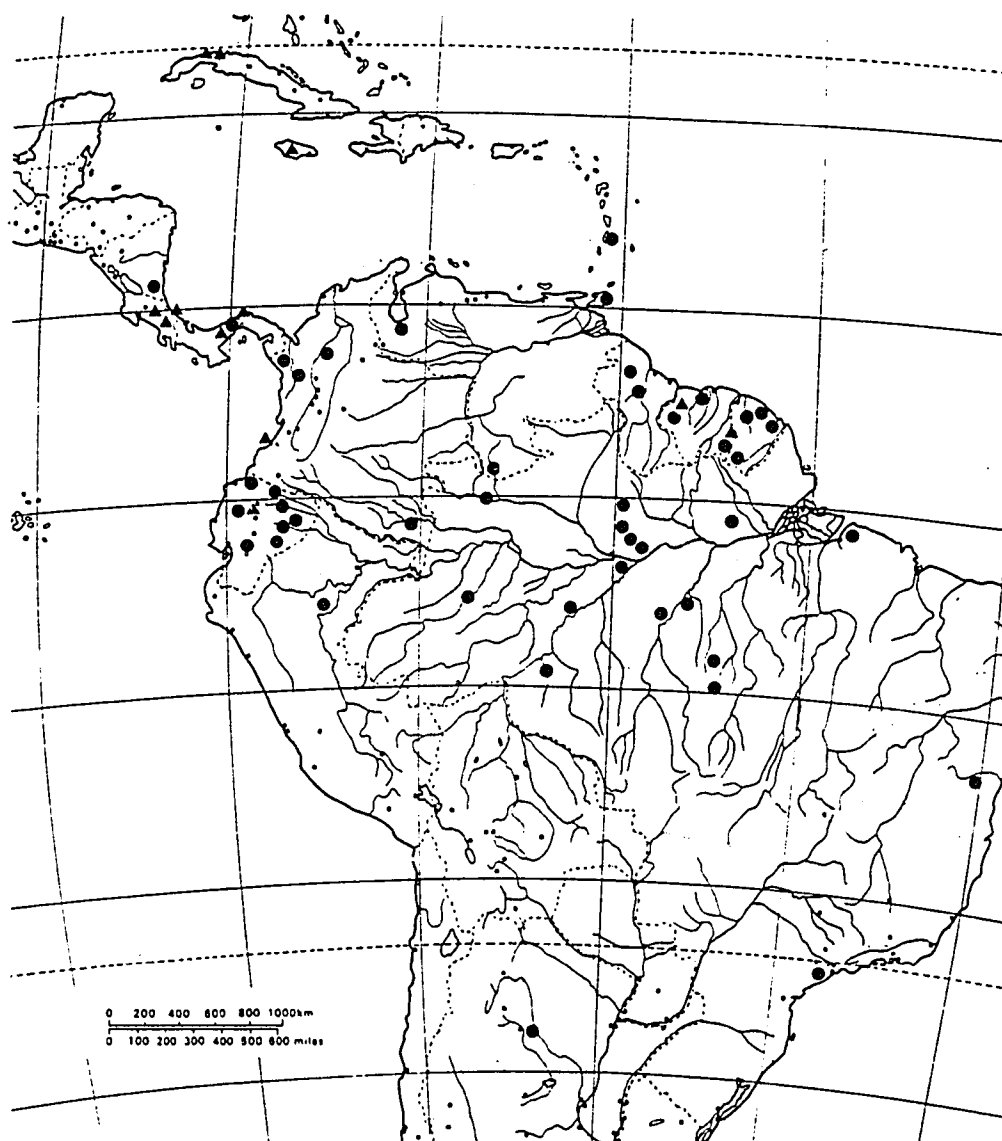
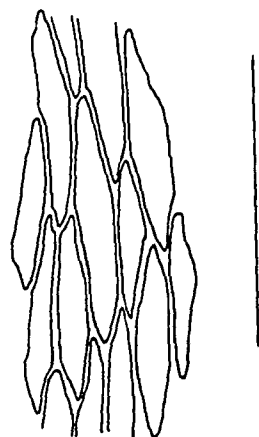


Fig. 16. Lepidopilum muelleri. A. Lateral leaves.
B. Median cells. (A-B. Moritz s.n.).



B

Fig. 17. Lepidopilum muelleri. A. Lateral (2 left; same leaf, left open, right folded) and median (1 right) leaves. B. Lateral (left) and median (right) leaf. C. Lateral leaf. (A. Pringle 10499, type of L. pringlei; B. Sehnem 6414, type of L. macrophyllum; C. Weberauer 819, type of L. splendens).

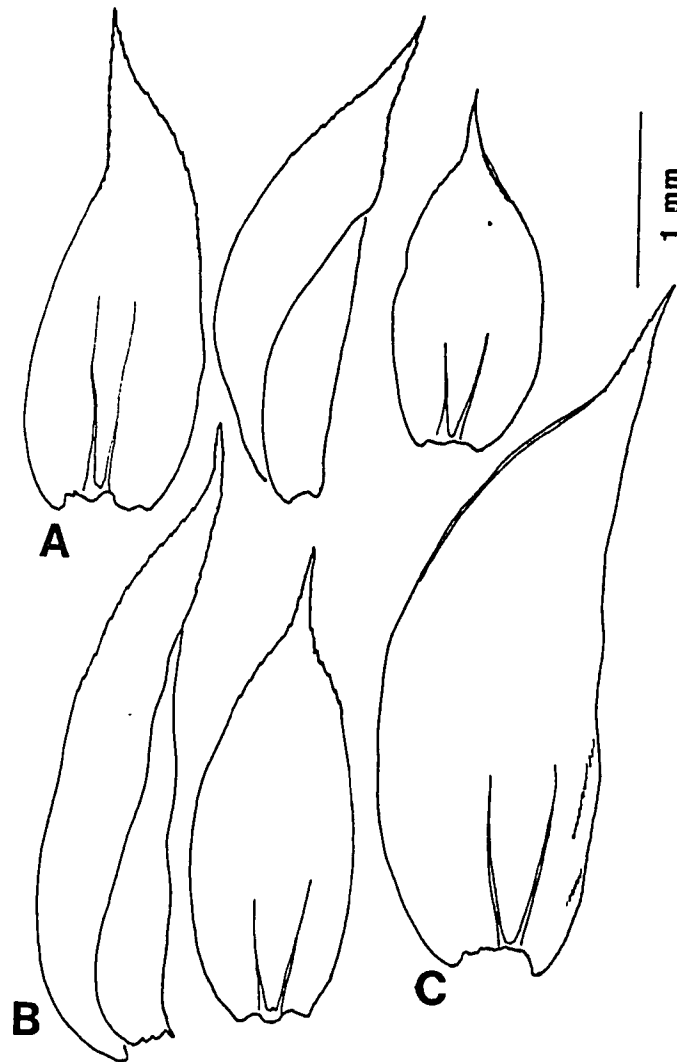


Fig. 18. Lepidopilum subsubulatum. A. Lateral leaves. B. Median leaves. C. Margin of lateral leaf. D. Median cells of lateral leaf. E. Perichaetial leaves. F. Sporophyte. (A-F. Puiggari 53).

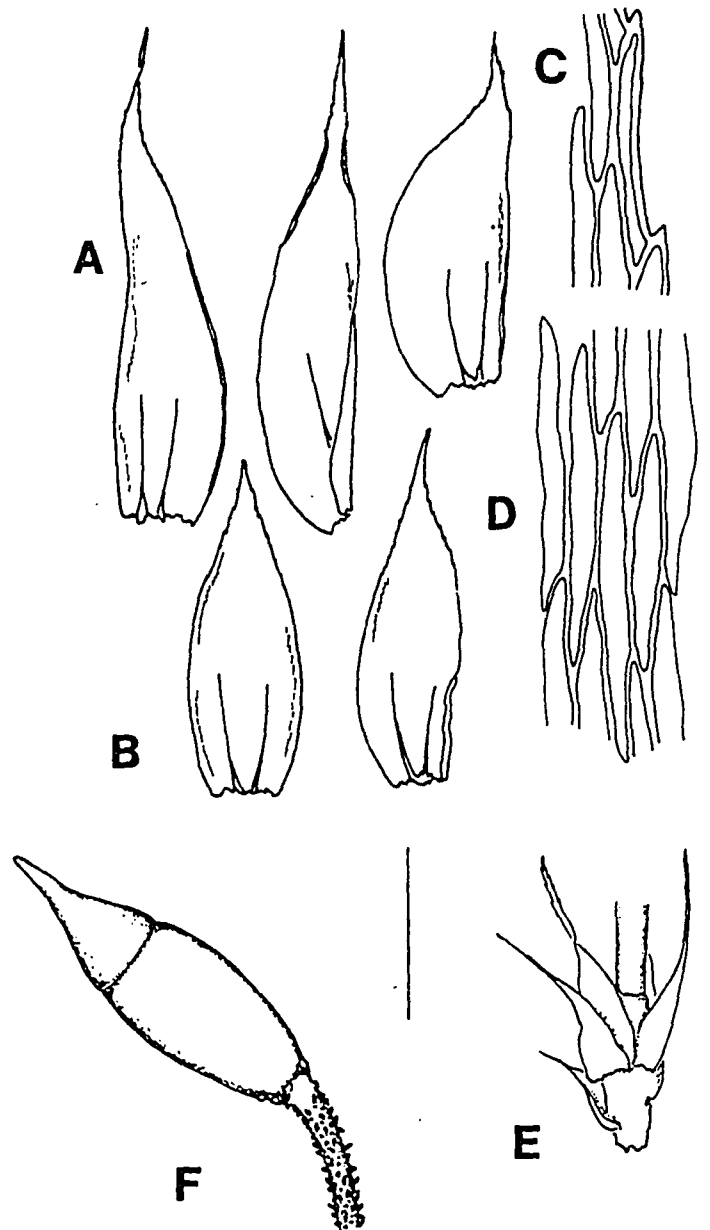


Fig. 19. Lepidopilum scabrisetum. A. Lateral (2 left) and median (1 right) leaves. B. Lateral (left) and median (right) leaf. C. Lateral (3 left) and median (1 left) leaves. (A. Richard s.n., type; B. Herzog s.n., type of L. ovatifolium; C. Sharp 2410).

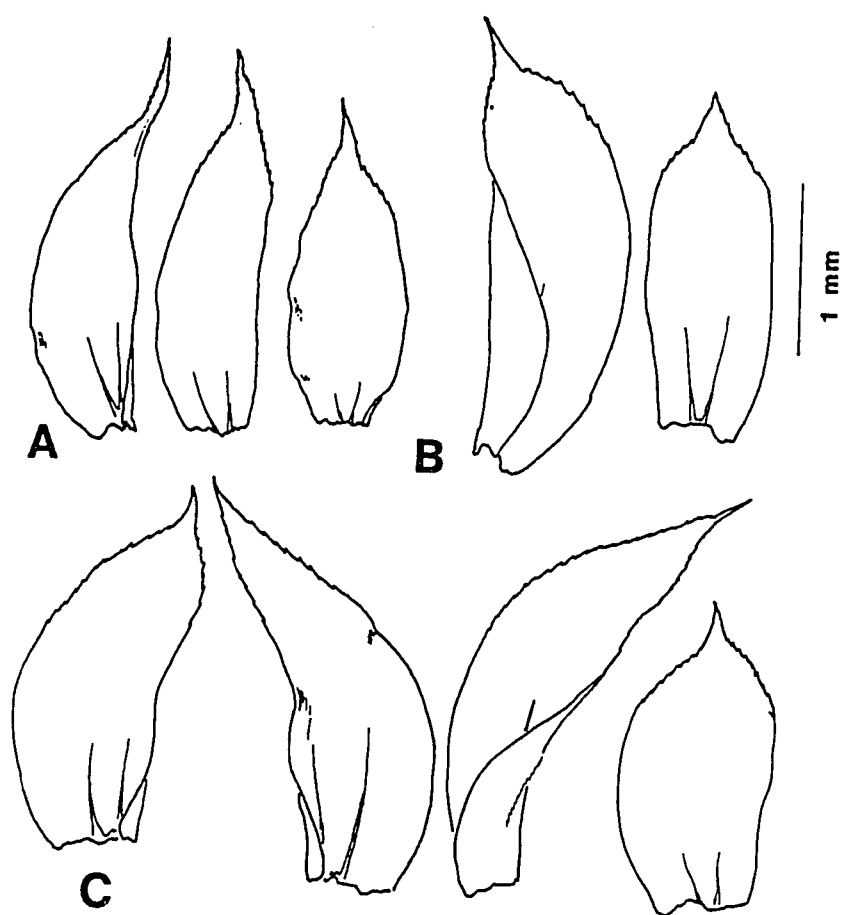


Fig. 20. Lepidopilum scabrisetum. A. Lateral dimorphic leaves; enlarged leaf (left), typical leaf of upper and lower secondary stem (right). B. Median cells. (A-B. Cruger s.n., type of L. latifolium).

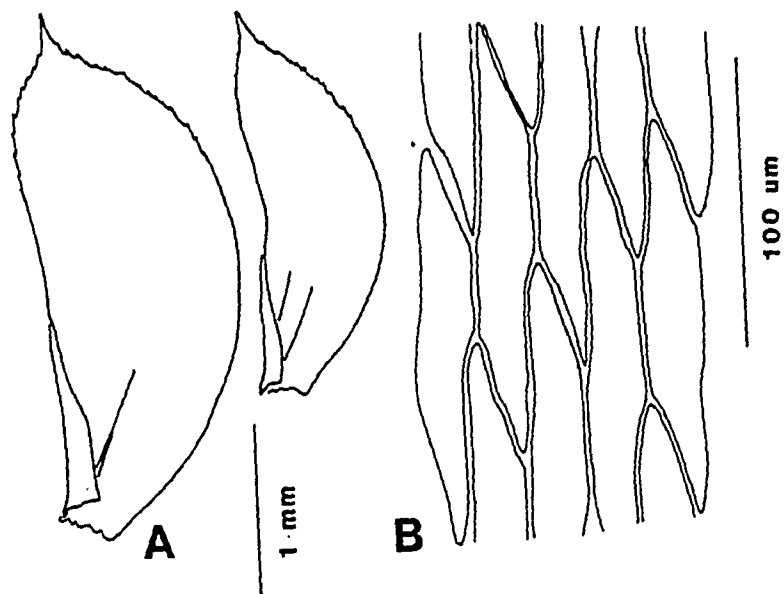


Fig. 21. Lepidopilum lastii. A. Lateral leaves (extreme right and left). B. Median leaf. C. Margin of lateral leaf. D. Median cells of lateral leaf (2 patterns from same plant). (A-D. Last s.n., type).

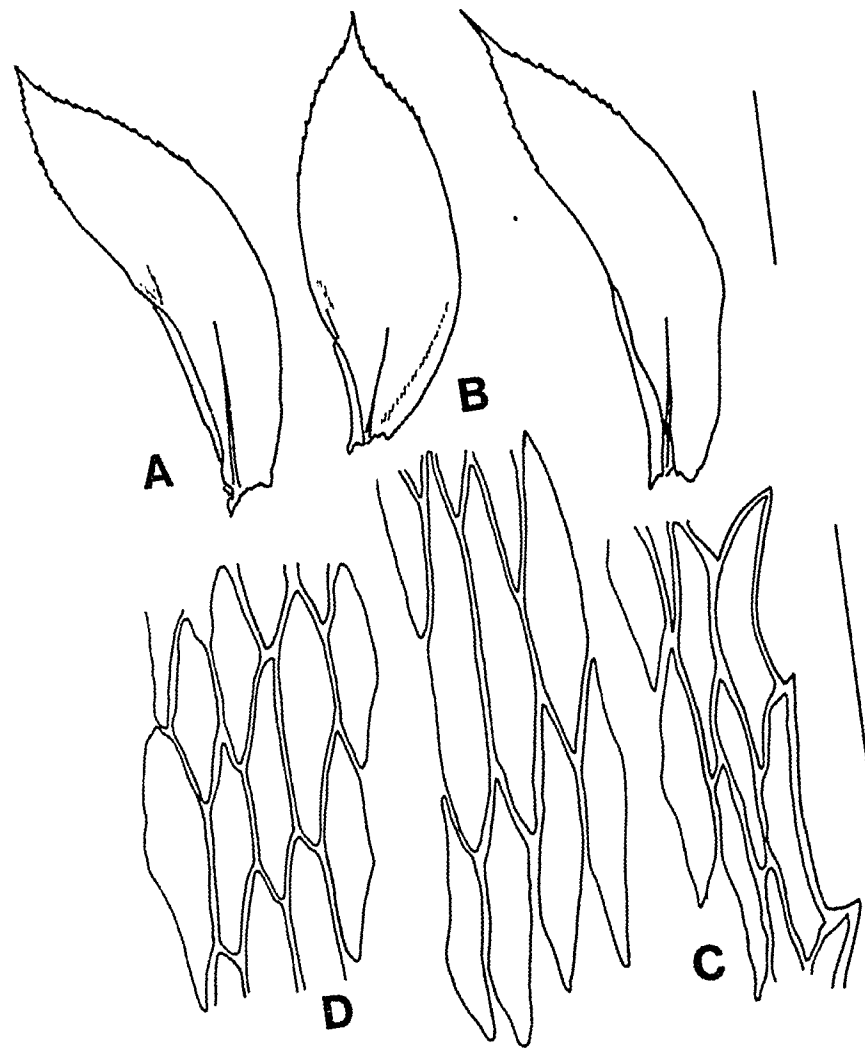


Fig. 22. Lepidopilum lastii. A. Lateral leaves
(extreme left & right). B. Median leaf. (Carrougeau
s.n., type of L. carrougeaunum).

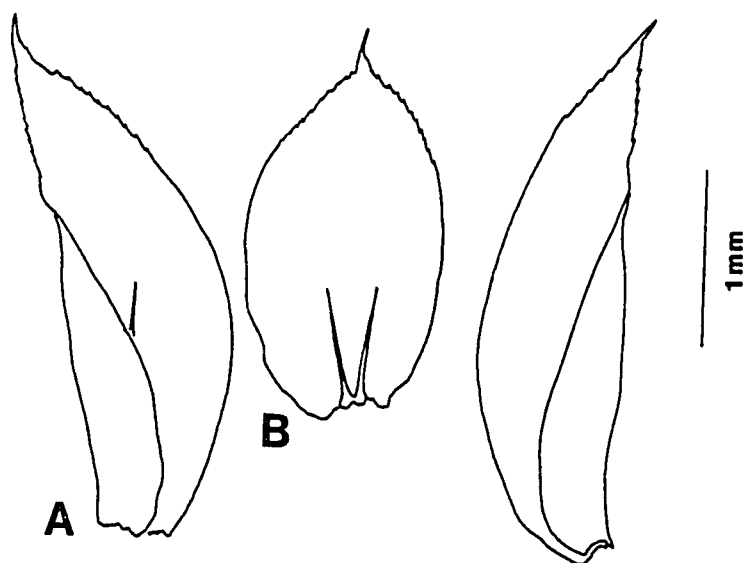


Fig. 23. Lepidopilum pallidonitens. A. Lateral leaves (right and left), and median leaf (center). B. Margin of lateral leaf. C. Median cells of lateral leaf. (A-C. Germain s.n., type).

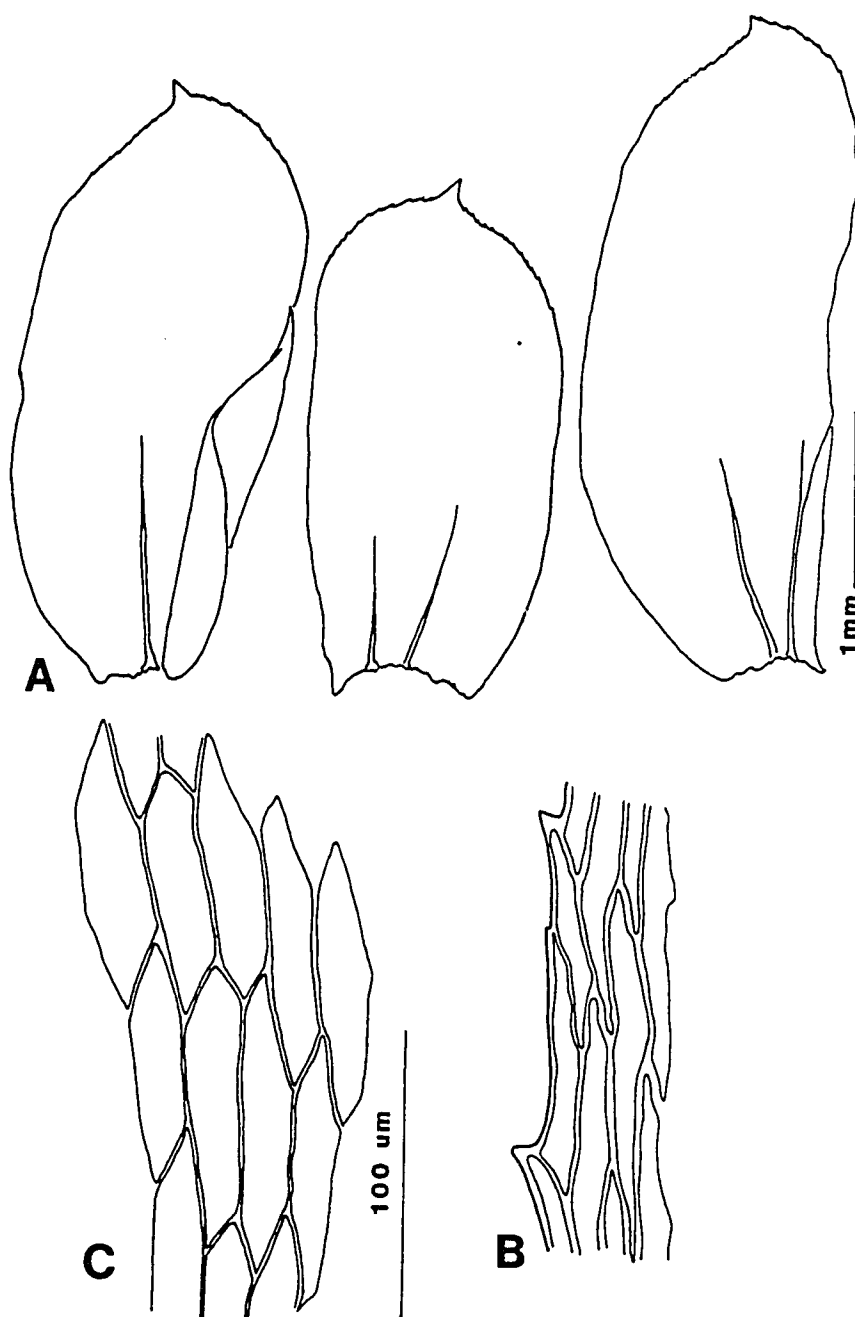


Fig. 24. Lepidopilum pallidonitens. A. Lateral leaves. B. Lateral leaves. C. Sporophyte. (A. Valerio 45, type of L. quadrifarum; B. Grubb 2939a, type of L. attenuatum; C. Germain s.n., type)

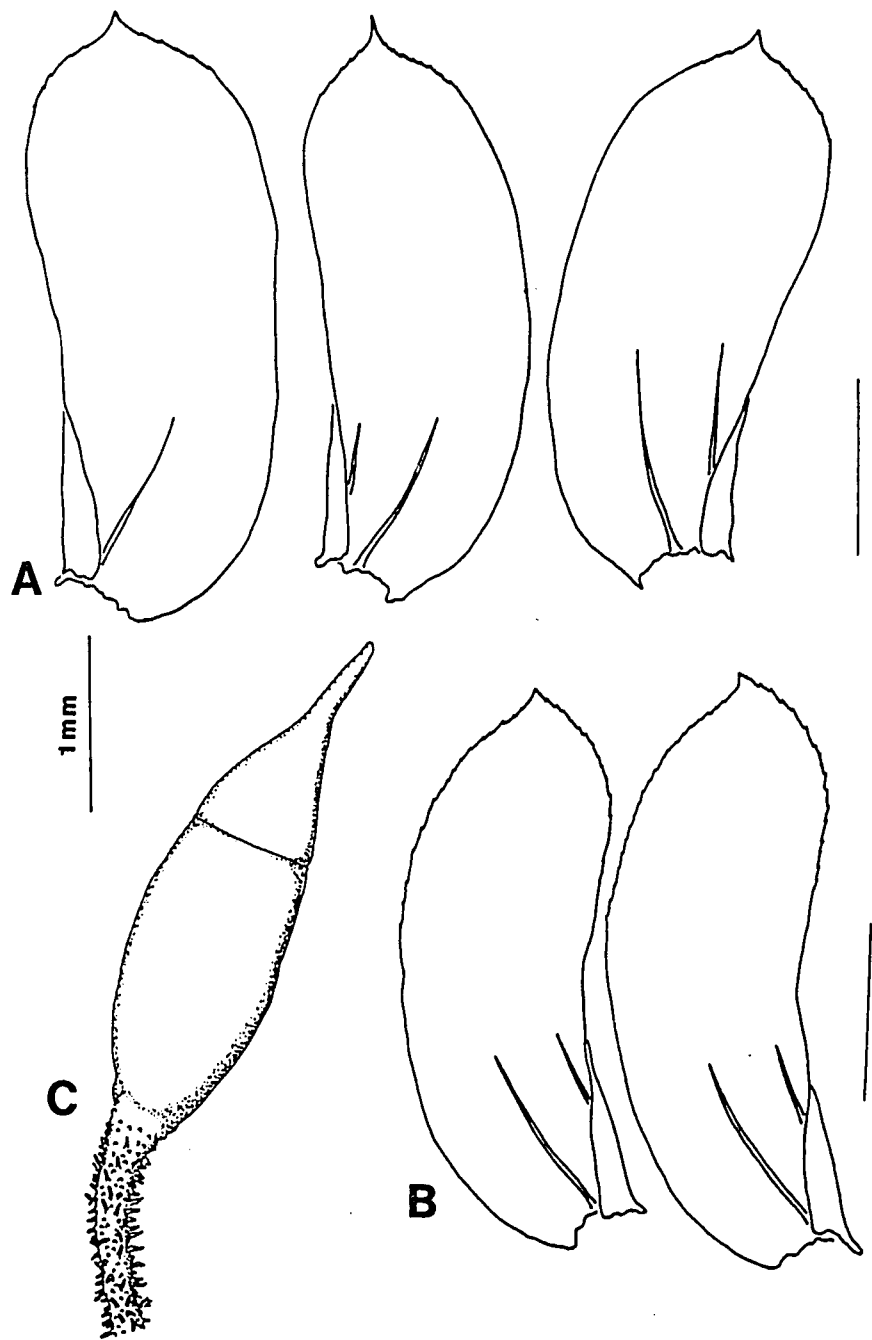


Fig. 25. Lepidopilum apophysatum. A. Lateral
leaves. B. Median leaf. (A-B. Bourgeau 2137, type).

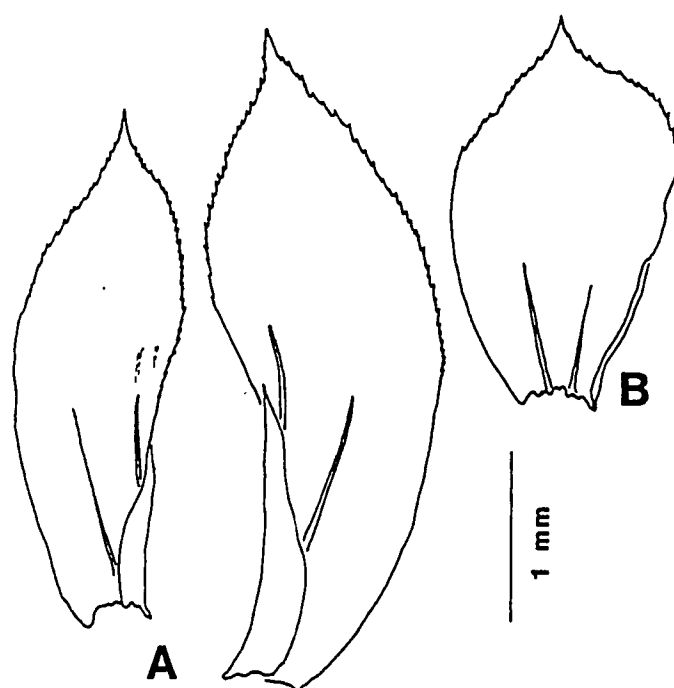


Fig. 26. Lepidopilum chloroneuron. A. Lateral leaves (2 left, 1 extreme right and below). B. Median leaf. C. Median cells of lateral leaf. D. Perichaetial leaf. E. Sporophyte. (A-E. Spruce 739, type).

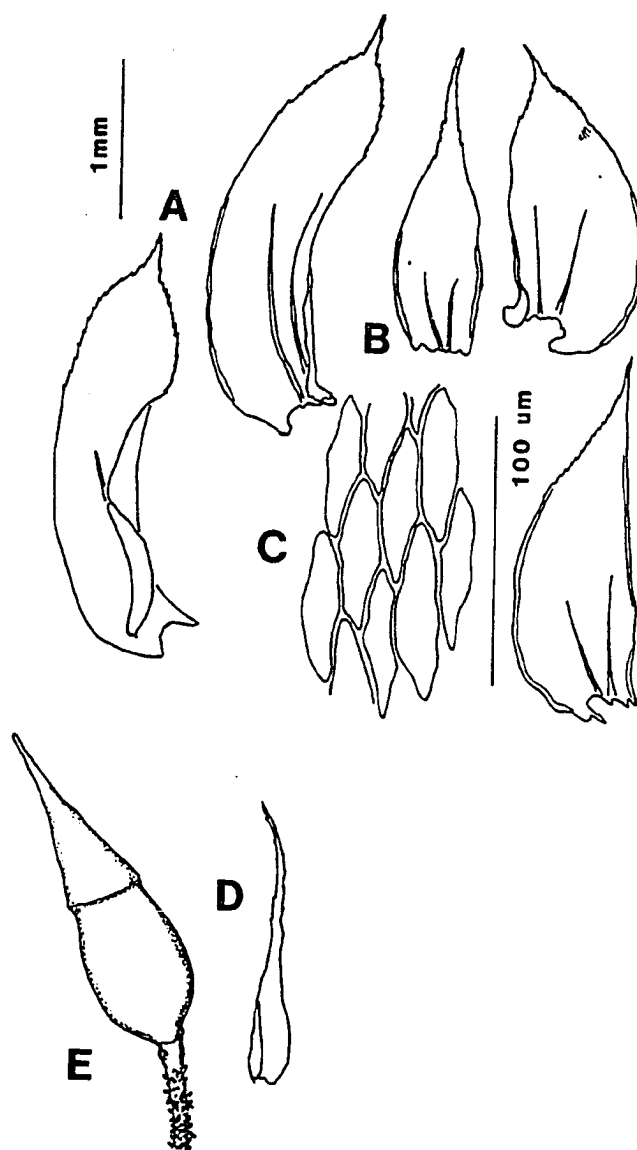


Fig. 27. Lepidopilum brevipes. A. Lateral leaves.
B. Median leaf. C. Margin and median cells of lateral
leaf. D. Calyptra. E. Sporophyte. (A-E. Churchill
et al. 13976).

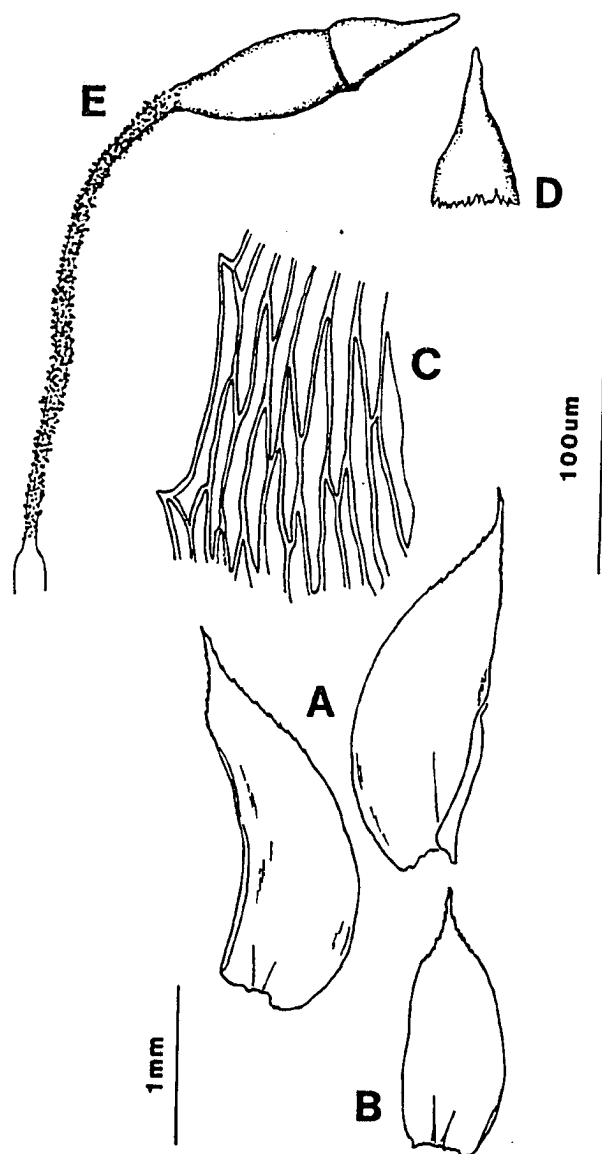


Fig. 28. Lepidopilum verrucipes. A. Lateral leaves. B. Margin of lateral leaf. C. Median cells of lateral leaf. (A-C. Mathieu s.n., type).

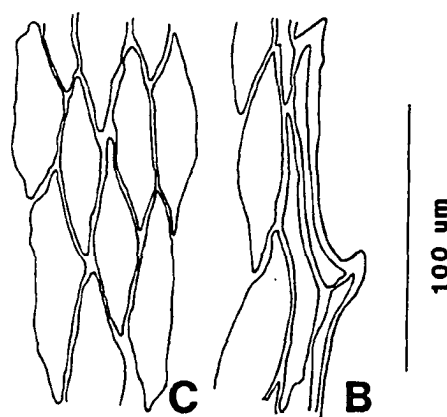
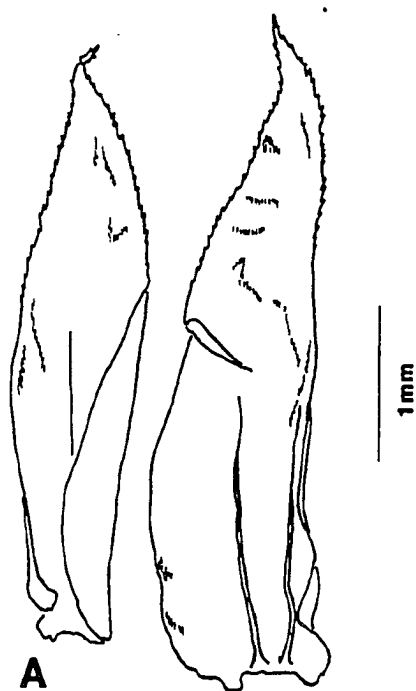


Fig. 29. Lepidopilum grevilleanum. A. Lateral
leaves. (A. Greville s.n., type).

**A**

1mm

Fig. 30. Lepidopilum affine; illustrating variation of leaves. A-D. Leaves. (A. Kegel 741, type ;B. Spruce 780, type of L. pumilum; C. Ule 298, type of L. subobtusatulum; D. Spruce 748, type of L. obtusulum).

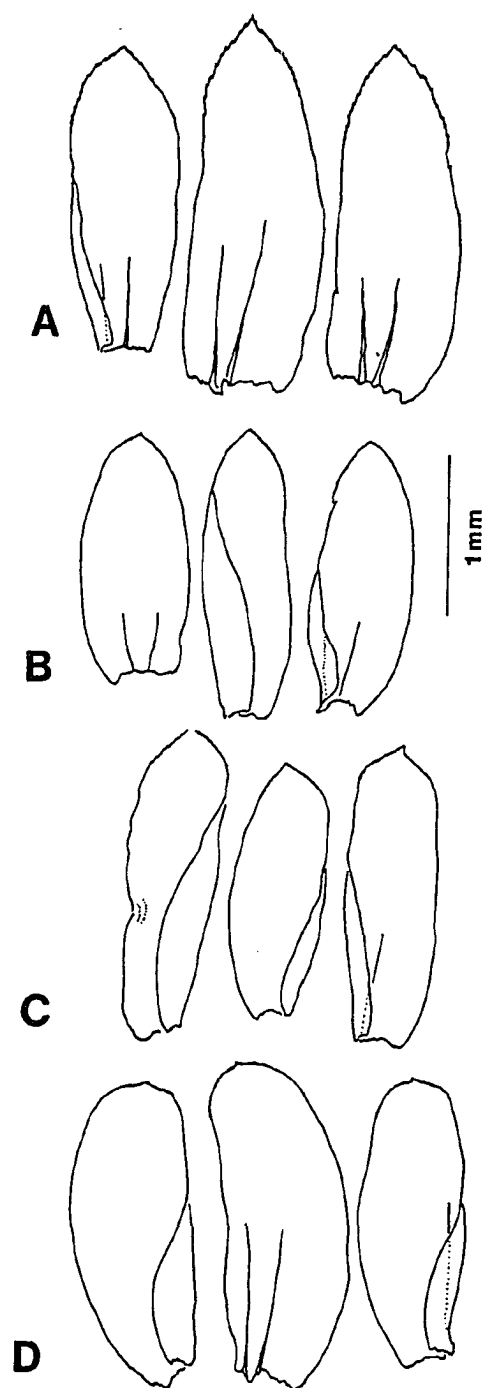


Fig. 31. Lepidopilum affine; illustrating variation of leaves. A-B. Leaves. (A. Krause s.n., type of L. undulatum; B. Allioni 625, type of L. allionii).

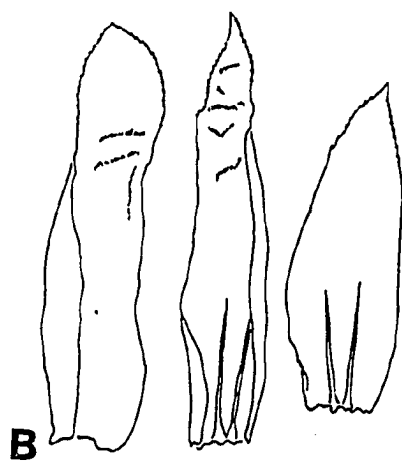
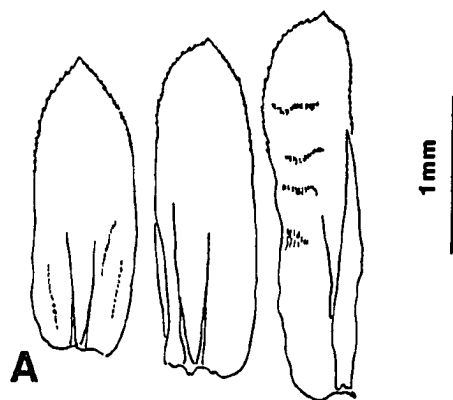


Fig. 32. Lepidopilum longifolium. A. Leaves. B. Median cells. C. Sporophyte. (A. Lindig s.n., 2 left, type; Weir 134, 2 right, type of L. robustum; B-C. Churchill et al. 13941)

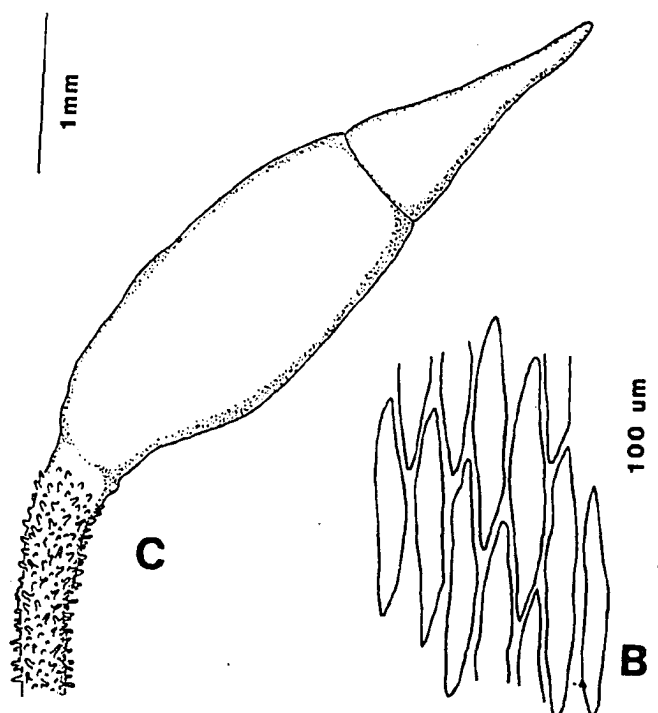
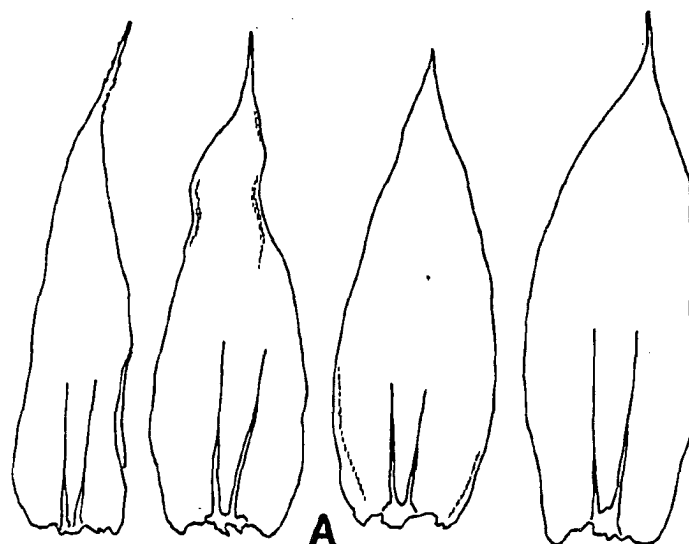


Fig. 33. Lepidopilum longifolium. A-C. Leaves.
(A. Spruce 755, 2 left, Spruce 752, upper right, Spruce 753, lower right, all types of L. integerrimum; B. Marie 43, type of L. cladorrhizans; C. Herzog 4097, type of L. herzogii).

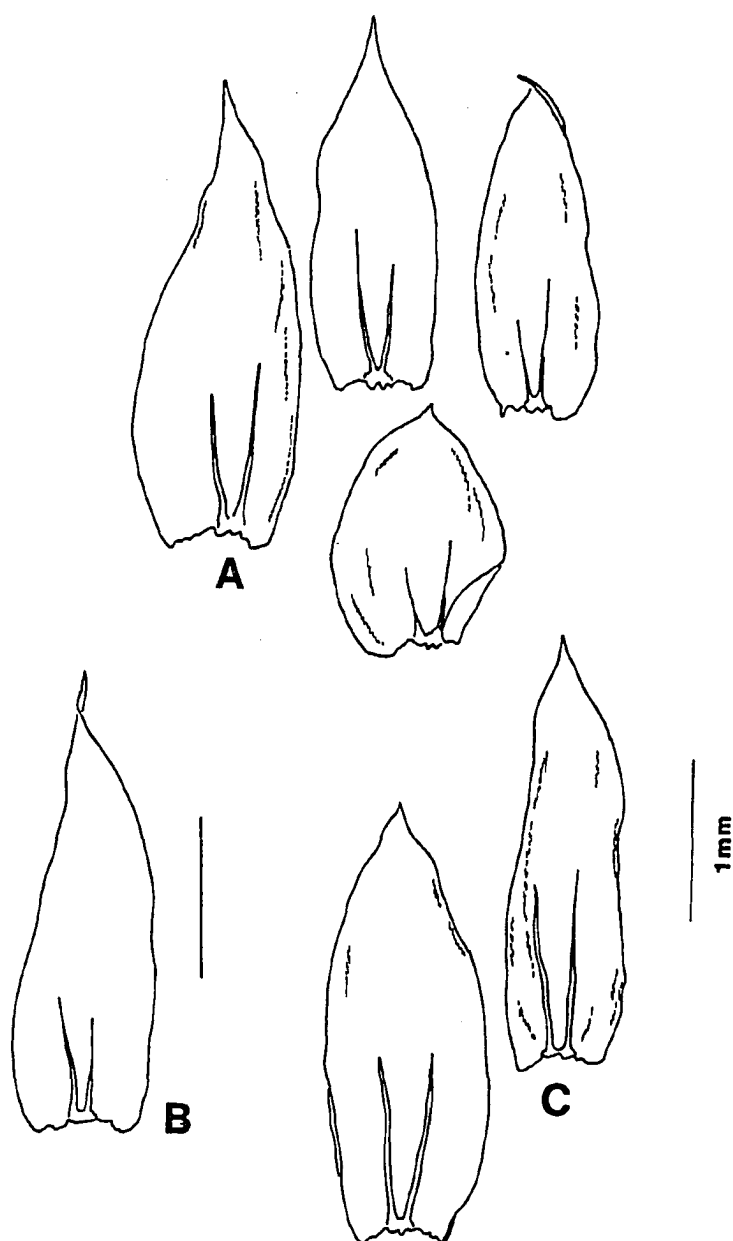


Fig. 34. Lepidopilum integrifolium. A. Leaves. B. Median cells. C. Sporophyte. (A-B. Duss 372, type; C. Steyermark & Dunsterville 92970).

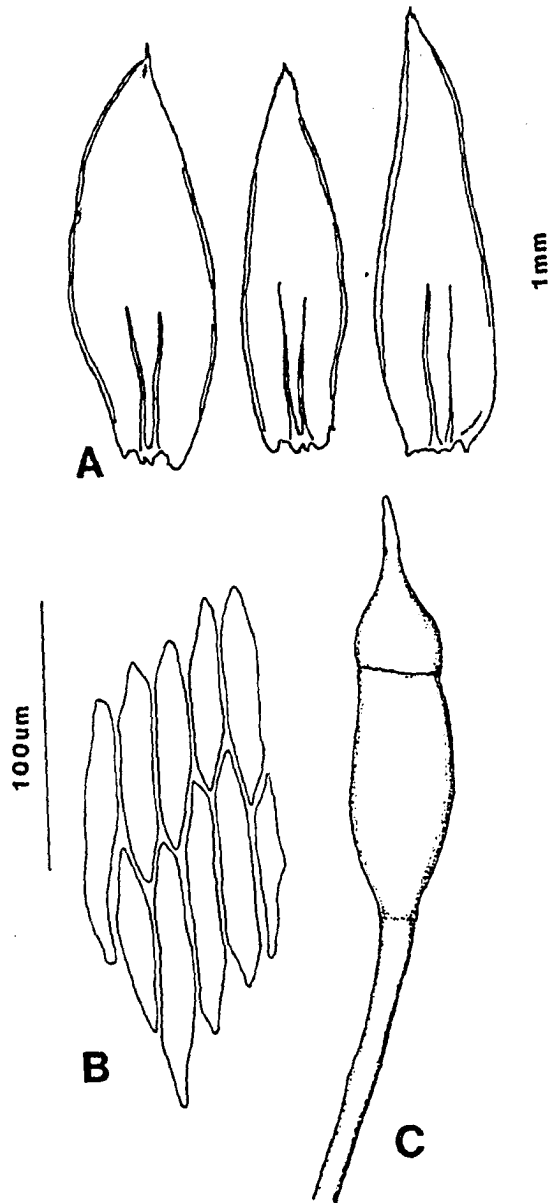


Fig. 35. Lepidopilum amplirete. A. Leaves. B.
Median cells. (A-B. Wright 72, type).

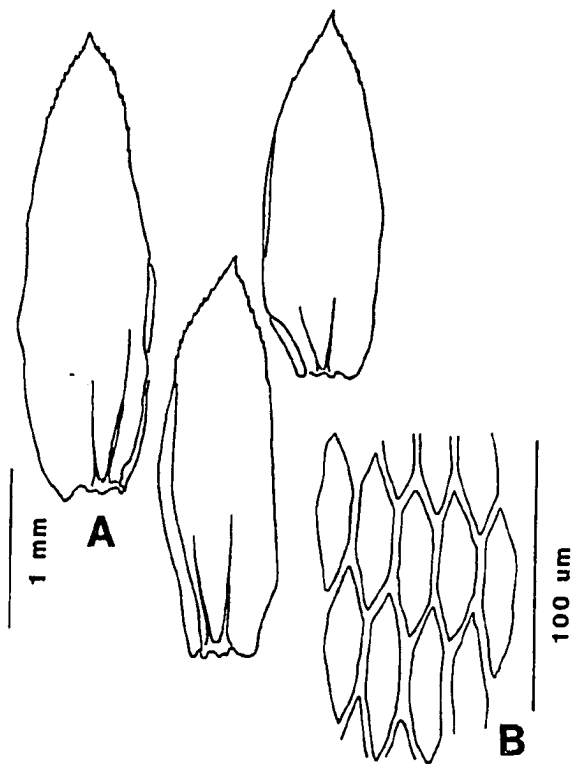


Fig. 36. Lepidopilum erectiusculum. A. Leaves.
(A-C. Spruce 734, type).

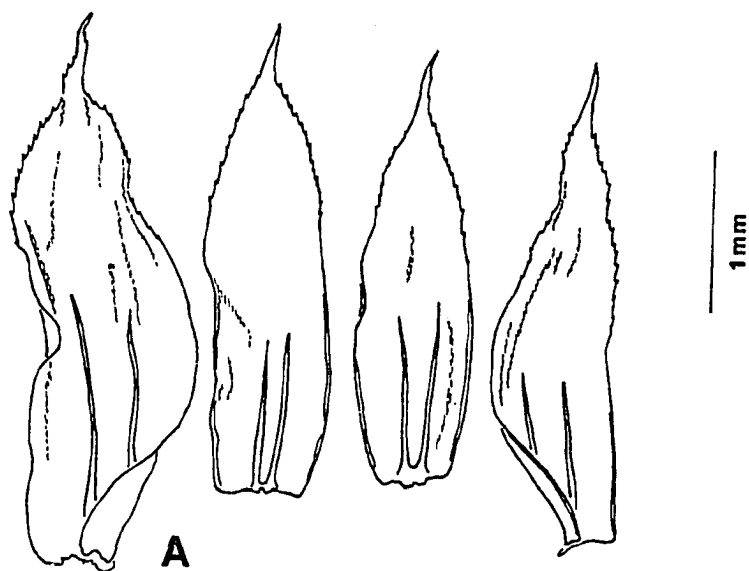


Fig. 37. Lepidopilum aurifolium. A. Leaves. (A.
Spruce 764, type).

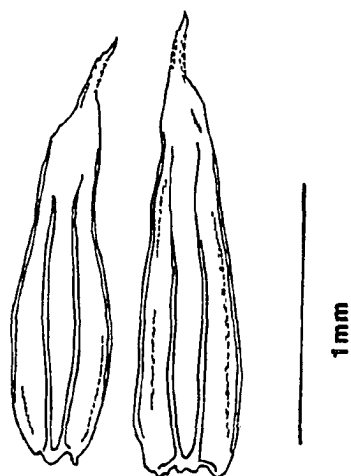
**A**

Fig. 38. Lepidopilum caviusculum. A. Leaves. B.
Margin. C. Median cells. (A-C. Spruce s.n., type).

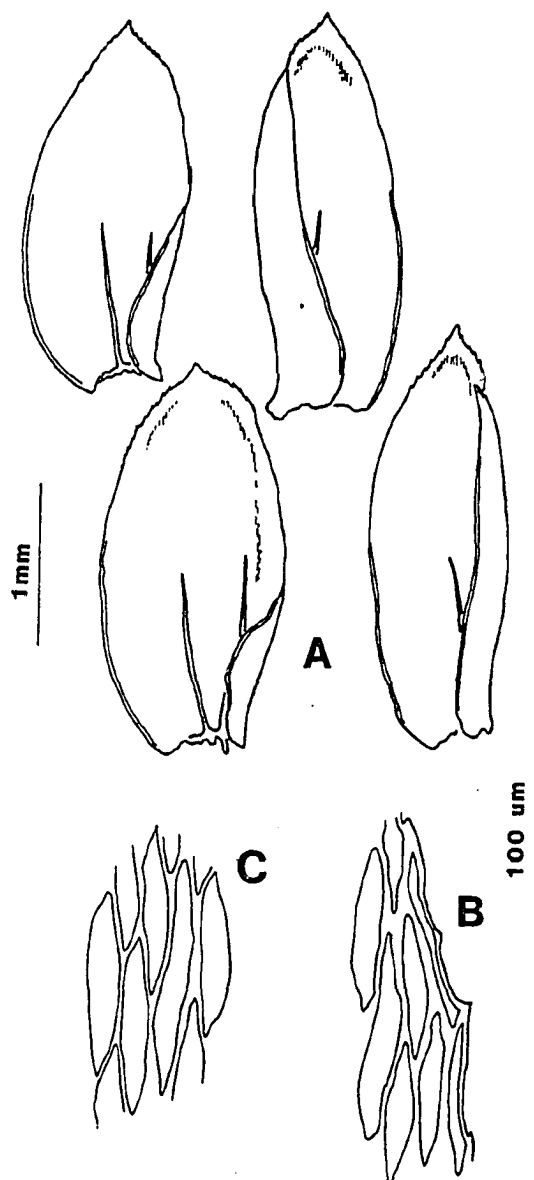


Fig. 39. Lepidopilum frondosum. A. Lateral leaves.
B. Median leaves. C. Margin of lateral leaf. D.
Median cells of lateral leaf. (A-D. Purdie s.n.,
type).

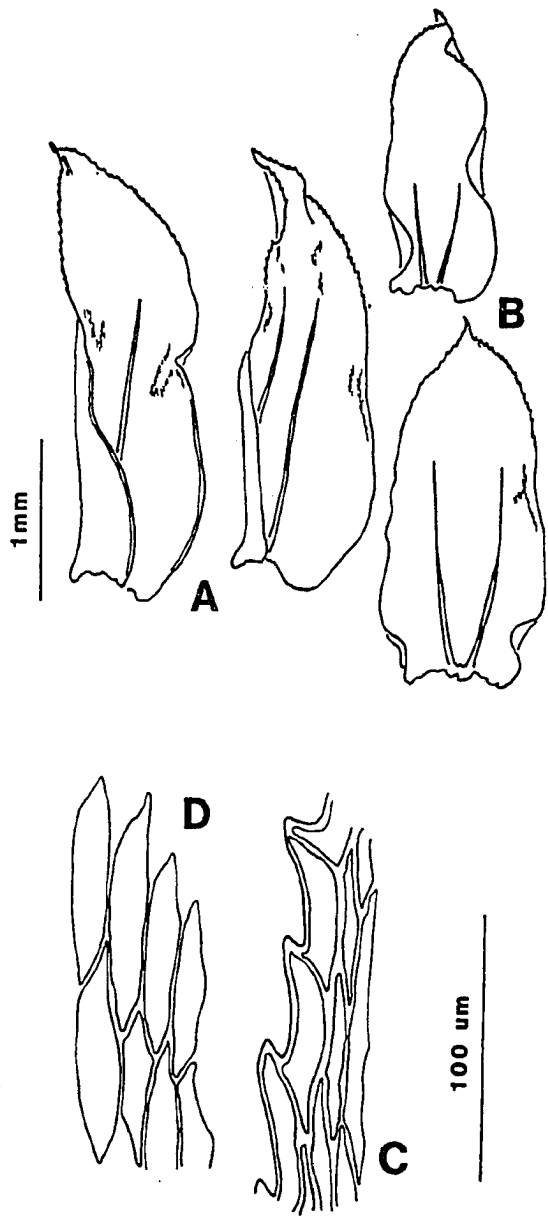


Fig. 40. Lepidopilum brevifolium. A. Leaves. B.
Branch leaves. (A-B. Spruce 784, type).

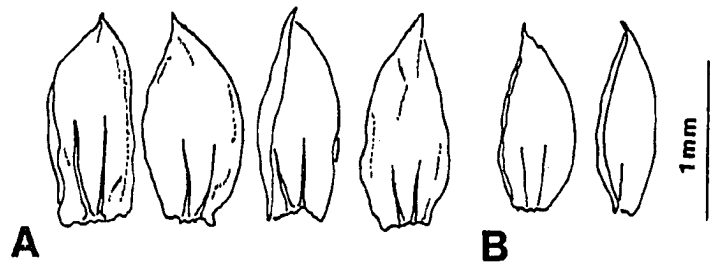


Fig. 41. Lepidopilum permarginatum. A. Leaves.
(A. Killip 11794, right and lower, type; Killip 35325,
upper left).

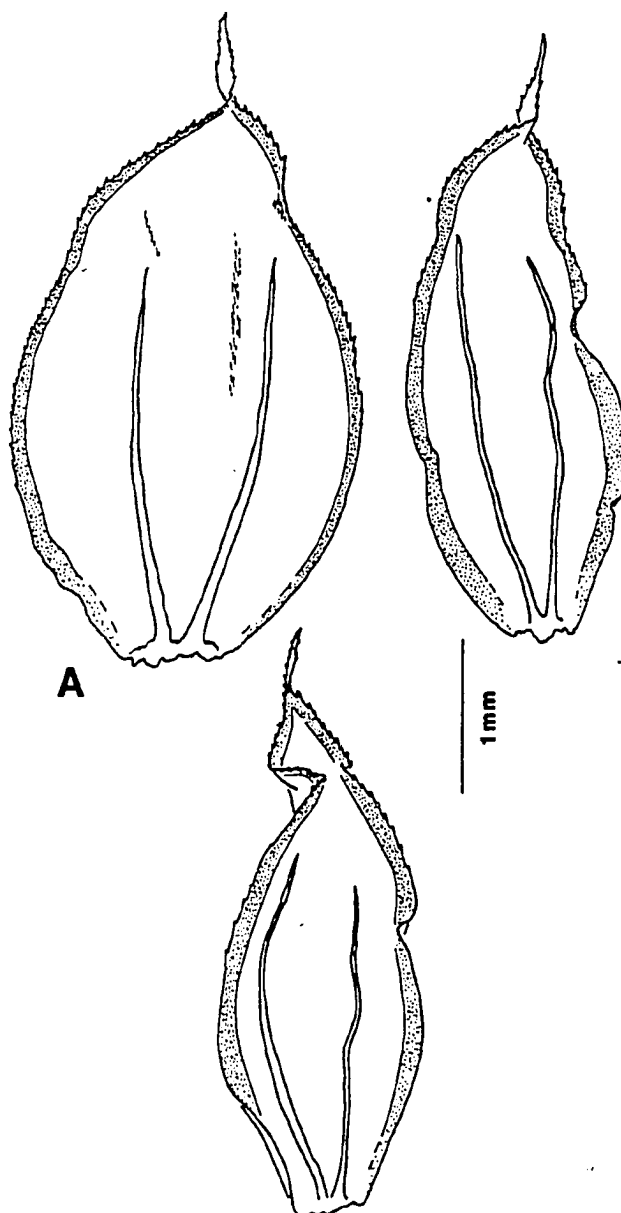


Fig. 42. Lepidopilum stillicidiorum. A. Lateral leaf. B. Median leaf. C. Attenuated leaf. (A-C. Spruce 735, type).

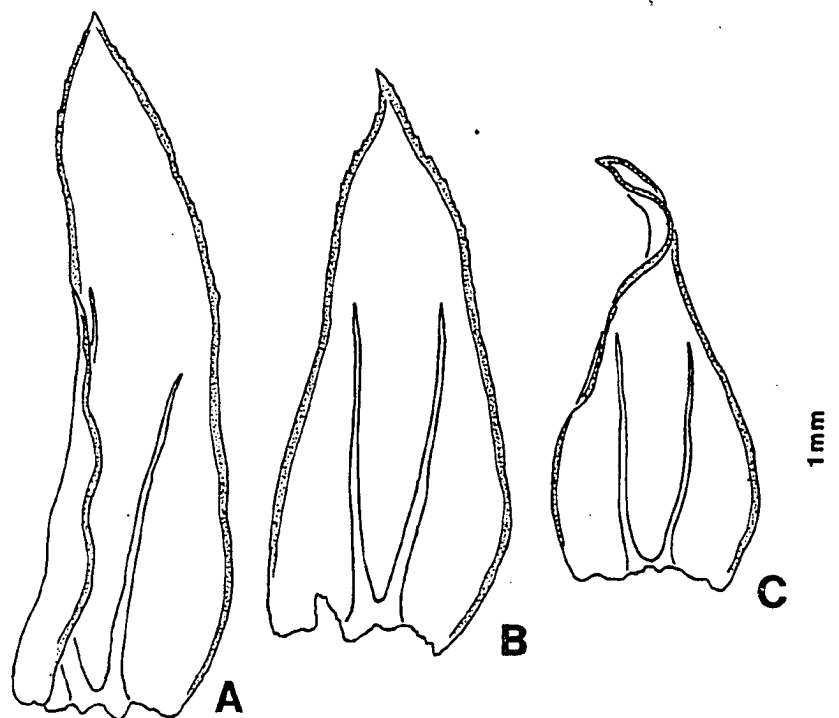


Fig. 43. Lepidopilum inflexum. A-C. Leaves. (A. Rue 132, type of L. perlaxum; B. Rue 133, type of L. aubertii; C. Spruce 726, type).

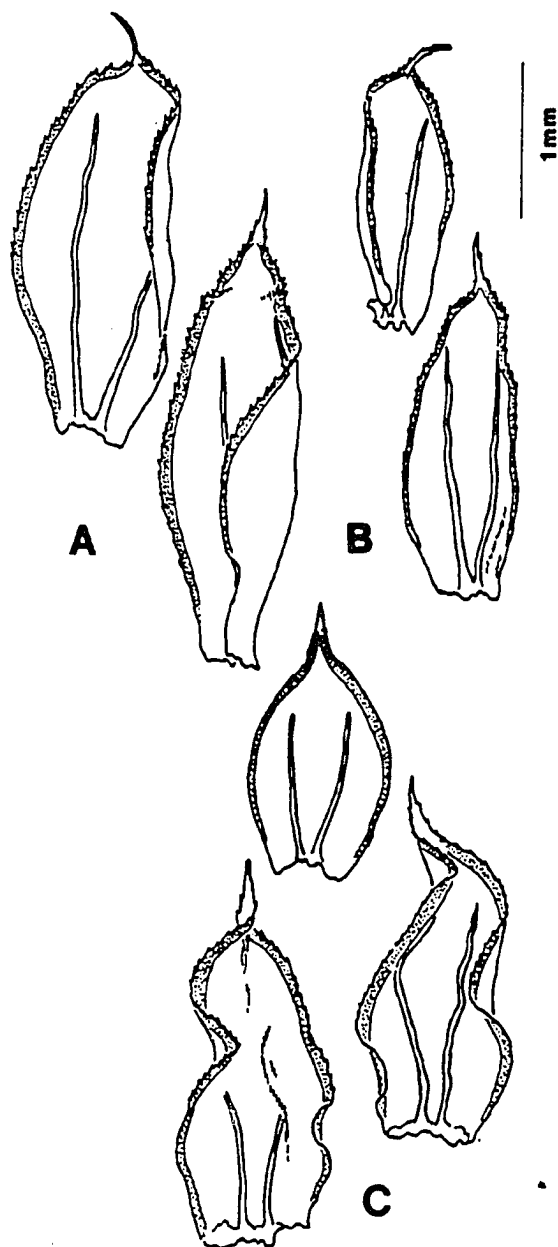


Fig. 44. Lepidopilum tortifolium. A. Lateral leaves (right and left), median leaf (center). B. Lateral leaf (left), median leaf (right). C. Lateral leaf (upper), branch leaves (lower). (A. Weir 147, type; B. Grubb et al. 2947, type of L. crispifolium; C. Frahm et al. 1606).

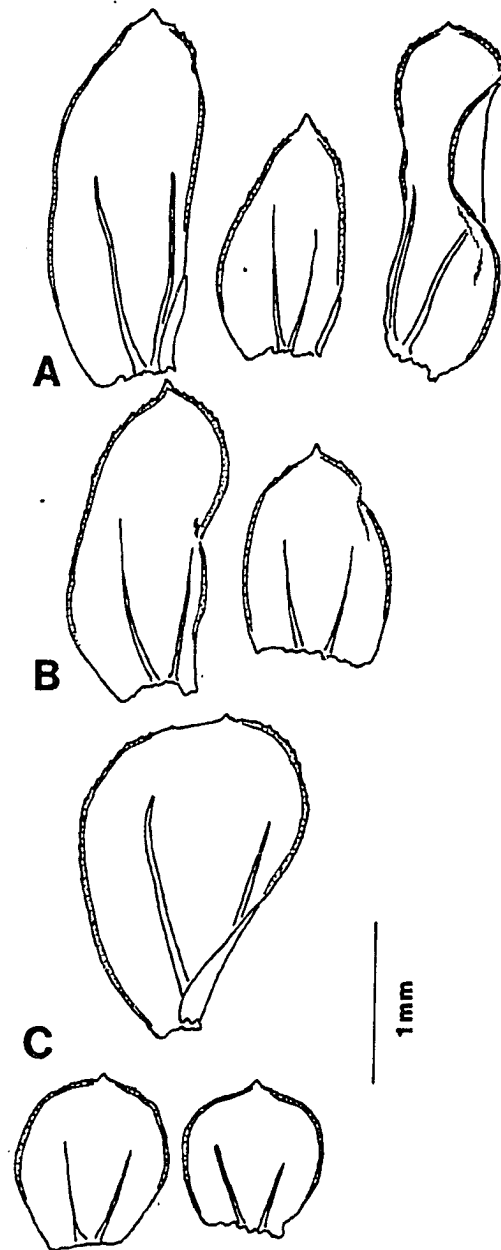


Fig. 45. Lepidopilum arcuatum. A. Lateral leaves.
B. Median leaf. C. Sporophyte. (A-C. Spruce 733).

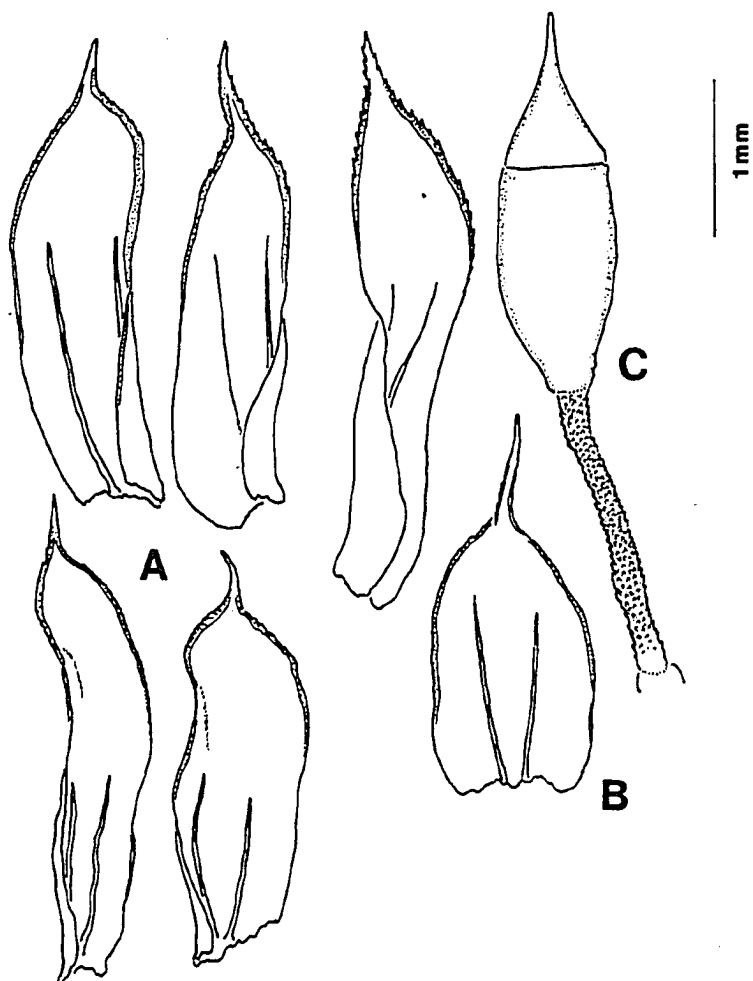


Fig. 46. Lepidopilum diaphanum. A. Lateral leaf (left), median leaf (right). B-C. Lateral leaves. D. Lateral leaf (right), median leaf (lower left). (A. Swartz s.n., type; B. Herzog 2724, type of L. brachyphyllum; C. Apollinaire s.n., type of L. apollinairei; D. Spruce s.n., type of L. tenuifolium).

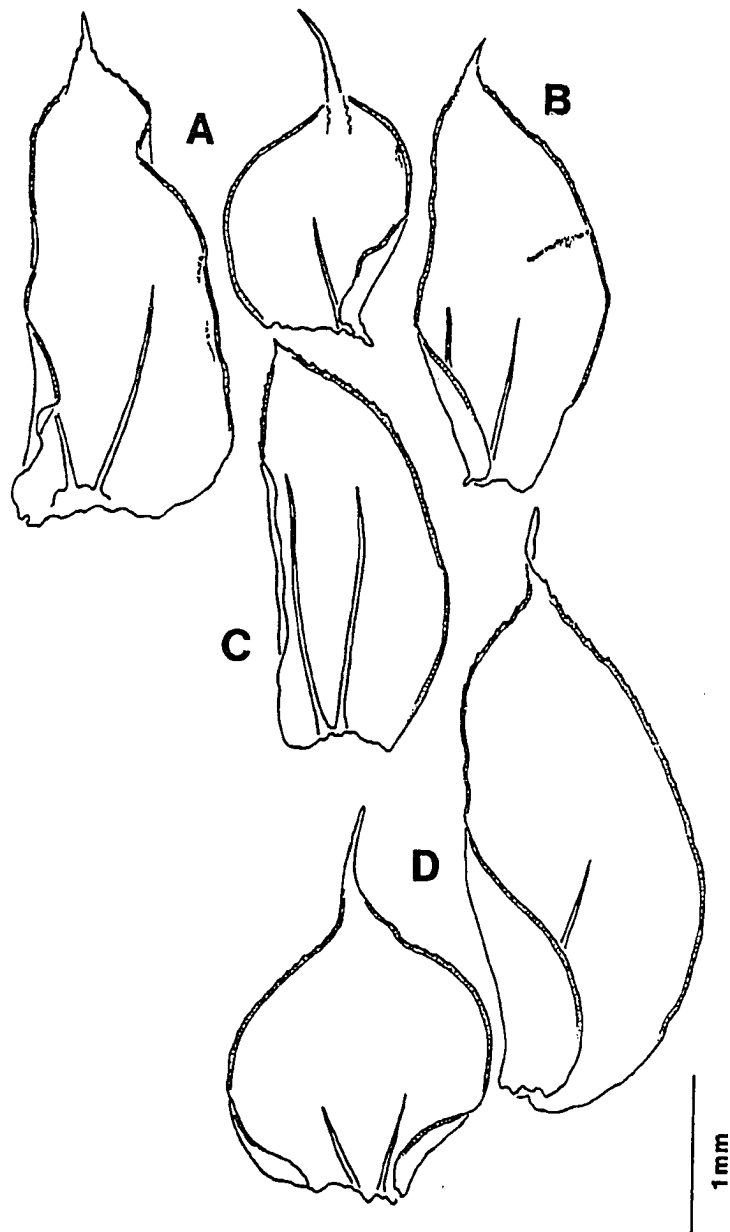


Fig. 47. Lepidopilum curvifolium. A-B. Lateral leaves. C. Median leaf. D. Branch leaf, with propagula along costa. E. Perichaetial leaf. (A, C. Spruce 724; B. Buchtier s.n.; D. Herzog 4020, type of L. gertrudis; E. Frahm et al. 185).

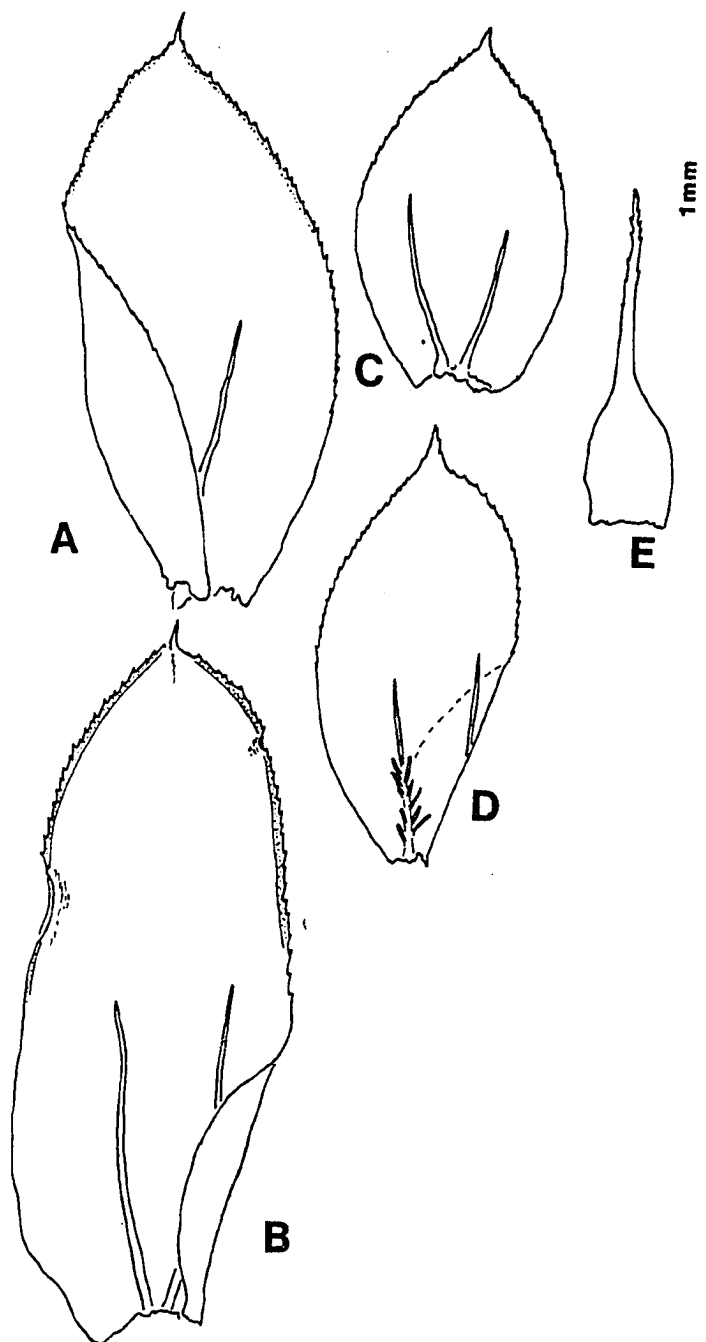


Fig. 48. Lepidopilum polytrichoides. A-B. Lateral leaves (upper), median leaves (lower) C-D. Lateral leaves (lower), median leaves (upper). (A. Pittier 5656, type of L. platyphyllum; B. Wallis s.n., type of L. excelsum; C. Swartz s.n., type; D. Fendler s.n., type of L. subpolytrichoides).

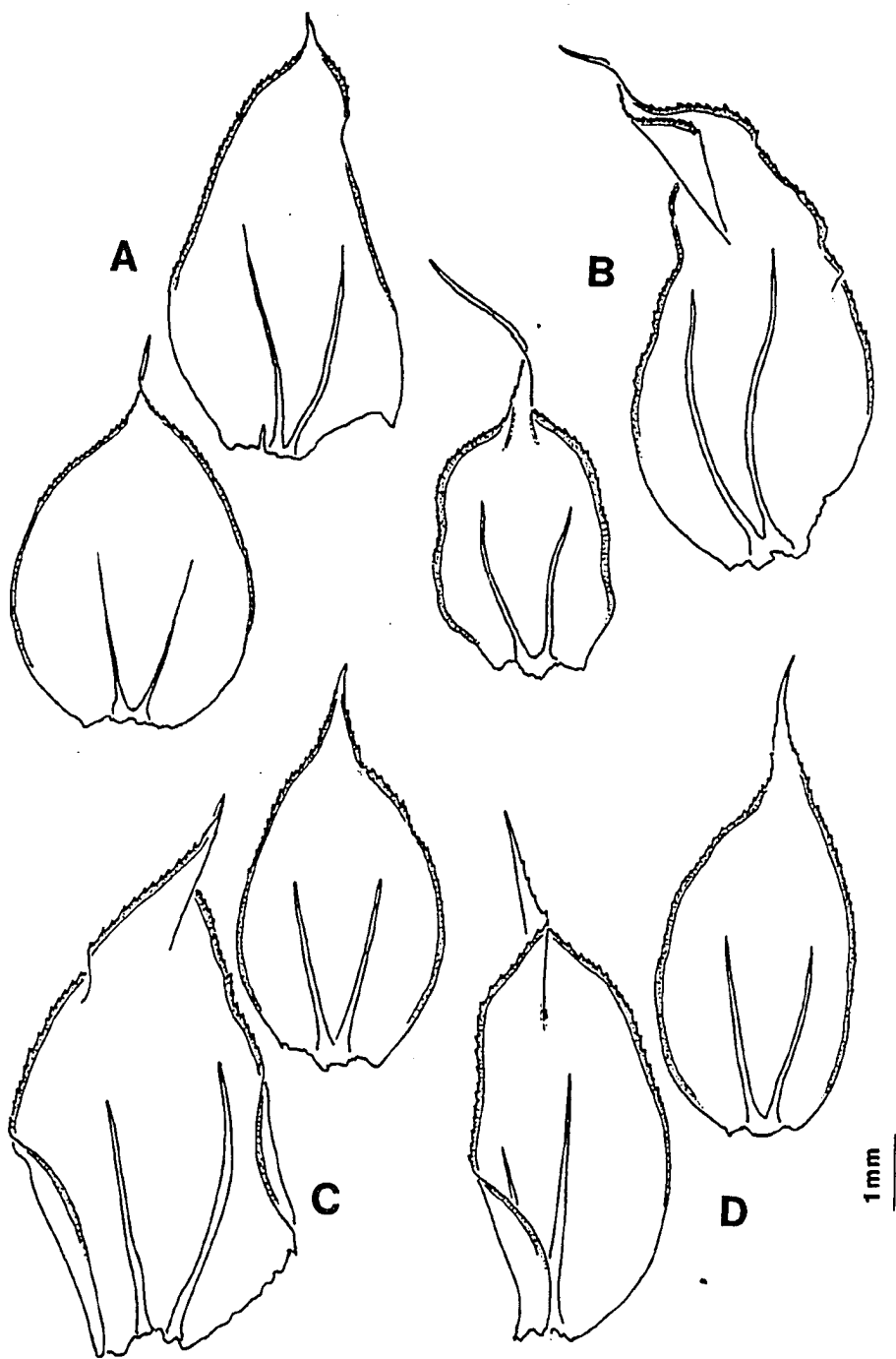


Fig. 49. Lepidopilum surinamense. A. Lateral leaf (left), submedian leaf (right). B. Margin of lateral leaf. C. Median cells of lateral leaf. D. Perichaetial leaf. E. Sporophyte. (A-B. Kegel 1406, type; C-E. Spruce 719, type of L. subflexifolium).

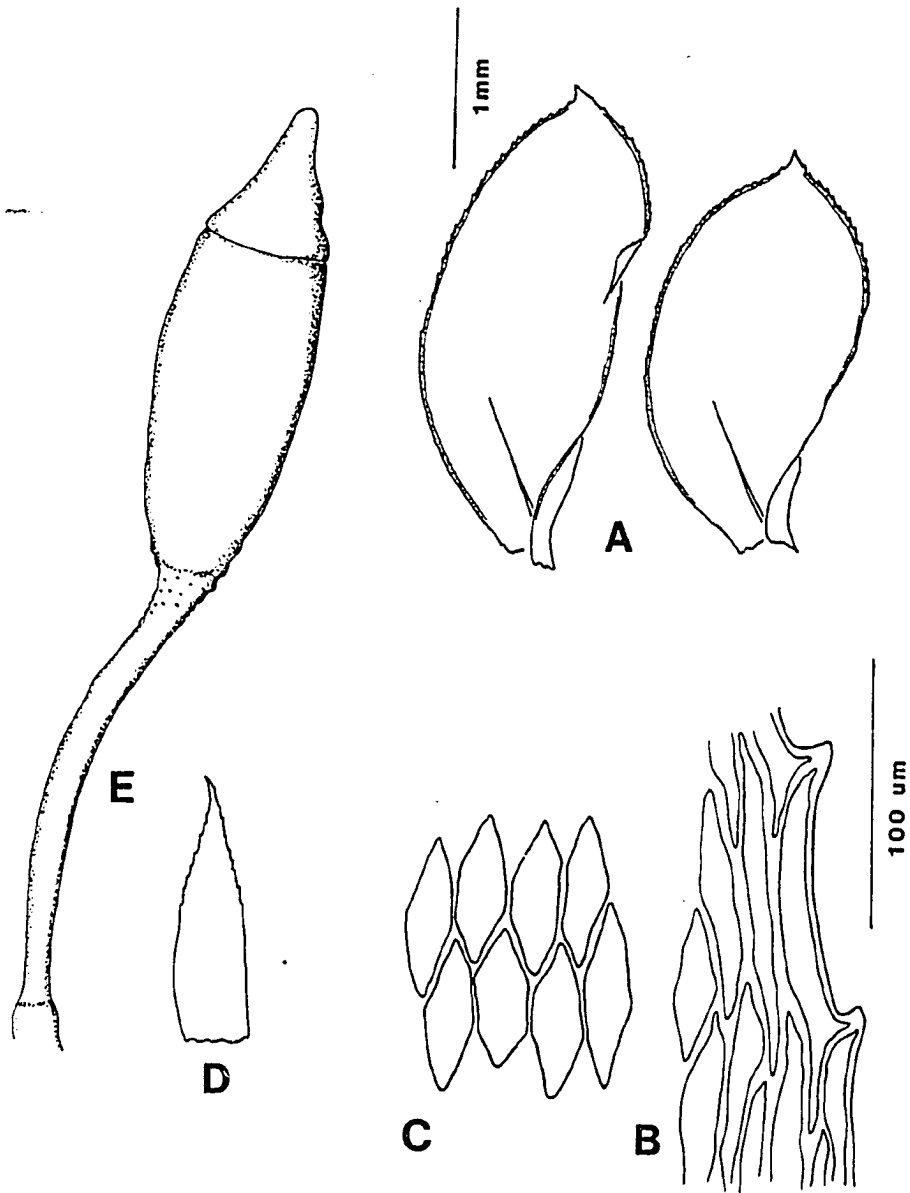


Fig. 50. Lepidopilum cubense. A. Leaf (lower left), branch leaves (upper). B. Leaf (lower center), branch leaf (upper center). C-D. Leaves. E. Margin. F. Median cells. (A. Skutch 2530, type of L. skutchii; B. Gutierrez 141, type of L. apiculatum; C. Williams 1054; D-F. Sinclair s.n., type of L. semilaeve).

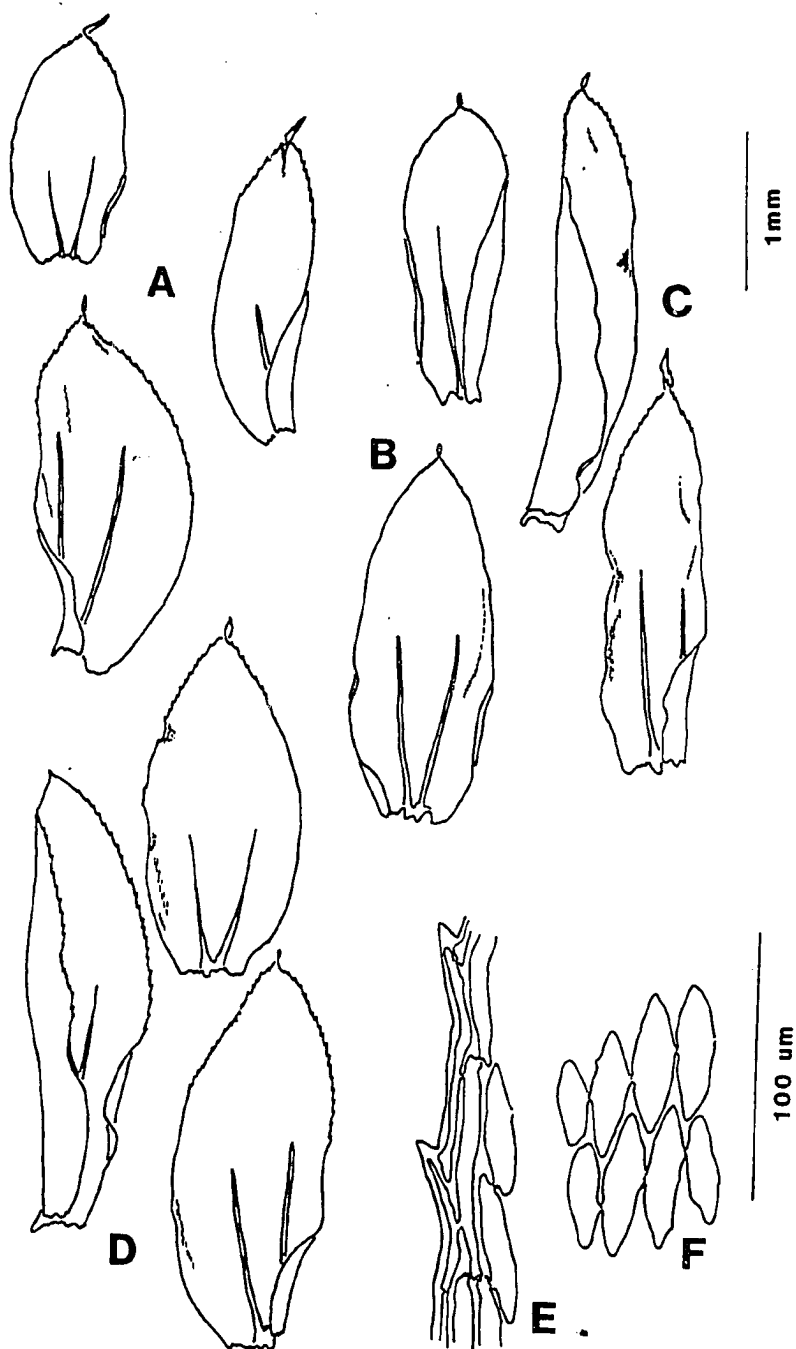
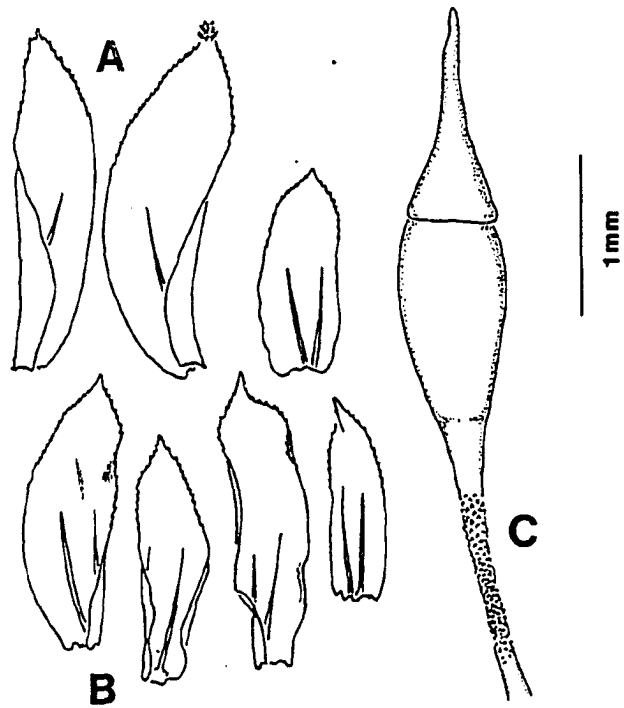


Fig. 51. Lepidopilum cubense. A. Lateral leaves (2 left; median leaf (right). B. Lateral leaves (3 left) median leaf (right). C. Sporophyte. (A. Buck 5923; B-C. Wright 85).



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