INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the original text directly from the copy submitted. Thus, some dissertation copies are in typewriter face, while others may be from a computer printer.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyrighted material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each oversize page is available as one exposure on a standard 35 mm slide or as a 17″ × 23″ black and white photographic print for an additional charge.

Photographs included in the original manuscript have been reproduced xerographically in this copy. 35 mm slides or 6″ × 9″ black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Accessing the World's Information since 1938

300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA

Order Number 8801758

A revision of the Neckeraceae Schimp. and the Thamnobryaceae Marg. & Dur. in the neotropics

Sastre-de Jesús, Inés, Ph.D.

City University of New York, 1987

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

A REVISION OF THE NECKERACEAE SCHIMP. AND THE THAMNOBRYACEAE MARG. & DUR. IN THE NEOTROPICS

by

INES SASTRE-DE JESUS

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1987

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.

14 July 87
date

William R. Buck
Chairman of Examining Committee
Prof. William R. Buck, New York Botanical Gardens

August 10, 1987
date

Executive Officer
Prof. Peter C. Chabora

Prof. Clark T. Rogerson, The New York Botanical Gardens

Prof. Noel H. Holmgren, The New York Botanical Gardens

Prof. Dana Griffin, III, University of Florida

Prof. Dennis Stevenson, Barnard College/Columbia Univ.

Supervisory Committee

The City University of New York

Abstract

A REVISION OF THE NECKERACEAE SCHIMP. AND THE THAMNOBRYACEAE MARG. AND DUR. IN THE NEOTROPICS

by

Inés Sastre de Jesús

Adviser: Dr. William R. Buck

Based on herbarium specimens and field work in Colombia, Venezuela and Ecuador the Neckeraceae and Thamnobryaceae were revised. The Neckeraceae in the neotropics are represented by two genera: **Neckera** and **Neckeropsis**. Asymmetric leaves in the family are considered a unique feature. Ten species are accepted in the genus Neckera. The ten species showed five basic patterns of distribution: Central America only (N. angustifolia, N. pachycarpa and N. ehrenbergii); Central America, West Indies and northern South America (N. urnigera); northern Andes (N. obtusifolia, N. spruceana, N. andina); Andes and southeastern Brazil (N. scabridens, N. chilensis) and southeastern South America (N. villae-ricae). In **Neckeropsis** three species are recognized (N. disticha, N. undulata and N. foveolata) which are lowland in distribution. A re-examination

of phyllotaxy in the familiy showed that it is not a useful taxonomic character at the generic level.

In the neotropics five genera are recognized in the Thamnobryaceae. **Homalia** and **Homaliodendron**, with one species each, are restricted to the West Indies and Central America. Two species are accepted in Pinnatella (P. minuta and P. callicostelloides). **Thamnobryum** is defined by dull plants with strong costae and short leaf cells. Generic separation between Porotrichum and Porothamnium was found ill-defined with unsuitable distinguishing characters. Nine species are recognized in Porothichum.

ACKNOWLEGMENTS

I thank Dr. W. R. Buck for reading the manuscript and for his many helpful suggestions during the course of this work. I am also grateful to the members of my supervisory committee, Dr. C. Rogerson, Dr. D. Stevenson, Dr. N. Holmgren, and Dr. D. Griffin, for their comments to the manuscript. I would like to thank all my friends and colleagues that helped me in one way or another, Dr. W. C. Steere, Steven P. Churchill, Pedro Acevedo, Dr. M. Richardson, Donald Black, C. H. Tsou, Lorinda Leonardi and Charlotte Labée. I am very grateful to the following institutions for the loan of herbarium specimens: B, BM, FH, FLAS, G, H, MO, NY, PACA.

I gratefully acknowlegde the financial support of the New York Botanical Garden and the use of laboratory facilities. I am also thankful to the personnel of the Centro Universitario de Cómputos at the Catholic University of Puerto Rico.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

Figure

INTRODUCTION

The objective of this investigation was to monograph the Neckeraceae and Thamnobryaceae in the neotropics. **Musci Austro Americani** (Mitten, 1869) and Brotherus (1925) have been the main references for the families in the neotropics. Mitten (1869) published 16 news species in his treatment of the Neckeraceae. He also included keys for all species of the family known at the time. Brotherus (1925) compiled all information available at his time and published keys to genera and species, and proposed some new combinations. The most recent neotropical treatment for the Neckeraceae (sensu Brotherus, 1925) was a revision by Wagner (1951) of the species from North and Central America. Some genera, such as Neckeropsis in Southeast Asis (Touw, 1962), Porotrichum and Porothamnium in Africa (De Sloover, 1983) and Homaliodendron in Indochina (Ninh, 1984), have been treated outside of the neotropics.

The lack of a modern treatment was the reason why I selected to study the Neckeraceae and Thamnobryaceae in the neotropics. Besides, the greatest number of species names for some genera in the Neckeraceae (e. g., Neckera) and Thamnobryaceae (e. g., Porotrichum and Porothamnium) are in the neotropics. Field collections and herbarium specimens from B, BM, FH, FLAS, G, H, MO, NY and PACA were the base for the taxonomic revision. During this investigation type material of most names available were compared to establish nomemclatural priorities.

All measurements given in the species descriptions are average values. The examined secondary stem leaves were observed from the middle-portion of the stem. Stipe leaves, when present, were studied from the middle area

of the stipe while branch leaves from the middle part of the main branches. Leaf lamina cells were described from the following areas: apical cells just below the apex, upper median cells and basal cells.

Ecological data at the end of each species description was obtained from herbarium labels and partly from personal field observations.

In this treatment 30 species are recognized between the two families. In the neotropics the Neckeraceae are represented by Neckera with 10 species and Neckeropsis with three species. Data from phyllotaxy studies showed that the two genera cannot be distinguished on the basis of this criteria as suggested by Wagner (1951). Five genera, Porotrichum, Pinnatella, Thamnobryum, Homalia, and Homaliodendron are included in the Thamnobryaceae. Generic delimitation between Porotrichum and Porothamnium was found ill-defined with unsuitable distinguishing characters.

HISTORY OF CLASSIFICATION

The genus Neckera was among the thirty-four genera described by Hedwig in his Species Muscorum Frondosorum (1801). Therefore, the genus is important nomenclaturally and, it is also the historical center of the Neckeraceae. Although not mentioned in Hedwig's treatment, it is believed that the genus Neckera was named to honor Noel J. de Necker (1730 - 1793), French-born botanist and historiographer. Sixteen species were included in the genus of which five are still in the family, three in Neckera (N. pennata, N, crispa, and N. pumila) and two in Neckeropsis (N. disticha and N. undulata). The other species are now placed in such genera as Anomodon, Antitricha, Cryphaea, Entodon, Pilotrichum, Pireella and Trachyloma. Hedwig's generic description of Neckera was rather

short and consisted only of sporophytic characters. He described the genus as mosses with a double peristome with sixteen acute external teeth and sixteen alternating inner teeth. The gametophytic characters of Neckera are found in his species descriptions. The plant habit was characterized as feather- or fern-like with complanate, alternating leaves. The leaves were described as lanceolate with an acute to truncate apex and sometimes rugose or undulate toward the apex. In his description of N. pennata two kinds of leaves were mentioned, anterior (and posterior) and lateral. The former are appressed whereas the latter are spreading from the axis. Neckera was divided into those species with short setae and those with long setae. Each group was further subdivided into species with distichous leaves or species with spirally arranged leaves. Hedwig did not give any name or rank to these divisions, but today they represent sections within Neckera and Neckeropsis.

Bruch, Schimper and Gümbel in their Bryologia Europaea (1855) gave very detailed generic descriptions, each accompanied by extensive comments. Their description of Neckera was not limited to sporophytic characters, it also contained descriptions of plant habit, stem, leaves, reproductive structures and the range of variability of these characters. Plant habit was characterized as creeping with pinnately branched, erect stems. The leaves were described as inserted in eight rows of which the anterior and posterior leaves are appressed, but the lateral ones diverge from the axis. Long perichaetial leaves with numerous paraphyses were reported as common. The sporophyte is without an annuals and has a cucullate calyptra, rarely with hairs. Like Hedwig (1801) they described a double peristome with 16 teeth in each ring, but in addition they noted articulations, trabeculae and perforations. Probably their most interesting remarks were on leaf insertation and arrangement in Neckera. Although the leaves of

Neckera appear to be inserted in two rows, they are disposed in a 3/8 phyllotaxis of obliquely inserted leaves. They were the first to point out that each leaf in Neckera is inflexed on one side of the leaf base, thus turning away from the axis and giving the plant a distichous appearance. If the inflection is on the right side the leaf will turn to the left and vice versa. This inflection point is stronger in the lateral leaves than in the dorsal and ventral ones.

According to Bruch, Schimper and Gümbel (1855) the genus was established solely on peristome characters and thus it comprised an assemblege of mosses with many dissimilarities. They compared their concept of Neckera to that of Bridel's (1827) Distichia. Although Bridel (1827) defined Neckera like Hedwig (1801) did, within the genus he segregated the species with distichous leaf arrangement into Distichia. This concept was not followed by bryologists of the time. Müller's Synopsis Muscorum (1851) was a step backwards in the concept of Neckera because it was so broad that it included nearly all pleurocarpous mosses known at the time (Bruch, Schimper & Gümbel, 1855).

Neither family concepts nor descriptions were included in Hedwig's (1801) work. These first appeared in Corollarium Bryologiae Europaeae (1855) published by Schimper as an appendix to Bryologia Europaea. Schimper's characterization of the Neckeraceae contained plant habit; leaf arrangement, shape, undulation, costa, aerolation; gametangial position, perichaetia, and vaginular shape; calyptra and seta length. The description did not include peristome features. The main defining characters of the Neckeraceae were the complanate leaf arrangement, ovate-lanceolate to ligulate leaf shape and the large perichaetial leaves with a perfectly cylindrical vaginula. Neckera and Homalia were the only genera included in the family. Neckera was divided into two sections (capsules immersed or exerted).

In Jaeger's review of the world moss flora (1870-1880) four genera (Trachyloma, Porotrichum, Camptochaete and Thamnium) were added to Schimper's Neckeraceae. Jaeger's addition to the family made it more heterogeneous because he placed mosses in the which did not show complanate foliation. He also included genera without perforate peristome teeth.

According to Fleischer (1906), the Neckeraceae represented a collection of genera that bryologists did not know where to place or for which they did not want to erect a new family. He considered Müller's (1851) and Mitten's (1869) concepts of the Neckeraceae artificial because in the former this group was within the Hypnaceae and in Mitten the Neckeraeae included a large range of unrelated mosses. Because he did not agree with such broad concepts he took up the task of rearranging the family (Fleischer, 1904-1923). He used Neckera as a center of radiation, from which he postulated a relationship for a series of genera. He claimed these should be kept together as a family. He saw a series of transitional stages starting with Neckera, through Pinnatella and Porotrichum, and ending in Thamnium. Another series began in some unspecified species of Neckera progressing to Lembophyllum, Camptochaete and Isothecium. He considered the external morphological similarities between Calyptotheciun and Pterobryopsis as parallelisms and for that reason segregated the Pterobryaceae from the Neckeraceae. Fleischer recognized eleven genera in the family which he divided into two subfamilies, the Neckereae and Thamnieae. The Neckereae were characterized as flattened plants with dimorphic, asymmetric, ligulate leaves, mostly transversely undulate with a weak costa and a lobed base. The exostome was described as papillose or transversely striate and the endostome was characterized as often keeled, perforate and mostly without cilia. This subfamily included Calyptothecium, Neckera, Bissetia, Baldwiniella,

Homaliodendron and Homalia. In the Thamnieae were included Cryptoleptodon, Leptodon, Pinnatella, Porotrichum and Thamnium. This subfamily differed from the Neckereae in the symmetric, oval to ligulate leaves, strong costa, and the presence of cilia or, a Hypnum-like peristome. In Die Musci der Flora von Buitenzorg (1922), Fleischer added a new subfamily, the Leptodonteae to accommodate Leptodon and Cryptoleptodon, previously included in Fleischer's (1906) Thamnieae and in Brotherus' (1906) Neckereae. Fleischer considered these genera distinct enough to form a separate group. Buck (1980) placed Leptodon in its own family and Cryptoleptodon was transferred to the Pterobryaceae. According to Buck (1980), Cryptoleptodon shares with the Pterobryaceae the general habit, colored auriculate alar cells and peristome characters.

Fleischer (1906) was the first to incorporate ecological comments about the family as its description. The group was characterized as forest dwelling mosses commonly growing on bark or rocks in moist tropical mountains. Fleischer's thorough analysis of the group set the groundwork for later treatment.

Brotherus (1925) basically followed Fleischer's (1906) concept of the Neckeraceae. Sixteen genera were recognized in three subfamilies. Cryphidium was added to the Leptodontoideae and Handeliobryum to the Thamnioideae.

Wagner (1951) segregated the Homalioideae from Brotherus' Neckeroideae on basis of leaf arrangement. According to his treatment, Homaliadelphus, Homalia and Neckeropsis have four rows of leaves as opposed to eight in the rest of the Neckeroideae. Wagner (1951) interpreted the four row leaf arrangement as an offshoot of the Neckeroideae. Touw (1962) considered Wagner's classification artificial and based on morphological misinterpretation. Touw agreed with van der Wijk (1957) that all Neckeraceae leaf insertation is in eight rows.

In 1982 Margadant and During raised the Thamnioideae to the family level. Buck and Vitt (1986) took a step further and transferred the family into the Hypnales to include those dendroid Neckeraceae with cross-striate exostomes.

Descriptive morphology of the Neckeraceae

1. Growth form and ramification. In the Neckeraceae one basic growth form is observed, that of Neckera. In this genus the plants are differentiated into a creeping rhizome and an erect to pendant branched part. This erect part may be regularly to irregularly pinnate. Stem and leaves are secondarily dorsiventrally arranged.

One kind of flagelliform branches is observed in the family. Neckera and Neckeropsis exhibit attenuation of branch tips.

2. Stem anatomy. In cross-section the stem is round to elliptic (Fig. 1). Small incrassate cells form the outer layers which surround the cortical layers of large parenchymatous cells. The central strand is absent in the two genera.

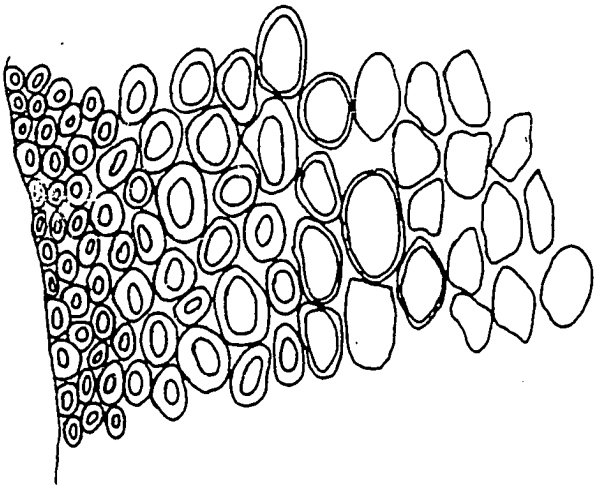
3. Branch primordia and paraphyllia. Many species of Neckera are characterized by abundant paraphyllia along the stem. Both types of paraphyllia, filamentose and foliose, are present in the genus. In some species, foliose paraphyllia can reach more than one millimeter. Neckeropsis is characterized by the absence of paraphyllia.

Branch primordia are present along the main stem and branches. Foliose and filamentose pseudoparaphyllia are observed in the family. The foliose pseudoparaphyllia may be obovate to lanceolate. The obovate ones tend to be appressed against the primordia.

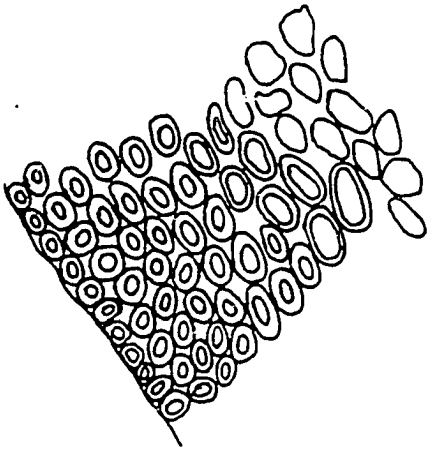
4. Phyllotaxy. The Neckeraceae are characterized by asymmetric, dimorphic leaves. Two kinds of leaves are present, outer and inner leaves. In the inner leaves the keel or folded part lies closer to the costa than in the outer ones (Wagner,

Fig. 1. Portions of stem cross-sections. A, Cross-section of Neckera andina (Spruce s.n., NY), x400. B, Cross-section of Neckeropsis undulata (Steere 6631, NY), x400.

A



B



1951). On each side of the stem, pairs of inner and outer leaves alternate. Along the stem a dorsal outer pair is adjacent to a ventral inner pair. The first detailed description of leaf arrangement in the family was given by Bruch, Schimper and Gümbel (1855). They noted that although the leaves in Neckera apper to be inserted in two rows, they are in eight rows. Bruch, Schimper and Gümbel were also the first to point out that each leaf is inflexed on one side of the leaf base. Therefore, the leaves turn away from the axis giving the plant a distichous appearance.

In mosses the shoot system originates from a three-sided apical cell (Berthier, 1971; Frey, 1970; Hallet, 1972). Leaves arise from the segmentation of the apical cell. According to Bopp (1984) the strong division pattern observed in the apical cell determines leaf position. The spindle position in the apical cell is turned by 120 degrees between divisions (Berthier, 1971). Three straight orthostichies will result when in two consecutive divisions the 120 degree angle prevails (e.g., Tetraphis pellucida and Fontinalis; Berthier, 1971). If the angle between successive divisions is enlarged the rows of leaves will be twisted producing a different phyllotaxy. This rotation could produce a 3/8 phyllotaxy as in Funaria and Bryum or a 2/5 like in Barbula and Bartramia. The phyllotaxy patterns observed in mosses follow the Fibonacci series or numbers (van der Wijk, 1957). Phyllotaxy has been useful in characterizing certain genera or families of mosses. For example a distichous phyllotaxy has been regarded as diagnostic for the Phyllogoniaceae.

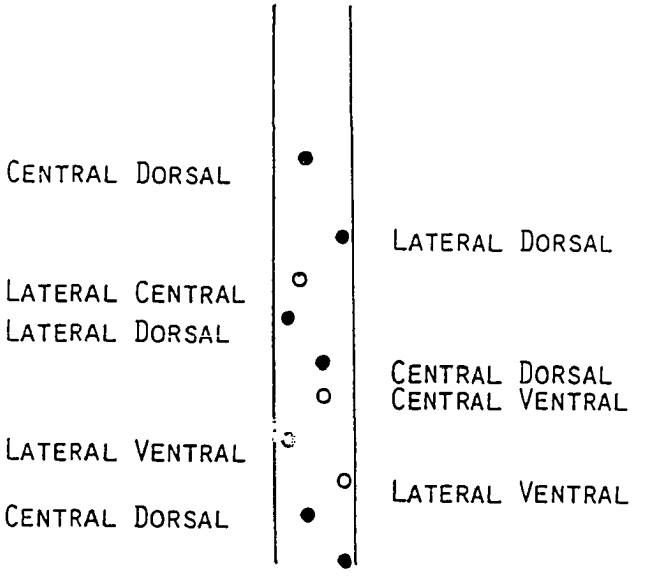
In the classification of the Neckeraceae phyllotaxy has been an important criteria. Fleischer in 1906 recognized two groups in the family using leaf arrangement. One group consisted of plants whit eight rows of leaves and the other with four. He did not describe how he reached those conclusions. Fleischer's criteria was followed by many others, such as Brotherus (1925) and Wagner (1951). Wagner, using leaf arrangement as the main criteria, created a new subfamily,

Homalioideae, to include Neckeropsis and Homalia. According to Wagner (1951), Neckera has the most complex leaf arrangement. He described the insertion cycle as eight consecutive leaves of two counter-clockwise spirals. Each spiral containing alternating inner and outer leaves. In Neckeropsis as well as Homalia he reported leaves in four rows. Wagner's conclusions were refuted by Touw (1962) in his revision of Neckeropis from Southeast Asia. Touw (1962), based on van der Wijk (1957) studies of distichous and pseudodistichous mosses, concluded that Neckera and Neckeropsis have eight rows of leaves.

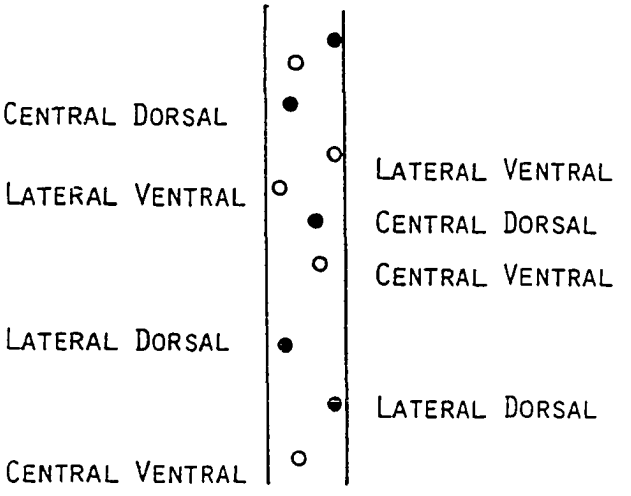
This controversy was approached by two methods. First using a dissecting scope, leaf sequence was followed along the stem, indentifying the orthostichies. Costa position of dorsal and ventral leaves was plotted on graph paper. This method, also used by Touw (1962), showed that leaves in Neckera and Neckeropsis for the most part are in eight rows (Fig. 2). Sometimes the phyllotaxy is altered and more than eight rows are observed. The phyllotaxies observed followed the main series or Fibonnacci numbers. The most common phyllotaxy was 3/8, but also 5/13 and 8/21 were observed.

The second method consisted of serial sectioning of shoot apices (for voucher specimens see Appendix A). Shoot apices were re-hydrated by bringing them to a boil in 10% multiterge for 5-10 minutes, washed in deionized water and fixed overnight in FAA. Samples were dehydrated in a TBA series and embedded in Paraplast Plus (62 degrees). They were sectioned on a Spencer rotary microtome and stained in Safranin-Fast Green. Sections were studied to determine the contact parastichys (Fig. 3). The number of contact parastichys found were 5, 8 and 13, but the most common one was eight. Results from this study also agree with those of Touw (1962) and van der Wijk (1957). Leaf arrangement in the family is not an important character at the generic level but it might prove to be useful at the family level.

Fig. 2. Stem leaf sequence. A, Leaf sequence in Neckera scabridens. B, Leaf sequence in Neckeropsis disticha. Open circles are ventral leaves and closed circles the dorsal ones.



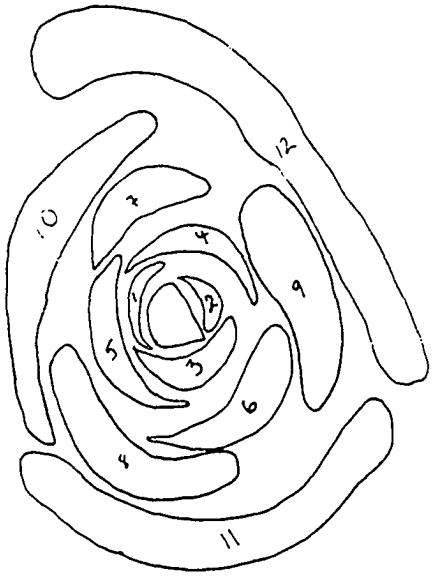
A



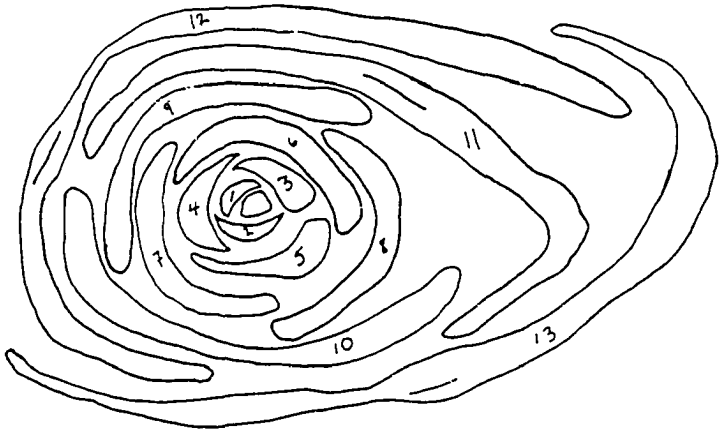
B

Fig. 3. Cross-sections of shoot apices. A, Cross-section of Neckera scabridens (Churchill & Sastre 12843-c, NY), x1000. B, Cross-section of Neckeropsis disticha (Sastre s.n., NY), x1000.

A



B



Leaves in the family range from distinctly undulate to not undulate.

5. Margins. Except some species of Neckera, leaf margins in the family are plane. Most species of Neckera and Neckeropsis have slightly serrate to crenulate margins.

6. Costa. The costa shows no internal differentiation. Its length varies in the family from short-double to single.

7. Gametangia and Sporophyte. Some species of Neckeropsis are dioicous, but others as in Neckera, may range from autoicous to synoicous. After fertilization two types of perichantial organization are observed in Neckera and Neckeropsis. In some species of Neckera (section Leiophylla) after fertilization the inner perichaetial leaves do not increase much in size, and the seta expands, extending the capsule beyond the perichaetial leaves. This type of maturation is also observed in some species of Neckeropsis from Southeast Asia (Touw, 1962), but not in the neotropical species. A second pattern of maturation is that of section Neckera in which the perichaetial leaves after fertilization expand, but the seta does not. Therefore, the capsule is immersed. Neckeropsis foveolata exhibits this kind of maturation. In the other neotropical species of Neckeropsis the vaginula elongates and it is mostly covered with ramenta. The ramenta, leaf-like paraphyses, develop after fertilization.

Seta length in the family is variable, it may be shorter than the capsule or much longer. Stomata are present at the capsule base in Neckera but absent in Neckerospsis.

8. Peristome. Exostome teeth in the family are lanceolate, striate at base and papillose above. The theet are mostly very pale to light orange. Some differences are observed in the arrangement of the exostome papillae. In some species of Neckera these may be arranged in rows, e. g., Neckera chilensis (Fig. 4).

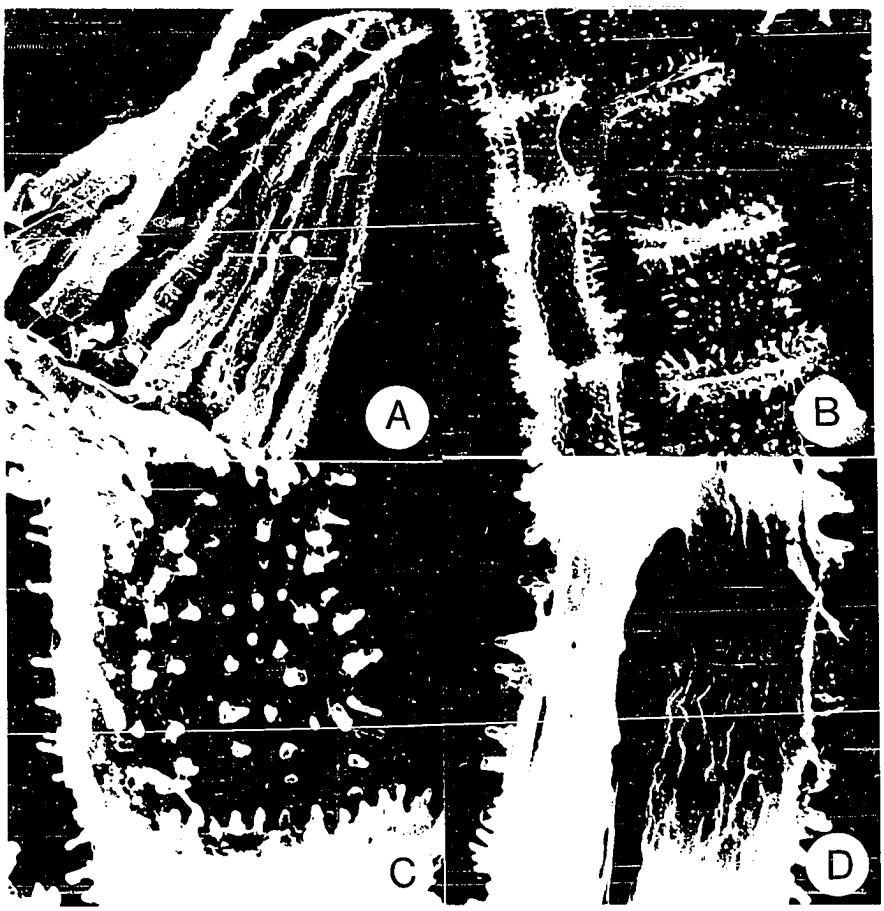
Fig. 4. Scanning Electron Micrograph of peristome of Neckera chilensis (Mahu 11837, MO). A, Exostome tooth, dorsal view, x800. B, Endostome segment, ventral view, x2000.

Longer papillae are observed in Neckeropsis disticha (Fig. 5). The endostme segments are smooth or papillose.

Neckeraceae Schimper, Coroll. Bryo. Eur. 99. 1855. Type. Neckera Hedwig, Spec. Musc. 200. 1801, nom. cons.

Small to robust plants, mostly forming mats, light to dark green, sometimes becoming yellowish, mostly shiny, complanate, unbranched or pinnate to dendroid, branches often becoming attenuate. Axillary hairs with short-quadrate stalk cell and long-rectangular apical cells; paraphyllia absent or present, filamentose to foliose; pseudoparaphyllia filamentose to foliose. Primary stem creeping, in cross-section, oval to elliptic, small rounded cells surrounding large hexagonal cells, central strand absent; primary stem leaves ovate, lanceolate to triangular, obtuse, broadly acute to acute; margins entire to serrulate; costa absent or present, short-double to single; marginal cells sometimes differentiated, upper median cells rhomboidal, fusiform to linear; alar cells distinct or undifferentiated. Secondary stem erect, perpendicular or pendent from substrate, complanate; stem leaves erect, erect-spreading to spreading, ovate, ovate-ligulate, oblong-ligulate or ligulate, asymmetric, some dimorphic, some auriculate, smooth to undulate; truncate, obtuse, acute to narrowly acute; margins entire, serrate to deeply serrate, distal margin sometimes folded; costa short-double or single; apical cells rhombic, rhomboidal to fusiform, upper median cells fusiform to linear, basal cells linear to rectangular, pitted to unpitted; alar cells distinct to undifferentiated. Autoicous, synoicous or dioicous. Perigonial leaves lanceolate, ovate to ovate-subulate; margins entire; costa absent; upper median cells fusiform, linear to rectangular. Ramenta present or absent. Perichaetial leaves oblong, oblong-subulate, broadly ovate-subulate, ovate-subulate; broadly

Fig. 5. Scanning Electron Micrograph of peristome of Neckeropsis disticha (Steyermark, 17261, G). A, Exostome and endostome, general view, x1000. B, Ventral view of exostome and endostome, x1500. C, Detail view of dorsal surface of endostome, x3000. D, Detail view of ventral surface of endostome, x3000.



acute to acute; margins entire to slightly serrate; costa absent or present, single; upper median cells fusiform to linear, pitted to unpitted. Setae short to long; capsule immersed to exserted, erect, cylindric, oblong to globose; exothecial cells short-quadrate to rectangular; stomata absent or present, phaneropore; annulus absent or rudimentary; operculum conic, short to long rostrate; peristome double, mostly hyaline or pale, exostome teeth lanceolate, smooth or striate al base, smooth or papillose above; endostome with a low to high basal membrane, segments linear to lanceolate, smooth to papillose, some keeled, perforate. cilia absent. Calyptra cucullate, mitrate, naked or with ramenta. Spores spherical, papillose.

The Neckeraceae are defined by a complanate stem, and asymmetric, dimorphic leaves, these being unique features in the order. Stem leaves are frequently undulate. The exostome teeth are lanceolate and papillose.

In the neotropics the Neckeraceae are represented by Neckera and Neckeropsis. Most of the genera still attributed to the Neckeraceae occur outside of the neotropics. In order to understand the relationships of the Neckeraceae further, studies at the species and generic levels outside of the neotropics should be carried out.

Key to genera

1. Stem leaves broadly acute to narrowly acute; costa mostly short-double to short single; ramenta absent

   1. Neckera

2. Stem leaves mostly truncate to obtuse; costa single; ramenta sometimes present on vaginula

2. Neckeropsis

1. **Neckera** Hedwig, Spec. Musc. 200. 1801, nom. cons. Type. Neckera pennata Hedwig, Spec. Musc. 200. 1801.

Plants medium-sized to robust, light to dark green, sometimes yellowish, mostly shiny, somewhat dendroid, complanate, mostly irregularly branched; branches sometimes becoming attenuate. Axillary hairs with short-quadrate stalk cell, mostly golden-brown, and long rectangular cells above; paraphyllia present or absent, scarce to abundant, filamentose to foliose; pseudoparaphyllia present, filamentose to foliose. Sometimes with a creeping primary stem; primary stem leaves erect, erect-spreading to falcate, triangular, lanceolate, broadly ovate to obovate, often decurrent, acute, narrowly acute or sometimes forming a long acumen; margins entire to slightly serrate, recurved to plane at base; costa absent or present, short-double to single; upper median cells fusiform to linear, basal cells mostly rectangular; alar cells undifferentiated to differentiated, short-quadrate. Secondary stem perpendicular to pendent from substrate, unbranched to pinnate, complanate; stem and branch leaves erect, erect-spreading to spreading, smooth to strongly undulate, ovate-ligulate, oblong-lugulate, oblong-lanceolate to ligulate, slightly concave to flat, sometimes secund, obtuse, broadly acute, acute to narrowly acute; margins entire to serrate, recurved to plane at base; costa short and double to sometimes single; apical cells rhombic, rhomboidal to fusiform, upper median cells fusiform to linear, basal cells linear to rectangular, pitted or unpitted; alar cells mostly short-quadrate. Autoicous. Perigonial leaves concave, lanceolate, slightly apiculate; margins entire; costa absent; upper median cells rectangular. Antheridia globose to cylindrical.

Perichaetial leaves oblong, oblong-lanceolate to ovate-subulate, abruptly to gradually acute; margins entire to slightly serrate at apex; costa absent or present, reaching mid-leaf; upper median cells fusiform to linear, pitted or unpitted. Seta short to long, smooth; capsule immersed to long-exserted, erect, cylindric, oblong, to globose; exothecial cells short-quadrate to rectangular; stomata present; annulus absent; operculum conic, short to long rostrate; peristome double, exostome teeth lanceolate, smooth to densely papillose, somewhat cross-striate at base, sometimes perforate; endostome rudimentary or well developed, with a low to high basal membrane, segments narrow-lanceolate, keeled, smooth to densely papillose, sometimes perforate. Spores spherical, papillose. Calyptra cucullate or mitrate.

This genus is defined by asymmetric and dimorphic leaves. According to Index Muscorum (van der Wijk et al., 1959-1969) there are 42 species of Neckera outside of the neotropics. Asia contains the largest number with 29. A chromosome number of 10 has been reported in Neckera complanata. N. crispa, N. himalayana, N. humilis and N. pennata (Fritsch, 1982). However, variations of 11 or 12 have been observed.

Key to sections

1. Capsules immersed; setae 0.5 mm long; perichaetial leaves ovate-subulate to oblong-subulate

   Sect. Neckera

2. Capsules mostly exserted; setae 2.0 mm long; perichaetial leaves oblong, obtuse to abruptly short apiculate

   Sect. Leiophylla

Neckera hedwig sect. Neckera

Neckera sect. Cryptopodia Röhling, Deutschl. Fl.

Crypt. Gew. ed. 2, 3: 82. 1813.

Key to species of sect. Neckera

1. Paraphyllia very abundant along stem, about 0.5–2.0 mm long

2.

2. Stem leaves mostly slightly concave to concave, not undulate

1. N. obtusifolia

2. Stem leaves mostly plane, not concave, mostly undulate

3.

3. Perichaetial leaves oblong-lanceolate, acute, 5.0–6.0 mm long; known only from Ecuador

2. N. spruceana.

3. Perichaetial leaves oblong-ovate, subulate, sometimes filiform 3.0–4.0 (6.0) mm long; known from Central America

4.

4. Stem leaves lanceolate, leaf apex narrowly acute

3. N. pachycarpa.

4. Stem leaves ovate to oblong-lanceolate, leaf apex acute to broadly acute

4. N. ehrenbergii.

1. Paraphyllia scarce to absent, when present mostly small sometimes reaching 0.5 (rarely 1.0) mm long

5.

5. Stem leaves mostly erect, lanceolate

5. N. angustifolia

5. Stem leaves erect-spreading to spreading, oblong-ligulate

6.

6. Plants very glossy (iridescent green); stem leaves mostly flat, rarely undulate; known only from southern Brazil, Paraguay, Uruguay and northeastern Argentina

6. N. villae-ricae.

6. Plants mostly dull to slightly shiny; stem leaves undulate, rarely flat; not restricted to southeastern South America.

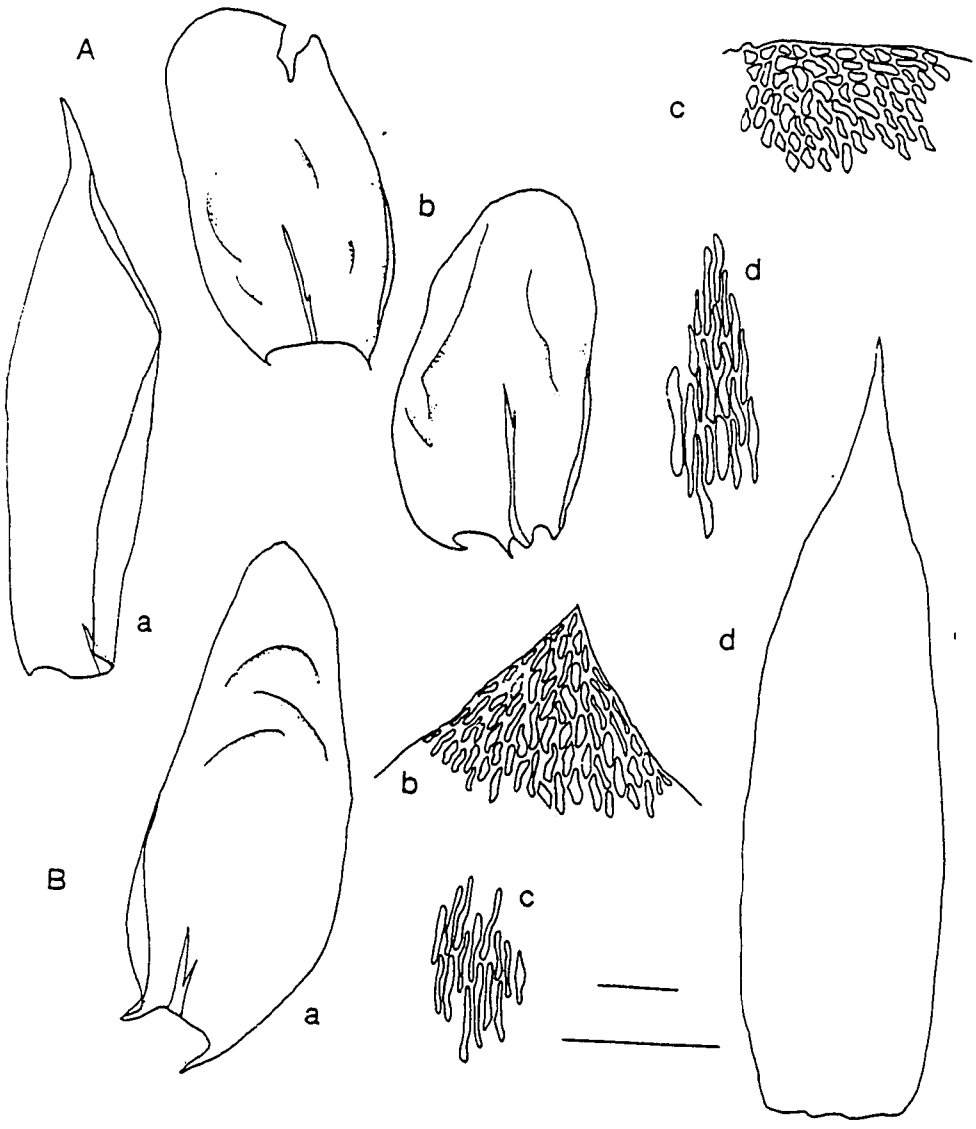
7. N. scabridens.

1. **Neckera obtusifolia** Taylor, London J. Bot. 7: 193. 1848. Type. Ecuador. Pichincha, 1827, Jameson s. n. (lectotype, FH!; isotype, NY!).

(Fig. 6A a-d).

Slender to slightly robust plants, 4.0-13.0 cm tall, dark-to light- green, to yellow, slightly shiny, irregularyly pinnate. Axillary hairs 6 cells long, the 2 stalk cells golden-brown, quadrate; paraphyllia abundant, filamentose to foliose, ca. 0.5-1.0 mm long; pseudoparaphyllia filamentose to foliose. Primary stem leaves appressed when dry, erect to erect-spreading when wet, obovate to lanceolate, 0.5-1.0 mm long; apical cells linear, 39-52 um long, 4 um wide, median cells linear, 39-52 um, long 6 um wide, rectangular basal cells, 39-65 um long, 6 um wide, alar cells differentiated, quadrate. Stem leaves erect to erect-spreading, oblong-ligulate, 2.0-3.0 mm long, 1.0 mm wide, slightly concave, sometimes secund, mostly not undulate obtuse to broadly acute; margins entire, margin recurved below (especially in central leaves); costa short and double,

Fig. 6. A, Neckera obtusifolia (Jameson s. n., FH). a, perichaetial leaf, x40; b, stem leaves, x40; c, stem leaf apex, showing cells, x40; d, stem leaf upper median cells, x40. B, Neckera spruceana (Spruce s. n., NY). a, stem leaf, x40; b, stem leaf apex, showing apical cells, x400; c, stem leaf upper median cells, x400; d, perichaetial leaf, x40.



1/4 to 1/2 of leaf length, sometimes single; aplical cells rhomboidal, 21-31 um long, 4-6 um wide, upper median cells linear, 52-60 um long, 4-6 um wide, basal cells linear to rectangular, 52-78 um long, 4-6 um wide, slightly pitted, alar cells distinct, quadrate; branch leaves somewhat smaller than stem leaves. Autoicous. Perichaetial leaves oblong, inner leaves 4-5 mm long, 1.0 mm wide, abruptly to gradually acute; margins entire; costa present or absent, reaching mid-leaf; apical cells linear, 52-78 um long, 4 um wide, upper median cells linear, 78-130 um long, 6 um wide, basal cells rectangular to linear, 78-130 um long, 6-8 um wide. Seta short, ca. 0.5 mm long; capsule cylindric, 2.0 mm long; exothecial cells rectangular, 52 um long, operculum conic, short-rostrate; peristome double, exostome lanceolate, striate at base, sparsely papillose to nearly smooth above; endostome slender, small, from a low basal membrane, nearly smooth, keeled. Calyptra cuculiate. Spores papillose, 39 um in diameter.

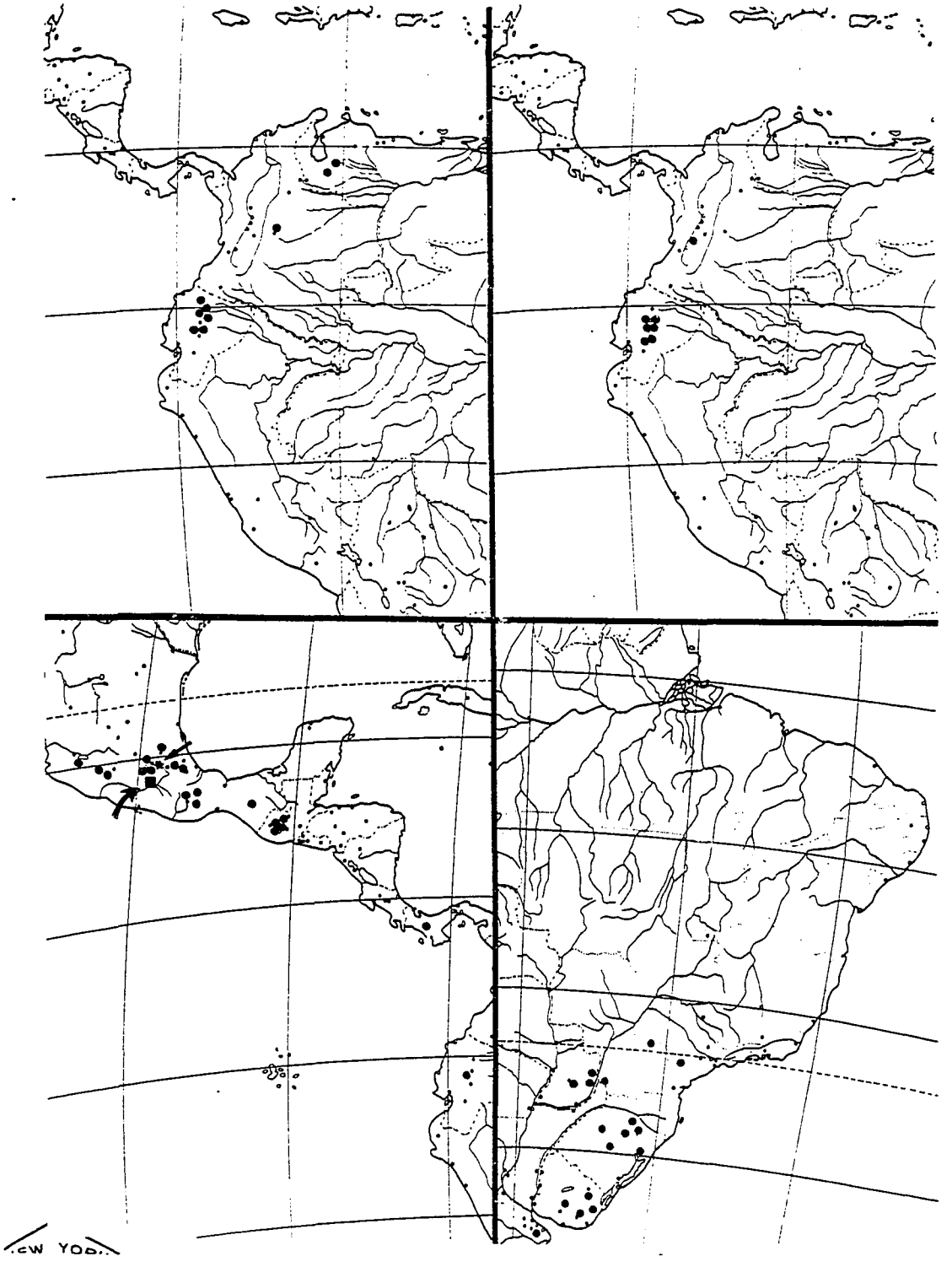
Distribution and Ecology. (Fig. 7A). Neckera obtusifolia is known form Venezuela, Colombia and Ecuador. It occurs in páramos from 2900 to 4000 m. It commonly grows epiphytically.

Specimens examined. COLOMBIA. Cundinamarca: Andes Bogotenses, between Tipaquira and Pacho, 2000 m, Weir s. n. (NY).

VENEZUELA. Mérida: Granates' Páramo, Granates' farm, along Río Granates, 3000-3100 m, 20 Feb 1985, Griffin PV-977 (NY); Trujillo: El Jabón, SE and above Carache, 2900-3300 m, 6-9 Mar 1985, Griffin et al. PV-1287 (NY).

ECUADOR. Cotopaxi: Páramo de Cotopilalán, 4000 m, 2 Feb 1984, Laegaard 51288G (NY), Parque Nacional Cotopaxi, ca 5 km from entrance, 3400 m, 30 Oct 1983, Steere 26973 (NY), Area Recreacional El Boliche along road ca 4 km S of Railroad Station, 3500 m, 15 Dec 1983, Buck 9901 (NY); Imbabura:

Fig. 7. Distribution maps of: A, Neckera obtusifolia; B, N. spruceana; C, N. pachycarpa (square), N. ehrenbergii, N. angustifolia (star); D, N. villae-ricae.



West slope of Cordillera Occidental, on old trail to Intag, via Selva Alegre region, 3500 m, 24 Nov 1943, Steere 9221 (NY), E side of Cerro Cotacachi, NW of Cotacachi, 3500 m, 21 Nov. 1978, Lewis 78-2620 (NY); Napo: Eastern Cordillera, E slope km 212.5 Quito-Baeza road, near head of Lago de Papallacta, 3200 m, 4 Nov 1983, Steere 27066 (NY); Pichincha: E slopes of Volcán Pichincha, above Quito, 3000-3500 m, 30 Jan 1981, Balslev 1769 (NY), Andes Quitenses, Spruce 1345 (NY), Pichincha, 3 Feb 1847, Jameson s. n. (FH), Cerro Pasochoa, S of Quito, 3200 m, Andrade 134 (NY), Western Cordillera, Laguna Mojanda-Malchingui road (old road Otavalo-Quito mule trail), 3500 m, 23 Oct 1983, Steere 26725 (NY).

Discussion. Neckera obtusifolia is easily recognized vegetatively by the abundant paraphyllia along the stem, and concave leaves with obtuse to broadly acute apices. These features are also diagnostic for N. andina. On the basis of the sporophyte the two species can be separated since in N. obtusifolia the short setae (reaching to 0.5 mm long) results in an immersed capsule. The setae in N. andina are 2.0-3.0 mm long, thus the capsule is exserted. Also in the N. obtusifolia there is a low basal membrane in the endostome. Perichaetial leaves in both species are very similar, if not identical. Plants bearing sporophytes are common. The presence of abundant paraphyllia, a single costa and autoicous sexuality were used by Steere (1948) to segregate N. obtusifolia, N. spruceana and N. menziesii into the genus Metaneckera. Paraphyllia are common in other species of South and Central America (three other), especially in those that reach higher elevations. A single costa may be frequently found within one plant of a species with double costae. In conclusion, the characters chosen to segregate these species fall within the limits of the genus Neckera.

This taxon is known from very few collections despite the extensive work done in páramos of South America. It seems to be limited to protected forest

areas in páramos of Venezuela, Colombia and Ecuador. The southernmost point in its range is the slopes of Cotapaxi in Ecuador. Neckera obtusifolia is one of the three species found at elevations higher than 3,000 m in the neotropics. This taxon seems to occupy the northern Andes while N. andina is found from Ecuador to Peru and Bolivia.

2. **Neckera spruceana** Mitten, J. Linn. Soc., Bot. 12: 456. 1869. Type. Ecuador. Andes Quitenses, in monte Titaicun, 11,000 ped., Spruce 1341 (holotype, NY!). (Fig. 6B a-d).

Medium sized to robust plants, to 15 cm tall, dark-to light-green, shiny, irregularly pinnate. Axillary hairs 4-6 cells long, stalk cell golden-brown, short quadrate; paraphyllia abundant, filamentose to foliose, (0.5)1.0-2.0 mm long; pseudoparaphyllia filamentose to foliose. Primary stem leaves obovate, 1.0 mm long, acute; margins entire to sometimes serrate at apex; costa present or absent; upper median cells fusiform, 26-39 um long, 4 um wide, alar cells slightly differentiated. Stem leaves erect to erect-spreading, oblong-ligulate, (3.0)4.0-4.5 mm long, 1.0 mm wide, undulate, acute to broadly acute, sometimes short apiculate; margins entire, sometimes recurved at base; costa short, double to single, 1/4 - 1/2 of leaf length; apical cells rhomboidal to fusiform, 15 um long, 8 um wide, upper median cells linear, (39)47-52 um long, 6 um wide, basal cells linear to rectangular, 65-100 um long, 8 um wide, pitted, alar cells distinct, short quadrate. Autoicous. Perichaetial leaves oblong-lanceolate, 5.5-6.0 mm long, 1.5-2.0 mm wide, acute; margins entire to slightly serrate at apex; costa present or absent, short and double to single, 1/4 to 1/2 of leaf length; upper median cells linear, 100 um long, 8 um wide. Setae short, 0.8 mm long, yellowish; capsule ovoid-cylindric, 2.0-3.5 mm long; exothecial cells irregularly short rectangular

to rounded-quadrate, 26-31 um long; peristome double, exostome on front surface striate at base, papillose above, sparsely papillose at back; endostome with a low basal membrane, segments narrow lanceolate, smooth on both surfaces, perforate, keeled; operculum conic-rostrate. Calyptra mitrate. Spores papillose, 39 um in diameter.

Distribution and Ecology. (Fig. 7B). This taxon is only known from Colombia and Ecuador where it is found in Polylepis forests. It occurs from 3000 m and higher.

Specimens examined. COLOMBIA. Valle: Páramo de Pan de Azúcar, 3700 m, 27 Jun 1987, Churchill et al. 15300 (NY).

ECUADOR. Azuay: Panamerican Highway S between Loja and Cuenca, 40-50 km N of Oña, 3350 m, 24 Sep 1982, Steere et al. 25932, 25937 (NY), around Laguna Toreadora in Parque Nacional de Cajas, ca 35 km WNW of Cuenca, 3950 m, 14 Jun 1979, Løjtnant 14823 (NY), from Soldados E along the road until Hda. San Vicente (W of Cuenca) 3300 m, 5 Jan 1981, Balslev 1561 (NY); Cotopaxi: Area Recreacional El Boliche, along road ca 4 km S of Railroad Station, 3500 m, 15 Dec 1983, Buck 9867, 9904 (NY), Páramo de Cotopilalán, 4000 m, 2 Feb 1984, Laegaard 51283B (NY), National Park Cotopaxi, on N slope of Cotopaxi volcano, 3950 m, 14 Jan 1984, Laegaard 51068B (NY), N slopes of Rumiñahui, 4100-4300 m, 28 Oct 1982, Balslev et al. 13387 (NY); Pichincha: Cordillera Oriental, just W of summit along Quito-Baeza road, 4000 m, 16 Jan 1981, Steere E-200 (NY); Tunguragua: Mount Carguairazo, Spruce 1340 (NY), Titiacun, Spruce 1341 (NY).

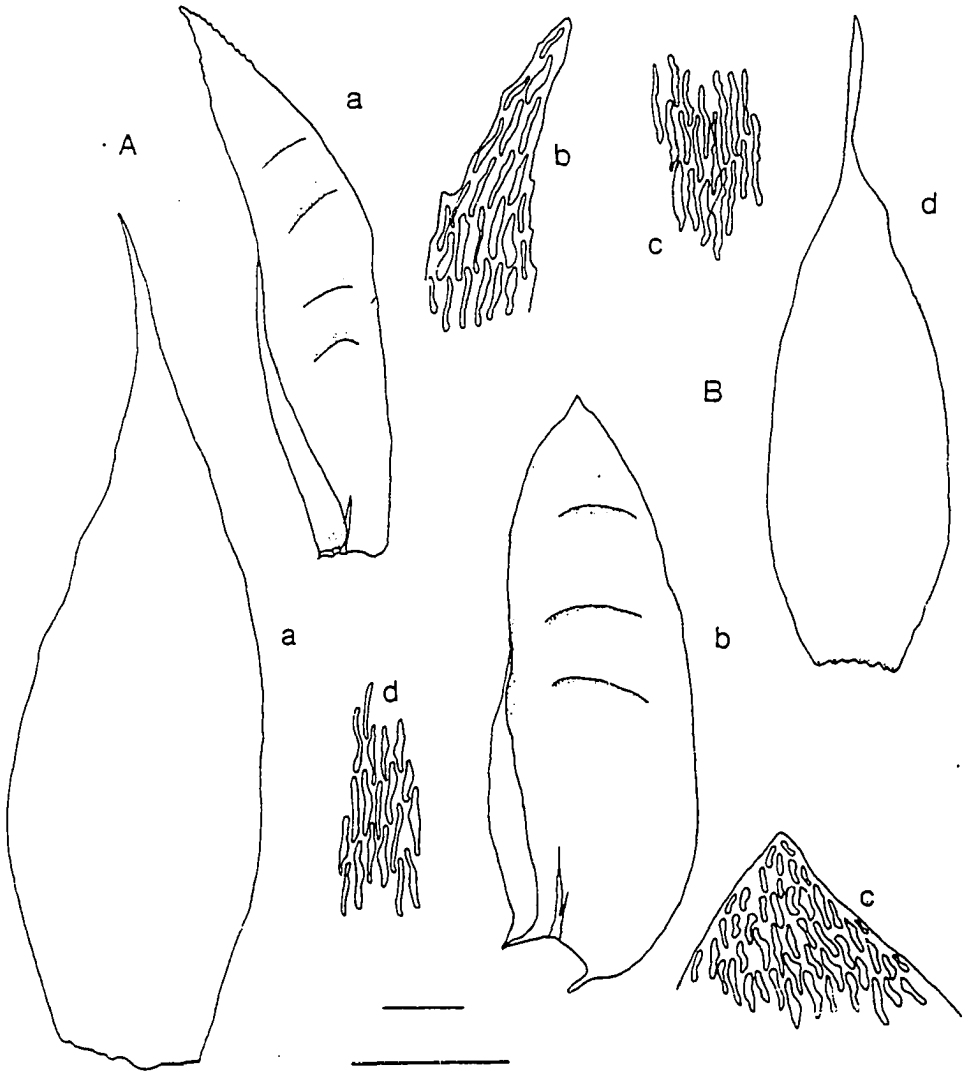
Discussion. The large perichaetial leaves in fully mature sporophytes are a good distinguishing character for this species. These may reach 6.0 mm long or more. Vegetatively, the species may be recognized by the abundant sometimes branched paraphyllia that reach 2.0 mm long. It is distinguished from N. obtusifolia by the distinctly undulate leaves with an acute apex. Neckera spruceana is probably most closely related to N. ehrenbergii since both share the same peristome type, leaf shape, and presence of paraphyllia, although in N. spruceana these are longer and more developed. The two taxa are kept separate because, in spite of the similarities, the perichaetial leaves are quite different in shape. In N. spruceana they are oblong-lanceolate to elliptic, not ending in a filiform apex while those of N. ehrenbergii range from obovate-ligulate to oblong and abruptly subulate (see N. ehrenbergii for further discussion).

Outside of Colombia and Ecuador no material studied showns the combination of characters described above. The species is only known from Pichincha, Parque Nacional de Cajas, slopes of Antisana and Cotopaxi. In these localities it appears to be found higher than 3000 m and commonly around 4000 m.

3. **Neckera pachycarpa** Schimper ex Bescherelle Mém. Soc. Sci. Nat. Cherbourg **14:** 220. 1872. Type, Mexico. Faro, Liebmann s. n. (in herb. Schimper) (holotype, BM!) (Fig. 8A a-d).

Plants medium sized, 4-5 cm tall, yellow-green, slightly glossy, irregularly pinnate. Axillary hairs 6-7 cells long, stalk cell short, quadrate; paraphyllia abundant, filamentose to foliose, mostly uniseriate to occasionally biseriate, 1.0 mm long; pseudoparaphyllia foliose. Primary stem leaves mostly erect, falcate at apex, lanceolate from a broad base, 0.5-1.0 mm long, 0.4-0.5 mm wide, acute to narrowly acute, sometimes forming a long acumen; margins entire to slightly

Fig. 8. A, Neckera pachycarpa (Liebman s.n., BM). a, lateral stem leaf, x40; b, stem leaf apex, showing apical cells, x400; c, stem leaf upper median cells, x400; d, perichaetial leaf, x40. B, Neckera ehrenbergii (Ehrenberg s.n., BM). a, perichaetial leaf, x40; b, lateral stem leaf, x40; c, stem leaf apex, showing apical cells, x400; d, stem leaf upper median cells, x400.



serrate, slightly recurved at base; apical and median cells linear, 39-52 um long, 4-6 um wide, basal cells mostly rectangular, 39-52 um long, 6 um wide, alar cells irregularly quadrate. Stem leaves erect to slightly erect-spreading, strongly undulate when dry, undulate when wet, oblong-lanceolate, 5.0-5.5 mm long, 1.0 mm wide, distal keeled margin 0.3 mm wide at base, narrowly acute, decurrent; margins serrate, recurved at base; costa short, double or absent; apical cells linear, 39 um long, 6 um wide, upper median cells linear, (65) 78 (92) um long, 6 um wide, basal cells rectangular, (65) 92-96 (100) um long, 6-8 um wide, alar cells mostly quadrate, 13-18 um long, thick-walled. Autoicous. Perichaetial leaves ovate-subulate, 6.0-8.0 mm long; margins serrate at apex; costa absent; apical cells linear, 65-84 um long, 4-6 um wide, upper median cells linear, 130-150 um long, 4 um wide, basal cells rectangular, (78) 130 um long, 8-10 um wide, pitted throughout, except at base. Setae very short; capsule erect, globose, 1.0-1.5 mm long, smooth; exothecial cells mostly short quadrate, 39-52 um; peristome double, hyaline, exostome lanceolate, densely papillose, trabeculate; endostome reduced, fragile, papillose, segments perforate. Spores 8 um in diameter, strongly papillose.

Distribution. (Fig. 7C). Only known form type collection in Mexico.

Specimens examined. MEXICO. Faro, Liebmann in herb. Schimper (BM).

Discussion. The erect, oblong-lanceolate leaves with narrow leaf apices help to identify this species. Some leaves may have distincly recurved basal margins.

Crum (1951), in his study of Mexican mosses, considered this species conspecific with N. ehrenbergii, a conclusion not followed in this treatment since a comparison of type materials suggested that these taxa are distinct. Wagner's

(1951) circumscription of N. pachycharpa as having stem leaves with a narrow leaf apex is followed here. This feature is not present in any of the high elevation paraphyllia-bearing species of South America (e.g., N. spruceana, N. obtusifolia, and N. andina).

4. **Neckera ehrenbergii** C. Müller, Syn. 2: 25. 1850. Type. Mexico: C. Ehrenberg (lectotype, BM!; isotype, NY!).

Neckera hornschuchiana C. Müller, Syn. 2: 51. 1850. Type. Mexico: Deppe & Schiede (lectotype, BM!).

Neckera remota Bruch & Schimper ex C. Müller, Syn. 2: 51. 1850, nom. nud. Based on: Mexico. Orizaba, Liebmann (BM).

Neckera chlorocaulis C. Müller, Syn. 2: 663. 1851, fide Wagner (1952). Type. Mexico. Michoacán, Cerro San Andrés, Mar 1849, Chrismar (n. v.).

Neckera liebmanni Schimper ex Bescherelle, Mém. Soc. Sci. Nat. Cherbourg **16**: 220. 1872. Type. Mexico. Orizaba, Liebmann (isotype, BM!).

Neckera leptophylla Schimper ex Bescherelle, Mém. Soc. Sci. Nat. Cherbourg **16**: 220. 1872. Type. Mexico. Orizaba, Liebmann (isotype, BM!).

(Fig. 8B a-d).

Robust to medium sized plants, 4-6 (10) cm tall, pale to dark-green, irregularly branched. Axillary hairs 4-5 cells long, stalk cell differentiated, 2 short quadrate cells; paraphyllia abundant along stem, especially in leaf axils, 0.5-1.0 mm long; pseudoparaphyllia mostly foliose. Primary stem leaves broadly ovate becoming triangular toward apex, 0.6-o.5 mm long, acute, decurrent; margins entire; costa very short or absent; apical cells linear, 26 um long, 4 um wide, upper median cells linear, 39-52 um long, 4 um wide, basal cells irregularly

rectangular to linear, 26-44 um long, 6-8 um wide, alar cells differentiated, irregularly quadrate. Secondary stem leaves erect-spreading to spreading, undulate, ovate-oblong-ligulate to oblong-lanceolate, (3.0) 3.4-3.7 (4.0) mm long, 1.0-1.4 mm wide at mid point, 1.2-1.4 mm wide at widest leaf base point, decurrent, acute to broadly acute; margins entire, sometimes slightly serrate, revolute at leaf base, to 1/4 of leaf length, sometimes only at auricles; costa short and double; apical cells rhomboidal, (23)31-39 um long, 6-8 um wide, upper median cells linear, 47-65 um long, 6 um wide, basal cells rectangular (52)65-78(100) um long, 8 um wide, pitted or unpitted, alar cells differentiated, quadrate to short rectangular. Autoicous. Perichaetial leaves oblong-subulate, 4.0-6.0 mm long, subulate short to long, smooth to sometimes rugulose; margins entire to slightly serrate above; costa present or absent; apical cells linear, 78-100 um long, 6-8 um wide, upper median cells linear, 100-140 um long, 6 um wide, basal cells rectangular, 130-170 um long, 10-13 um wide. Setae 0.5 mm long; capsules cylindric, 1.5-2.0 mm long; exothecial cells quadrate to short-rectangular, 30-50 um long; exostome well developed, teeth lanceolate, papillose, sometimes perforate in the upper half; endostome well developed to slightly reduced, with a high basal membrane, segments keeled, perforate in the upper half, slightly papillose to smooth. Spores 28 um in diameter, densely papillose.

Distribution and Ecology. (Fig. 7C). This species is an epiphyte in cloud to oak forests at elevations from 2000 to 3500 m from Mexico to Panama, Ecuador and Peru.

Representative specimens examined. MEXICO. Chiapas: Southwest of Mexican Highway 190 near Rancho Nuevo, about 9 mi SE of San Cristóbal las Casas, 3000 m, 20 Aug 1966, Breedlove 15143 (MO); Distrito Federal: About 43 km southward from Mexico City along highway to Cuernavaca, 2600 m, 7 May 1938, Frye 2728 (G, NY), Desierto de los Leones, 2990 m, 15 Jan 1967, Delgadillo 1284 (NY); Hidalgo: 5 mi E of Acaxochitlan edge of Lake Tejocotal, 2000 m, 21 Feb 1961, McGregor 16386 (NY); Hidalgo: 5 mi E of Acaxochitlan edge of Lake Tejocotal, 2000 m, 21 Feb 1961, McGregor 16386 (NY); Jalisco: El Cuartón, above Manantlán, 2500 m, 30 Jul 1949, Crum 1204 (NY); México: Volcán de Toluca, 3500 m, 7 Sep 1892, Pringle 18a (G, MO, NY), West slope of Popocatepetl, Sierra Nevada, 3500 m, 23 Oct 1966, Hermann 20776 (FH, NY); Michoacan: 6 miles E of Pulvilla on Hwy, 15 Aug 1970, Norris et al. 15684 (NY); Oaxaca: Llano de las Flores, 20 km beyond Ixtlan de Juarez toward Tuxtepec in the Sierra Juarez, 3000 m, 3 Jan 1960, Sharp M59170 (MO); Veracruz: Jalapa, 1400 m, Dec 1907, Arsène 7996 (NY).

GUATEMALA. Chimaltenango: Along road near Chimaltenango, 1950 m, 23 Jan 1974, Richards et al. 2904 (MO); Huehuetenango: Sierra de Cuchumatanes, beyond La Pradera, km 32, 3300 m, 31 Dec 1940, Standley 81742 (NY), 81764 (FH); Quetzaltenango: Las Majadas, near Quetzaltenango, 2300 m, Jan 1962, Vogel B-9020 (NY), mountains SE of Palestina on old road to San Juan Ostuncalco, 2550-2850 m, 21 Jan 1941, Standley 84243 (FH); Quiché: 8 km E of Los Cinquenteros, 2550 m, 25 Jan 1974, Richards et a. 2957 (MO, NY); San Marcos: Mt. between San Marcos and Serchil, 2700-3150 m, 30 Jan 1941, Standley 85419 (FH, NY); Sololá: Volcán San Pedro, north-facing slopes towards Lago de

Atitlán above San Pedro Village, 1800-3200 m, 7 Jun 1942, Steyermark 47240 (NY), Volcán de Agua, 3000-3300 m, 22 Mar 1905, Maxon 3716 (NY); Totonicapán: María Tecún forest, 3000 m, 15 Jan 1974, Molina et al. 30397 (NY).

PANAMA. Chiriqui: Alto Pineda, Cerro Punta, 11 Apr 1979, Salazar 1142 (NY), E slope of Volcán de Chirique (Barú) WNW of Boquete, 2200-2300 m, 19 Nov 1975, Davidse et al. 10183 (MO).

ECUADOR. Pichincha: Andes Quitenses, Spruce 1343 (BM, G, NY).

PERU. Amazonas: Chachapoyas, Chanchillo, 31 Aug 1973, Hegwald et al. 6746 (NY).

Discussion. Although N. ehrenbergii is quite a variable taxon both gamethphytically and sporophytically, it may be distinguished by the recurved margin toward the leaf base and paraphyllia from 0.5-1.0 mm long. A major source of variation in this species is the perichaetical leaf apex ranging from short- to long-subulate. These two extremes do not seem to be related to any specific pattern.

Previous author (Thériot, 1928; Barthram, 1949; Wagner, 1951) suggested the same synonyms given here for this taxon. There is no clear cut distinction between specimens showing perichaetial leaves with a long filiform apex and

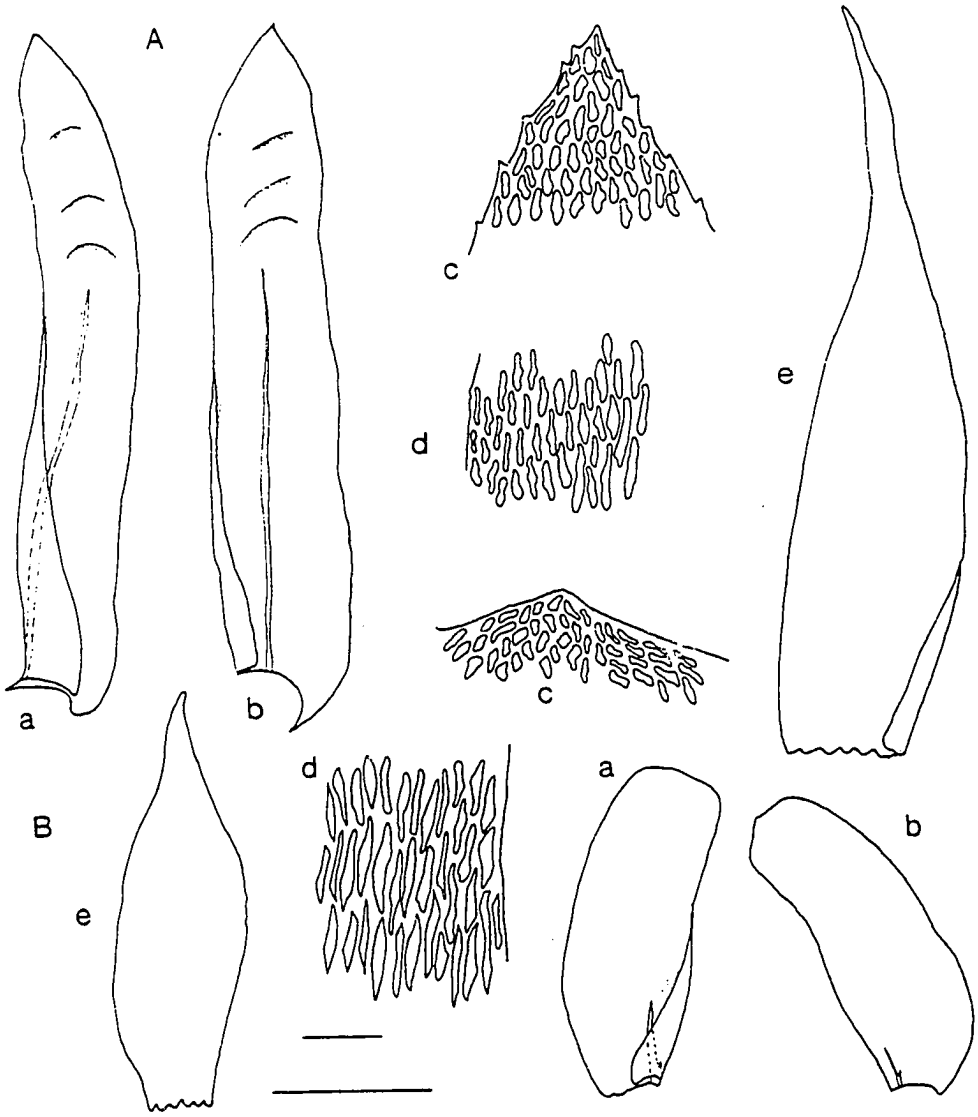
short endostome to those with short subulae with well developed peristome, especially since in many of the collections studied the combination of perichaetial leaves with long subulae and well developed endostomes, was commonly found.

At the same elevational range (2000-3000 m) at which this species occurs, is found N. scabridens in the Andes. Material from the Andes is considered distinct because is does not show the clearly recurved margin and paraphyllia, diagnostic features of N. ehrenbergii. Also, the endostome in N. ehrenbergii is not trabeculate as in the Andean counterpart.

5. **Neckera angustifolia** C Müller, Bot. Zeit. **5**: 828, 1847, Type. Mexico. Cl. Miguel communicavit. (lectotype, BM!). (Fig. 9A a-e).

Mostly robust to medium sized plants, 6-10 cm tall, irregularly branched. Axillary hairs 4-5 cells long, 2 short quadrate stalk cells; paraphyllia scarce or absent; pseudoparaphyllia foliose. Primary stem leaves lanceolate, plane, falcate, 1.0-1.5 mm long, acute; margins entire; costa absent; apical cells linear, 44 um long, 6 um wide, upper median cells linear, 39-52 um long, 6 um wide, basal cells rectangular, 52 um long, 3 um wide, pitted. Secondary stem leaves erect to slightly erect-spreading, oblong-lanceolate to lanceolate, 4.5-5.0 mm long, 1.0 mm wide at leaf mid point, 1.0-1.4 mm wide at widest point at base, deeply undulate when dry, slightly decurrent, acute; margins entire; costa mostly single, 1/2 to 2/3 of leaf length; apical cells rhombic to rhomboidal, 21-26 um long, 8 um wide, upper medial cells linear, (50) 52-63 (92) um long, 6-8 um wide, sometimes pitted, based cells rectangular, (63) 65-78 (100) um long, 6-8 um wide, pitted, alar cells weakly differentiated in distal margin of folded lamina. Autoicous. Perichaetial leaves oblong-lanceolate-subulate, 6.0-7.0 mm long;

Fig. 9. A, Neckera angustifolia (Juárez 964, MO). a, lateral stem leaf, x40; b, central stem leaf, x40; c, stem leaf apex, showing apical cells, x400; d, stem leaf upper median cells, x400; e, perichaetial leaf, x40. B, Neckera villae-ricae (Herter 9377, NY). a, lateral stem leaf, x40; b, central stem leaf, x40; c, stem leaf apex, showing apical cells, x400; d, stem leaf upper median cells, x400; e, perichaetial leaf, x40.



margin serrate at apex; costa present; apical cells linear, 65-92 um long, 6-8 um wide, slightly pitted, median cells linear, 65-78 um long, 8 um wide, pitted, basal cells rectangular, 39-65 um long, 13 um wide. Setae very short, 0.5 mm long; capsule globose, 1.5 mm long; exothecial cells mostly rectangular, thin-walled, 52-92 um long, 21 um wide; peristome single, exostome teeth lanceolate, striate below, smooth above. Calyptra not seen. Spores 26-28 um in diameter, papillose.

Distribution and Ecology. (Fig. 7C). It is known only from Mexico in the Quercus forest at 2000 meters. Neckera angustifolia grows as an epiphyte in shaded and wet areas.

Specimens examined. MEXICO. no collector (BM); Veracruz: Tlacotepec, 13 km N of Huayacocotla, 2000 m, 29 Mar 1979, Gil Juárez 964 (MO).

Discussion. This species is easily recognized by its erect, narrowly lanceolate leaves and presence of exostome only. It is known only from the type locality and Tlacotepec in Veracruz.

6. **Neckera villae-ricae** Bescherelle, Mém. Soc. Sci. Nat. Cherbourg **21:** 264. 1877; Neckeropsis villae- ricae (Bescherelle) Brotherus, Nat. Pfl. ed. 2, 11. 188. 1925. Type. Paraguay. Guairá: Villa Rica, Balansa 1254 (holotype, BM!). (Fig. 9B a-e).

Plants small to medium sized, 3-5 cm tall, light green, glossy, sometimes dendroid to irregularly pinnate. Axillary hairs of 3-4 rectangular cells, stalk cell golden-brown, short quadrate; paraphyllia absent; pseudoparaphyllia foliose

or filamentose, 0.5-1.0 mm long. Primary stem leaves erect, deltoid, subulate, 0.4-0.5 mm long, acute; margins entire; costa absent or present and very short and double; upper median cells fusiform, 26-39 um long, 6 um wide, alar cells short quadrate. Stem leaves erect-spreading to spreading, ligulate, 2.5-3.0 mm long, 1.0 mm wide, flat, plane, truncate to obtuse or broadly acute, short apiculate; margins entire to slightly crenulate; costa single or double, short, 1/4 of leaf length, apical cells rhombic to rhomboidal, 26-39 um long, 8-13 um wide, upper median cells fusiform 39-78 um long, 6-8 um wide, basal cells fusiform to linear, sometimes rectangular, (52)65-100 um long, 6-8 um wide, slightly pitted, alar cells scarcely differentiated. Autoicous. Perichaetial leaves oblong-subulate, (3.0)4-4.5 mm long, 1.0 mm wide, acute; margins entire; costa absent; upper median cells, 78-100 um long, 6 um wide. Setae short, 1.0-2.0 mm long; capsules ovoid, 1.5-2.0 mm long; exothecial cells quadrate to irregularly rectangular, 26 um in diameter; peristome double, exostome teeth lanceolate, striate below, densely papillose above, with branched papillae, at back papillose; endostome from a high basal membrane, densely papillose, segments narrowly perforate, papillose at back. Spores 26 um in diameter, papillose.

Distribution and Ecology. (Fig. 7D). This taxon is known only from southeastern Brazil, Uruguay, Paraguay and northeastern Argentina. It is frequently found as an epiphyte at 0-200 m.

Specimens examined. BRAZIL. Paraná: Foz do Iguacu, Parque Nacional do Iguacu, along Rio Iguacu, 100-200 m, 22-23 Sep 1984, Vital 12018 (NY); Rio Grande do Sul: São Marinho, Forqueta, 26 Aug 1984, Dal Pont et al. 244 (NY), Dois Irmãos, Aug 1934, Sehnem s. n. (FH), Colonia Nova, Cruz Alta 450 m, 10 Aug 1905, Bornmüller 6539 (FH), Municipio de Lagoa Vermelha, along Rio Ligeiro,

along BR-285, km 111, 11 Mar 1976, Vital 5699B, 5703B (NY), Municipio de Vacaria, 21 Jul 1980, vital 9328 (NY); São Paulo: Municipio de Sarapui, Chácara dos Piavas, Rio Itapetininga, 7 Sep 1978, Yano 1186 (NY).

PARAGUAY. Alto Paraná: Ciudad Presidente Stroessner, 8 Oct 1984, Bordas 123A (NY); Itapúa: Centro de Desarrollo Forestal at km 428 on Ruta 6, just W of Arroyo Pirapó, 100 m, 10 Oct 1984, Buck 12168 (NY); Paraguari: Parque Nacional Ybycui, along trail to mirador, 200 m, 4 Oct 1984, Buck 11768 (NY).

ARGENTINA. Buenos Aires: Punta Lara, 23 Aug 1936, Kühnemann 199 (NY).

URUGUAY. Florida: Rincón del Yi, 200 m, Sep 1926, Herter 424 (G, MO, NY); Lavalleja: Sierra de Animas, ca 65 km E of Montevideo, 22 Nov 1981, Landrum 3860 (NY); Saralleja: Villa Serrana 1 Nov 1959, Garcia Zorrón 1905 (FH); Treinta y Tres: Tacuari, 50 m, Nov 1933, Herter 93977 (G), Tucuari, 7 Oct 1961, Gracia Zorrón 2877 (NY).

Discussion. Macroscopically, this species is easily recognized by the lustrous, light green color and non-undulate leaves. The general aspect is of a Neckeropsis, especially the leaf shape and cell pattern, and indeed Brotherus proposed that this taxon belongs there but it is here considered more appropriate in Neckera on the basis of the following characters: short costa, perigamial structure (no leaf like paraphysis, perichaetial leaf shape), capsule with stomata, and branched papillae on the exostome teeth. This taxon is an example of the problem that exists in delimiting the two genera (Neckera and Neckeropsis). Neckera probably includes the species attributed to Neckeropsis. A detailed study including Old World tropical taxa is needed to clarify this problem.

7. **Neckera scabridens** C. Müller, Bot. Zeit. **5:** 828. 1947. Type. Chile australis in truncis sylvarum umbrosarum ad Antuco Novbr, (no collector given) (lectotype, BM!).

Neckera lindigii Hampe, Linnaea **32:** 149. 1863, **syn . nov.** Type. Colombia. Bogotá, Lindig s. n. (lectotype, BM!); Monserate, Tequendama, Canoas et Fusagasuga ad arbores, 1900-2900 m, Jan-Majo-Junio Lindig s. n. (syntypes, BM!).

Neckera berteroana Schimper ex Mitten, J. Linn. Soc., Bot. **12:** 454. 1869, **syn, nov.** Type. Chile. Ad Quillota, Bertero; Arrique, Lechler 670 (holotype, NY!; isotype, BM!).

Neckera bogotensis Mitten, J. Linn. Soc., Bot. **12:** 454. 1869, **syn. nov.** Type. Colombia. Andes Bogotensis, inter Tipaquira et Pacho 2000 m, ad arbores, Weir 275 (holotype, NY!).

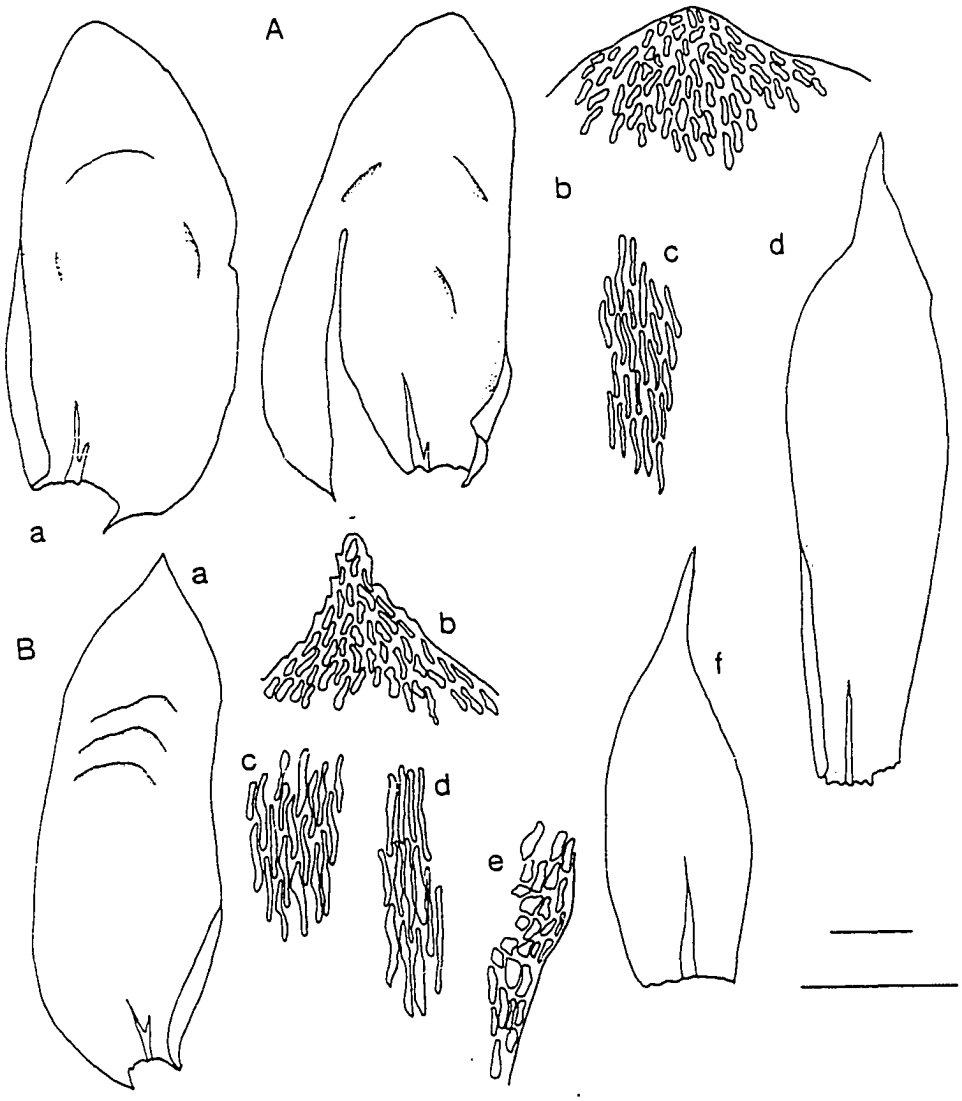
Neckera argentinica Lorentz ex C. Müller, Linnaea **42:** 411. 1879, **syn. nov.** Type. Argentina. Cuesta de Buyuyu, 15 Jun 1873, Lorentz s. n. (isotype, NY!).

Neckera araucarieti C. Müller, Bull. Herb. Boissier. **6:** 115. 1898, **syn. nov.** Type. Brazil. Sa. Catharina: Serra Geral, Jan 1890, Ule 647 (syntype, NY!); Serra do Itatiaia, Capão, 2000 m, 1894, Ule 1847 (syntype, H-BR!).

Neckera missionum Sehnem, Pesquisas **34:** 87. 1980, **syn. nov.** Type. Brazil. Rio Grande de Sul: São Luiz dad Missões, Bossoroca, 300 m, 12 Jan 1953, Sehnem 6225 (holotype, PACA!). (Fig. 10B a-f).

Plants mostly small to medium sized, 3-5 cm tall, irregularly branched. Axillary hairs 4-5 cells long, stalk cell differentiated; paraphyllia scarce or absent; pseudoparaphyllia foliose. Primary stem leaves obovate to lanceolate, 0.5-1.0

Fig. 10. A, Neckera andina (Spruce s. n., NY). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaves upper median cells, x400; d, perichaetial leaves, x40. B, Neckera scabridens (Steere 7937, NY). a, stem leaf, x40; b, stem leaf apex, x400; c, stem leaf upper median cells, x400; d, stem leaf basal cells, x400; e, stem leaf alar cells, x400; f, perichaetial leaf, x40.



mm wide; apical cells rhomboidal to linear, 18-26 um long, 6 um wide, upper median cells 39-52 um long, 6 um wide, basal cells linear to rectangular, 26-34 um long, 6 um wide. Secondary stem leaves erect-spreading to spreading, undulate, oblong-ligulate, 2.8-4.0 mm long, 1.0-1.5 mm wide at leaf mid point, 1.0-1.3 mm wide at leaf base widest point, acute, slightly decurrent; margins entire to slightly serrulate at apex, plane, if revolute only at auricles; costa short and double; apical cells rhombic to rhomboidal, 23-28 um long, 8-10 um wide, upper median cells linear, 52-78 um long, 6 um wide, basal cells long to short rectangular, 65-100 um long, 8 um wide, pitted, alar cells weakly differentiated. Autoicous. Perichaetial leaves oblong to oblong-ovate, short to long subulate, 3.0-4.0 mm long, 1.0-1.5 mm wide; margins entire; costa present or absent; apical cells linear, 52-92 um long, 6 um wide, upper median cells linear, 65-120 um long, 6 um wide, basal cells rectangular, 39-78 um long, 8 um wide, pitted throughout. Setae short, 0.5 mm long; capsule cylindric-ovoid, 2.0 mm long; exothecial cells irregularly rectangular, thick-walled, 39-78 um long, 18-26 um wide; peristome double, exostome teeth lanceolate, striate at base, densely papillose above, trabeculate; endostome with a high basal membrane, segments keeled, perforate, papillose. Spores 28 um in diameter, densely papillose.

Distribution and Ecology. (Fig. 11). Neckera scabridens is a common epiphyte of subpáramo, montane to Nothofagus forest in Argentina and Chile north to Venezuela and eastern Brazil. It is also known from the Dominican Republic and Costa Rica.

Representative specimens examined. COSTA RICA. San José: Along Inter American Highway about 10 km NW of summit at La Ascención, 3130 m, 15 Mar 1973, Crosby et al. 6109 (MO).

Fig. 11. Distribution map of Neckera scabridens.

DOMINICAN REPUBLIC. Independencia: Sierra de Baoruco, 30.5 km S of Puerto Escondito, 1940 m, 25 Jan 1987, Buck 14667 (NY).

COLOMBIA. Antioquia: La Ceja, 5.5 km SE of La Ceja and La Unión, 2420 m. 21 Jun 1985, Churchill & Sastre 12843-c (NY), Medellín, Piedras Blancas, 2338 m, 25 Jun 1985, Churchill & Sastre 13132 (NY); Boyacá: On road Chiquinquira-Pauna, below San Antonio, 2300 m, 3 Sep 1967, Hammel et al. 1960 (MO); Cauca: Nevado del Huila, Rio López, above Tacueyo, 2300-2700 m, 4 May 1943, Steere 7937 (NY); Cundinamarca: 20 km SE of Bogotá, on road to Villavicencio, 3000 m, 28 Feb 1943, Steere 7855 (NY), Andes Bogotenses, Bogotá 2000 m, Weir 184 (BM, NY); Nariño: Baños Termales above village of Chiles W slope of Volcán Chiles, 3300 m, 20 Aug 1943, Steere 8703 (NY); Santander: Páramo de Romeral, 3800-4100 m, 29-30 Jan 1927, Killip at al. 18598 (FH).

VENEZUELA. Táchira: Junín, roadside of Rubio-Delicias, 1700 m, 28 Jul 1975, Griffin et al, 31 (FLAS, NY); Trujillo: Boconó, along the old Boconó-Trujillo highway, base of páramo La Cristalina, Aug 1975, Griffin et at. 1260 (FLAS, NY).

ECUADOR. Azuay: San Joaquín-Soldados road, W of Cuenca, bank of Rio Yanuncay, 3020 m, 24 Oct 1984, Steere 27836 (NY); Carchi: Páramo El Angel, road Tulcán-El Angel 36.5 km S of Tulcán, 3630 m, 4 Apr 1976, Gradstein et al. 3482 (G); Cotopaxi: Cotopaxi National Park, W slope of Volcán Cotopaxi, 3500 m, 2 Oct 1982, Steere et al. 26123 (NY); Imbabura: Cordillera Oriental, Ibarra-Mariana Acosta Road, E slope above Mariana Acosta, 3700 m, 27 Oct 1983, Steere 26830 (NY); Loja: Loja-Zamora highway 9 km E of Loja, 2350 m, 23 Sep 1982, Steere et al. 25757 (NY); Napo; 34.7 km W of Baeza, above Río Papallacta, 3300 m, 21 Jul 1985, Churchill & Sastre 13570 (NY); Pichincha: E slope of Volcán Pichincha above Quito, 3000-3500 m, 30 Jan 1981, Balsley 1771

(NY); Tungurahua: 14-19 km W of Baños along road 78, 1650-1800 m, 10 Jun 1985, Crosby 10619 (MO, NY).

PERU. Amazonas: Chachapoyas-Cajamarca, 2600 m, 6 Sep 1982, Frahm et al. 946 (NY); Ayacucho: Huanta, 25 km from Tapuna, 5 Jul 1977, Hegewald 9015 (NY); Cuzco: Urubamba, 17 Jul 1911, Ward 24 (NY); Junín: Huacapistana, 1800 m, 6 Jun 1929, Killip et al. 24302 (NY); Pasco: Oxapampa, 1780 m, 12 Jun 1977, Hegewald 8480 (NY).

BOLIVIA. Cochambamba: Florida de San Mateo, 2000 m, Apr 1911, Herzog 3627 (NY); La Paz: Near Pelechuco, 2500 m, 30 Apr 1902, Williams 2810 (BM, NY); Santa Cruz: Comarapa, Apr 1911, Herzog s. n. (NY); Tarija: Casteón, at summit of mountain above and W of Entre Ríos, 1900-1950 m, 2 Feb 1979, Lewis 79-515 (NY).

BRAZIL. Minas Gerais: Fazenda Boa Esperanca, 15 Aug 1966, Vital 1020 (MO), Serra do Itatiaia, 6 Jun 1902, Dusén s. n. (NY); Santa Catharina: Serra Geral, Jan 1890, Ule 82 (G), Sep 1889, Ule 763 (BM); Sao Paulo: Pindamonhangaba, 2 km NE of Pico do Itapeva, 6 Apr 1977, Vital 7076 (MO).

CHILE. Maule: In Cordillera de la Costa, ca 43 km SE of Constitución, Aug 1970, Landrum 323 (MO); Valparaiso: Capt, Wilkes s. n. (NY), Santiago, 1915, Costes s. n. (BM); Quillota: Palma forest, 1829, Bertero 1053 (BM, NY), Arique, Lechler 670 (BM, NY): Valdivia: Dec 1911, Herzog 5226 (BM, FH).

ARGENTINA. Chubut: Menéndez lake, 2 Feb 1945, Castellanos 2174 (FH); Tucumán: Tucumán, 24 Aug 1915, Rose et al. s. n. (NY).

Discussion. Neckera scabridens is characterized by the scarce paraphyllia, and oblong-ligulate leaves with plane margins. A unique feature that helps segregate this species from N. ehrenbergii is the peristome ornamentation. In N. scabridens the exostome teeth are distictly trabeculate.

It is a widely distributed and highly variable species as evidenced by the numerous synonyms. Two modalities may be observed in the stature of this species. In the northern Andes plants tend to be very handsome, robust (7-15 cm tall) and sometimes with narrow leaf apices. In the southern range of the species, it is mostly small.

Type studies of N. lindigii, N. berteroana and N. scabridens show no differences other than variation in size. Similarities in peristome morphology of this group can be found in Mitten's descriptions. Mitten's leaf drawings (in herb. NY) of N. lindigii and N. bogotensis show no differences.

Gametophytically, this species seems to intergrade with N. ehrenbergii, but the trabeculae in the exostome of N. scabridens aid in the recognition of the two species. Perichaetial leaves in both species range from oblong subulate to obovate-subulate.

Neckera sect. Leiophylla (C. Müller) Braithwaite, Brit. Moss Fl. **3**: 201. 1905.

Neckera subsect. Leiophyllia C. Müller, Syn. **2**: 41. 1850. Lectotype (chosen here): Neckera leiophylla Gümbel ex C. Müller, Syn. **2**: 44. 1850.

Key to species of sect. Leiophylla

1. Paraphyllia abundant; stem leaves mostly concave

   8. N. andina

1. Paraphyllia scarce or absent; stem leaves mostly flat

   2.

   2. Plants generally slender; stem and branch leaves spreading, equal in size

      9. N. urnigera

2. Plants slender to robust; stem leaves mostly erect-spreading, larger than branch leaves

10. N. chilensis

8. Neckera andina Mitten, J. Linn. Soc., Bot. **12:** 457. 1869. Type. Ecuador. Andes Quitenses, in monte Pichincha, 3000 m, Spruce 1344 (holotype, NY!; isotype, BM!).

Neckera amblyoglossa C. Müller, Linnaea **42:** 409. 1879, **syn. nov.** Type. Argentina subtropica, montibus inter Siambon et Tafi, Martio-Aug 1872, Lorentz s. n. (syntypes, H-BR!, NY!)

Neckera eucarpa Schimper ex C. Müller, Nuovo Giorn. Bot. Ital. ser. **4:** 146. 1897. Type. Bolivia. Sorata, Panguasi, Apr 1858, Mandon s. n. (holotype, G!; isotype, NY!).

Neckera eucarpa Schimper ex C. Müller var. secundifolia Williams, Bull. New York Bot. Gard. **6**(21): 241. 1910, **syn. nov.** Type. Bolivia. Tacacoma, 3150 m, 10 Jun 1902, Williams 1997 (holotype, NY!).

(Fig. 10A a-d).

Plants mostly medium sized to small, 7-10 cm tall, dark green, mostly dull, irregularly pinnate. Axillary hairs 3-4 cells long, stalk cell short quadrate; paraphyllia abundant, mostly foliose, 0.8-1.0(2.0) mm long; pseudoparaphyllia filamentose to foliose. Primary stem leaves obovate-lanceolate, 1.0-2.0 mm long, acute; margin entire; costa present or absent, double; upper median cells fusiform, 26-39 um long, 4-6 um wide, alar cells short quadrate. Secondary stem leaves erect to slightly erect-spreading, slightly concave, sometimes secund, mostly smooth, sometimes undulate, ovate-oblong, base slightly auriculate, 2.8-3.5 mm long, 1.1-1.7 mm wide, broadly acute; margins entire, rarely slightly serrulate,

plane; costa short and double or single, 1/4 or less of leaf length; apical cells rhomboidal, (18)23-31 um long, 6-8 um wide, upper median cells rhomboidal to linear, 65-78 um long, 6 um wide, basal cells linear to rectangular, 65-94(130) um long, 6-8 um wide, alar cells quadrate, thick-walled, 18-23 um long, 10 um wide. Autoicous. Perichaetial leaves oval to oblong-lanceolate, inner leaves 3-5 mm long, 1.0 mm wide, abruptly to gradually acute; margins entire; costa present or absent, 1/4 to 1/2 of leaf length; apical cells linear, 52-78 um long, 4 um wide, upper median cells linear, 92-105 um long, 4-6 wide, unpitted to slightly pitted, basal cells linear to rectangular, 100 um long, 6 um wide, slightly pitted to pitted. Setae short to long, 2.0-4.0 mm long, sometimes slightly twisted; capsule erect, ovoid-cylindric to cylindric, 1.5-2.0 mm long; exothecial cells quadrate to rectangular toward base, 13-18 um long; peristome double, exostome teeth lanceolate, striate toward base, finely papillose above; endostome segments with a high basal membrane, segments keeled, perforate. Spores papillose, 39 um in diameter.

Distribution and Ecology. (Fig. 13). This species occurs from Ecuador southwards to Peru, Bolivia and Argentina at elevations of 3000-3300 m, mostly an epiphyte.

Specimens examined. ECUADOR. Cotopaxi: Cotopaxi National Park, on W slope of Volcán de Cotopaxi, 3500 m, 2 Oct 1982, Steere et al. 26114 (NY); Napo: Banks of Río Napo, Villavicentia s. n. (FH); Pichincha: Pichincha, Spruce 1344 (BM, G, NY), Quito, Jameson s. n. (NY), 136 (G).

PERU. Ancash. Yungay, Laguna Llanganuco, 4035 m, 17 Jan 1973, Hegewald et al. 7518 (NY); Apurimac: Andahuaylas, Pampa Runtojocha, 20 km from Uripa, 4 Jul 1977, Hegewald et at. 8948 (NY); Cajamarca: Cajabamba Luchumbamba, 3050 m, 17 Nov 1983, Sagastegui et al. 11165 (MO, NY); Cuzco: La Convención, 3000-3030 m, Oct 1920, Bües 1444, 1185 (NY), Anta, Indahuaco, 2 Jul 1977,

Hegewald et al. 8877 (NY), Urubamba, between Penas and Panticalla, 3500 m, 24 Jul 1944, Vargas 4417 (G), Urubamba, 3160 m, 17 Jul 1911, Foote 23 (NY), Ollantaytambo, 3000 m, 15 May 1915, Cook & Gilbert 763 (NY).

BOLIVIA. Cochabamba: Choquecamata, Jun 1889, Germain 1192 (G); La Paz: Larecaja, Sorata, Nov 1859, Mandon s. n. (NY), vicinity of Sorata, 3200 m, Nov 1859, Mandon 1690 (BM, G), Canyon 1 km E of Cachipata, SE of Sorata, 3250 m, 6 Apr 1979, Lewis 79-1594A (NY), Parachital, 3000 m, Jun 1911, Herzog 3323 (NY), Pelichuco, 3300 m, 4 May 1902, Williams 2808 (NY), Nururata, 4500 m, Sep 1924, Jatterel s. n. (BM), Tacacoma, 3150 m, 10 Jun 1902, Williams 1997 (BM); Unduavai: Dec 1910, Buchtien s. n. (NY).

ARGENTINA. Between Siambom and Tafi, Lorentz s. n. (NY).

Discussion. Neckera andina is distinguished gametophytically by the abundant foliose paraphyllia along the stems, and concave, secund (leaf apex is pointing inward), and mostly non-undulate leaves. Plants are mostly golden-brown, slightly shiny and somewhat tumid. Two trends in perichaetial leaf size and setae length are observed. Plants with longer perichaetial leaves and shorter setae are more common from Ecuador to Peru. Longer setae and smaller perichaetial leaves are mostly from Peru, Bolivia and Argentina. Variation was observed within the same plant in perichaetial leaf apex, i.e., gradually to abruptly acute. Differences were also noticed in mature capsule size within one plant. This species is probably related to N. laevigata from Australia. Both share concave stem leaves and the same perichaetial leaf shape.

9. **Neckera urnigera** C. Müller, Syn. 2: 57. 1850. Type. Mexico. Xalapa, Deppe & Schiede s. n. (lectotype, BM!; isolectotype, H-BR!).

Neckera mollusca Mitten, J. Linn. Soc., Bot. **12:** 455. 1869, **syn. nov.** Type. Peru. Cuzco: Lucmas, 1500 m, Spruce 1338 (lectotype, NY!); Ecuador. Titaicun, 3300 m, Spruce 1337 (syntypes, BM!, G!).

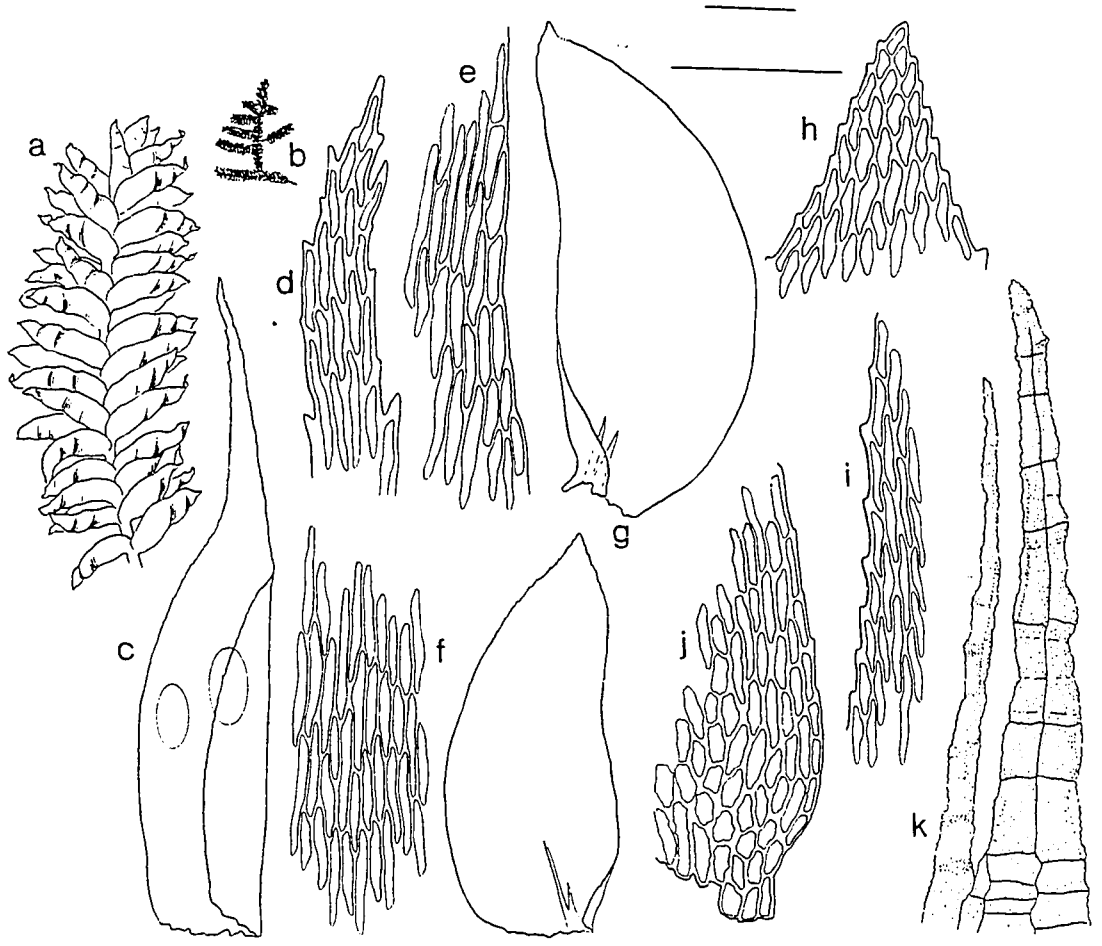
Neckera microcarpa Schimper ex Bescherelle, Mém. Soc. Sci. Nat. Cherbourg **16:** 221. 1872, **syn. nov.** Type. Mexico. Mirador (Liebmann in herb. Mus. Par.) (isotype, BM!).

Neckera marchalii Herzog, Biblioth. Bot. **87:** 116. 43. 1916, **syn. nov.** Type. Bolivia. Florida de San Mateo, 2000 m, Herzog 3635; Coranital, 1800 m, Herzog 4739; Tres Cruces, Santa Cruz, 1400 m, Herzog 3907 (syntypes, H-BR!).

(Fig. 12 a-k).

Slender plants, mostly small, 4-8 cm tall, light green to yellow green, shiny, mostly irregularly branched. Axillary hairs 4-5 cells long, stalk cell short-quadrate; paraphyllia sparse, mostly absent; pseudoparaphyllia foliose. Primary stem leaves obovate, acute; margins entire; costa absent; apical and median cells rhomboidal to linear, 26-39 um long, 6 um wide, basal cells linear to rectangular, 26-52 um long, 6 um wide, alar cells differentiated. Stem and branch leaves mostly spreading, rarely erect-spreading, oblong-laceolate, decurrent, sometimes slightly falciform (especially lateral leaves), slightly undulate to sometimes smooth, 3.0-4.5 mm long, 1.0-1.3 mm wide at mid-leaf, 1.0-1.4 mm wide at middle of leaf base, acute; margins serrulate to entire; costa short and double, sometimes one fork reaching 1/4 of leaf length; apical cells rhomboidal to linear, 26-39 um long, 6-8 um wide, upper median cells linear, 52-78 um long, 6-8 um wide, basal cells rectangular, 52-78 um long, 6-10 um wide, alar cells slightly differentiated, short quadrate to irregularly quadrate. Autoicous. Perichaetial leaves oblong-subulate, 2.4-3.0 mm long; margins entire; costa absent; apical cells linear, 65-78 um long, 8 um

Fig. 12. Neckera urginera (Buck 7965, NY). a, stem moist, x12; b, habit dry, x1; c, perichaetial leaf, x40; d, perichaetial leaf apex, x400; e, perichaetial leaf margin cells x400; f, perichaetial leaf median cells, x400; g, stem leaves, x40; h, stem leaf apex, showing apical cells, x400; i, stem leaf marginal cells, x400; j, stem leaf basal and alar cells, x400; k, peristome, x400.



wide, upper median cells linear, 65-130 um long, 6 um wide. Setae 2.0-2.5 mm long; capsules erect, oblong, 1.0-1.5 mm long, light brown; exothecial cells quadrate to short rectangular, thick-walled, 26-52 um long, 26 um wide; exostome on front surface striate at base, papillose above; endostome with a high basal membrane, papillose, segments slightly trabeculate above. Spores 23-31 um in diameter, papillose.

Distribution and Ecology. (Fig. 13). This species occurs in Central America, northern South America, southeastern Brazil and the West Indies at elevations of 1300 to 2500 m.

Representative specimens examined. MEXICO. Veracruz: Close to Consolapan, 1 km NW of Caotepec, old road Coatepec-Xalapa, 1320 m, 23 may 1975, Juárez 64 (MO, NY), Huayacocotla Natural Park, 2040 m, Juárez 1372 (MO), 1 km from Ixhuacan de los Reyes, 1610 m, 12 Feb 1976, Juárez 604 (MO, NY), Jalapa, Coatepec road, 1500 m, Barnes 558 (NY), Mirador, Liebmann 31 (BM).

GUATEMALA. Jalapa: High hills east of Jalapa, 20 Jan 1947, Clover 10199 (FH); Quetzaltenango: along ridge about 2 mi W of road 95 at 197 km, 4 km S of Santa María de Jesús, 1300-1500 m, 18 May 1966, Crosby 2839 (MO).

COSTA RICA. Alajuela: Just above Poasito on road to Volcán Poás, 30 km NWN of city center of San José, 2000 m, 24 Mar 1973, Crosby et al. 6289 (MO); Heredia: Porrosati area, valley of Río Ciruelas at end of regional road 114, N of village of Barba, 2250 m, 30 Mar 1973, Crosby et al. 6478 (MO); Puntarenas: Talamaca ridge, 3000 m, 11 Aug 1971, Spellman et al. B123a (MO); San José: Cerro Daser area, 5 km S of Asseri, 10 km SSE of city center of San José, 2250 m, 19 Mar 1973, Crosby et al. 8568 (MO).

Fig. 13. Distribution map of Neckera andina and N. urnigera.

PANAMA. Chiriqui: Mountain directly S of Cerro Respinga, 18 Mar 1977, D'Arcy 10796D (MO).

HAITI. Sud'est: Massif de la Selle, 8 km N of Seguin on road to Kenscoff, 1900 m, 21 Nov 1982, Buck 9455 (NY).

DOMINICAN REPUBLIC. La Estrelleta: Sierra de Neiba, along road from La Descubierta to Valle Hondo, from 8-15 km N of Angel Feliz, 1500-2000 m, 16 Mar 1981, Buck 4600 (NY); Independencia: Sierra de Baoruco, at the 2nd house of Dirección Nacional de Foresta, 17-21 Oct 1983, Bolay 55 (NY); Pedernales: 9 km of Los Arroyos, 2000 m, 6 May 1982, Buck 8255A (NY); San Rafael: Sierra de Neiba, along the Haiti border, vic. line between San Rafael and Independencia Province, 1400 m, Jul 1967, Norris et al, 6805 (NY); La Vega: South bank of Río Los Guanos, just above confluence with Río de la Izquierda, 1100-1200 m, Jul 1967, Norris et at. 5205A (NY).

COLOMBIA. Antioquia: Near Medellin, Feb 1931, Archer 1570 (FH, NY).

VENEZUELA: Mérida: Libertador, El Maciegal, farm of Dr. L. Ruiz-Terán, along La Pedregosa stream, 1900-2000 m, Jul-Aug 1972, Griffin et al 765 (FLAS, NY).

ECUADOR. Pichincha: Andes Quitenses, s.d., Spruce 1339 (BM, G, NY); Tunguarahua: At base of Tunguarahua, s. d., Spruce s. n. (NY).

BRAZIL. Paraná: Castro, 660 m, Weir 58 (NY).

PERU. Cuzco: Lucmas, Spruce s. n. (NY).

ARGENTINA. Tucumán: Famaitlá, 1100, 13 Jul 1922, Venturi 1106 (FH).

Discussion. A distinct species, N. urginera is easily recognized its small, slender stature and conspicuous spreading leaves. If the sporophyte is present the small size of the capsule helps to identify it. Neckera urnigera is related to N. chilensis with both sharing the same peristome type. Macroscopically, leaf orientation easily segregates the two species: in Neckera urnigera the leaves are wide

spreading, and erect-spreading in N. chilensis. Alar cells in N. urnigera are not as well differentiated as in N. chilensis.

Wagner (1951) had included N. microcarpa as a synonym of N. ehrenbergii, but the type of the former perfectly matches that of N. urnigera.

10. **Neckera chilensis** Schimper ex Montange, Ann. Sci. Nat. Bot. sér. 2, **6:** 147. 1836. Type. Chile. Bertero s. n. (isotypes, BM!, NY!).

Neckera jamesonii Taylor, London J. Bot. **5:** 59. 1846, **syn. nov.** Type. Ecuador. Andes Quitensis, Jameson 1845 (holotype, FH!; isotype, NY!).

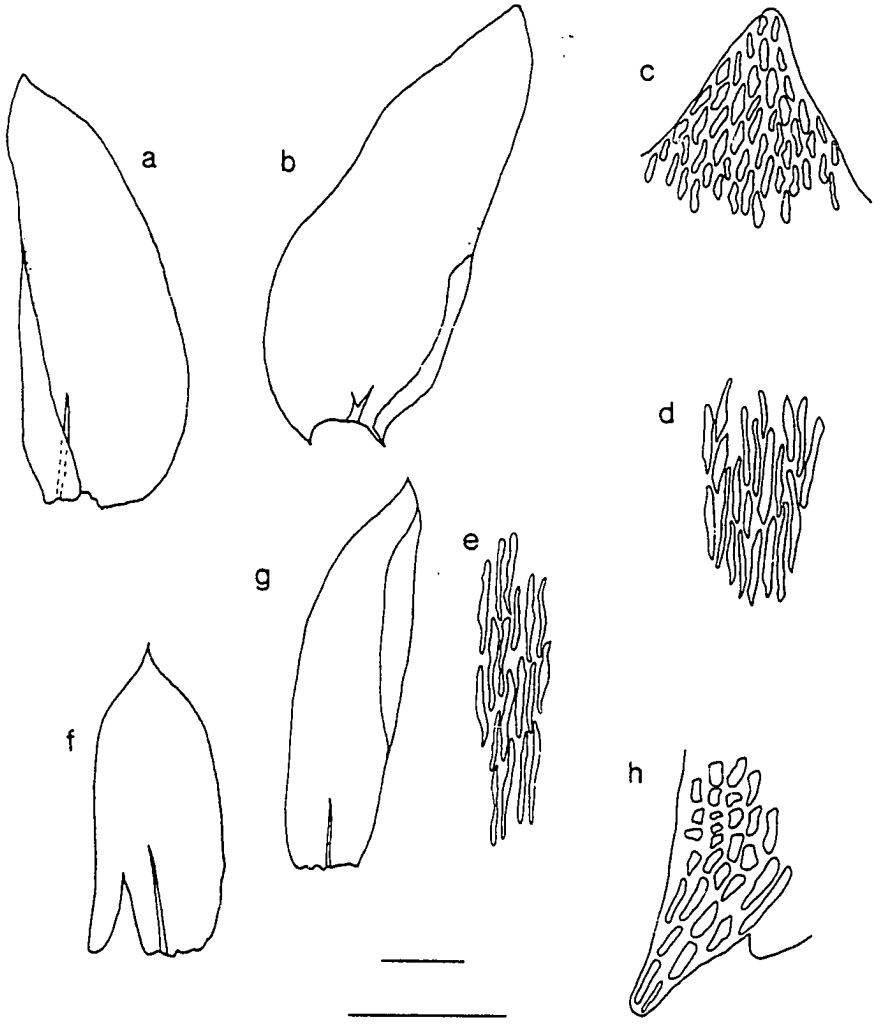
Neckera novae-granadae C. Müller, Bot. Zeit. **15:** 581, 1857, **syn. nov.** Type. Colombia. Río Hacha, Sierra Nevada, Taquinaar, 2400 m, Schlim 871 (lectotype, G!; isolectotype, NY!).

Neckera osculatina De Not, Mem. Reale Accad. Sci. Torino ser. 2, **18:** 440. 1859, **syn. nov.** Type. Colombia?. Osculati s. n. (isotype, BM!).

(Fig. 14 a-h).

Plants mostly medium sized to robust, 7-15 cm tall, green to yellow-green, shiny to slightly dull, irregularly to regularly pinnate, forming wefts. Axillary hairs 4-6 cells long, stalk cell short-quadrate; paraphyllia sparse, mostly absent; pseudoparaphyllia foliose. Primary stem leaves obovate, 0.5-1.0 mm long, acute; margins entire, plane; costa present or absent; apical cells linear, 26 um long, 6 um wide, median and basal cells 34-52 um long, 6 um wide, alar cells quadrate. Stem leaves mostly erect-spreading to spreading, ovate-lanceolate, slightly decurrent, 3.1-3.8 mm long, 1.2-1.3 mm wide at mid-leaf, 1.4-1.5 mm wide at base, not concave, undulate, acute to narrowly acute; margins entire to slightly serrulate; costa short and double, rarely single; apical cells rhombic to rhomboidal, 28-39 um long, 6-8 um wide, upper median cells linear, 52-78 um long, 8 um wide,

Fig. 14. Neckera chilensis (Bertero s. n., BM). a, lateral stem leaf, x40; b, central stem leaf, x40; c, stem leaf apex, showing apical cells, x400; e, stem leaf alar cells, x400; f, outer perichaetial leaf, x40; g, inner perichaetial leaf, x40; h, perichaetial leaf upper median cells, x400.



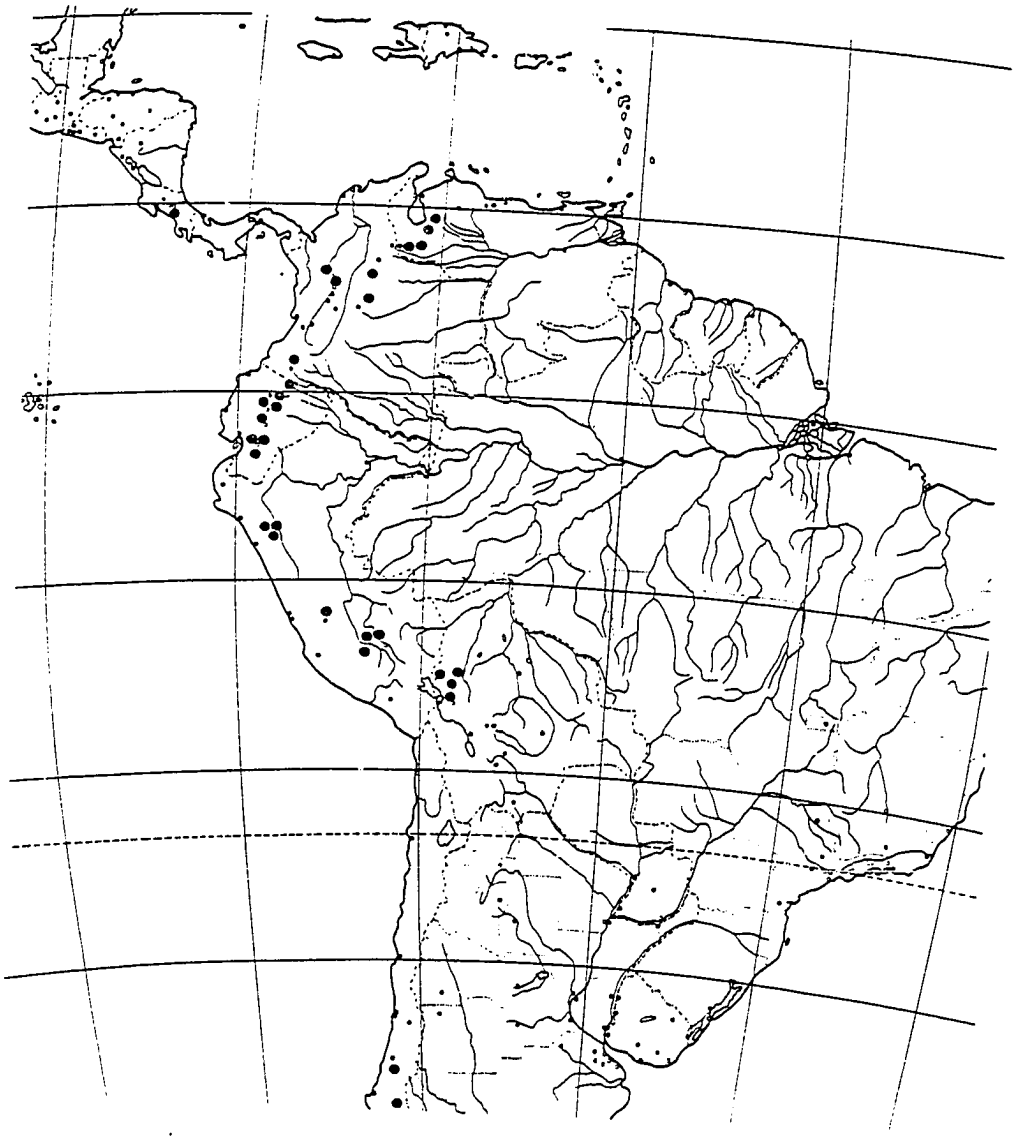
basal cells linear to rectangular, 52-78 um long, 8 um wide, alar cells short quadrate, thick-walled; branch leaves smaller. Autoicous. Perichaetial leaves oblong-lanceolate, 2.0-3.0 mm long, gradually or abruptly acute to acuminate; margins entire; costa mostly absent; apical cells irregularly rectangular, 34-52 um long, 6 um wide, upper median cells linear, 78-100 um long, 6 um wide, basal cells rectangular, 78-100 um long, 8-13 wide, pitted throught. Seta 2.0 mm long; capsule erect, ovoid-cylindric, 1.5-2.0 mm long; exothecial cells irregularly quadrate to rectangular, 21-31 um long, thick-walled; exostome teeth lanceolate, very long, to 1.0 mm, on front surface cross striate below, papillose above, papillae mostly arranged in rows, upper part becoming trabeculate, papillose at back, lamellae projecting; endostome with a high basal membrane, segments lanceolate, keeled, papillose throughout. Spores 39 um in diameter, densely papillose.

Distribution and Ecology. (Fig. 15). A widespread taxon occurring from Venezuela to Chile. Neckera chilensis is a páramo and subpáramo species. It is commonly an epiphyte at elevations of 2500-4000 m. Less frequently, it is found growing on the ground.

Representative specimens examined. COSTA RICA. Heredia: Volcán Barba, 2600 m, 6 Feb 1979, Griffin et al. D-219 (NY); San José: Cerro de las Vueltas, 2700-3000 m, Dec 1925, Standley et al. 368 (MO).

COLOMBIA. Antioquia: Sonsón, 12 km E of Sonsón on road to Nariño, 2580 m, 23 Jun 1985, Churchill & Sastre 13004 (NY); Cundinamarca: Near Bogotá, on road to Páramo el Palacio, 3000 m, 3 Jun 1976, Zarucchi 1687 (NY); Nariño: E slopes of Volcán Chiles, Baños Termales above village of Chiles, 3100-3300 m, 17 Aug 1944, Steere 9470 (NY); Santander: S slopes of Páramo de Romeral,

Fig. 15. Distribution map of Neckera chilensis.



3800 m, 29-31 Jan 1927, Killip et al. 18707 (FH, NY), Cerrito, road Presidente-Cerrito, Páramo Almorladero, 3400 m, 26 Jul 1985, Escobar et al. 342 (HUA, NY).

VENEZUELA. Mérida: Rivas Davila, Páramo la Negra above from of Bailadores, 2900 m, Jul-Aug 1972, Griffin et al. 1986 (FLAS, NY), along highway 139 km NW of Barinitas and ca 20 km E of Santo Doming, 1900 m, 28 Jul 1979, Nee et al. 16951 (NY); Táchira: Jauregui, páramo El Batallón, above the town La Grita, 3340 m, Aug 1975, Griffin et al. 508 (FLAS, NY); Trujillo: Urdaneta, páramo La Estrella, to the south and above the town of La Mesa de Esnujaque, 3100 m, Aug 1975, Griffin et al. 1344 (FLAS, NY).

ECUADOR. Azuay: Panamerican Highway S between Loja and Cuenca, 40-50 km N of Oña, 3350 m, 24 Sep 1982, Steere et al. 25937A (NY): Carchi: Páramo el Angel, just before the pass on road El Angel-Tulcán, 3450-3500 m, 14 May 1973, Nielsen et al 5261 (NY); Cotopaxi: Parque Nacional Cotopaxi, N slopes of Rumiñahui, 4100-4300 m, 28 Oct 1982, Balslev et al. 3383 (NY), N slopes of Mt. Cotopaxi, 3500 m, 12 Jun 1975, Crosby 10675 (MO, NY); Imbabura: Western Cordillera, road Otavalo-Laguna de Mojanda, 3700 m, 29 Oct 1983, Steere 26927 (NY); Napo: Eastern Cordillera, Quito-Baeza road, Papallacta, 3500 m, 4 Nov 1983, Steere 27049 (NY); Pichincha: W side of Volcán Atacazo, ca 5 km S of Campamento, 3750 m, 24 Oct 1984, Laegaard 53274G (NY), new Quito-Santo Domingo de los Colorados highway, 6 km W of Aloag, 3100 m, 26 Sep 1982, Steere et al. 26001 (NY), W slope of Pasachoa 30 km SSE of Quito, 2900 m, 20 Dec 1983, Buck 10164 (NY).

PERU. Aprurimac: Andahuaylas, Pallcamayo to Huancarama, 3700 m, 9 Apr 1973, Hegewald 5743 (NY); Cajamarca: Cajabamba-Luchubamba, 3050 m, 17 Nov 1983, Sagastegui et al. 11227 (MO, NY); Cuzco: Urubamba, between

Peñas and Panticalla, 3500 m, 24 Jul 1944, Vargas 4417 (MO), La Convención, Oct 1920, Bües 1045 (MO, NY); Junin: Huancayo, 56 km from Huancayo, 3000 m, 8 Jul 1977, Hegewald 9264 (NY).

BOLIVIA. Cochabamba: Choquecamata, Jun 1889, Germain 1191 (G); La Paz: Sorata, 3000 m, Feb 1886, Rusby 3169 (FH), Saavedra, on mountain side directly N of river beneath Niño Karine NNW of Chuma, 3250 m, 6 Mar 1979, Lewis 79-1037 (NY).

CHILE. Biobio: Salto de El Laja, 150 m, 19 Jan 1977, Mahu 11277 (MO, NY); Choapa: Cerro Talinay, 5 km N of Huentelau, 600 m, 15 Dec 1978, Mahu 12534 (MO); Curico: Fundo el Manzano 40 km E of Curico, 30 Apr 1970, Weber 152 (MO); Maule: Between Quirihue and Cobquecura, 21 Mar 1971, Landrum 1543 (NY).

Discussion. Variation in N. chilensis resides principally in leaf shape which ranges from ovate-lanceolate to oblong-lanceolate. Even within a single plant the different grades may be observed, assuming that leaves from the same position are compared. Leaf apex is quite variable also, but branch leaves are consistently narrowly acute. This taxon is characterized by the absence of paraphyllia, and fully exserted capsules. Plants from higher elevations (3000 m) tend to be larger than those found at lower elevations. Plants from lower elevations also may exhibit narrower leaf apices. The type of Neckera jamesonii is an example of the robust growth form and that of Neckera novae-granadae of the smaller form.

2. **Neckeropsis** Reichardt, Verh. Zool. Bot. Ges, Wien 18: 192. 1868. Type. Neckeropsis undulata (Hedwig) Reichardt.

Plants unbranched, irregularly branched to dendroid, light green to yellow-green, glossy. Axillary hairs 3-4 cells, stalk cell differentiated, golden-brown; paraphyllia absent; pseudoparaphyllia filamentous to foliose. Primary stem creeping, in cross-section with 3-4 outer rows of thick-walled cells, 3-4 inner rows of thin, lax cells; leaves broadly ovate, rounded acute; margins serrulate to entire; costa single; apical cells rhomboidal, upper median cells long rhomboidal, distal marginal cells differentiated, mostly linear to long rhomboidal, basal cells rectangular. Secondary stem mostly perpendicular from substrate, unbranched to irregularly pinnate to dendroid, complanate. Secondary stem leaves pseudotetrastichous (3/8), spreading to squarrose, undulate to smooth, dimorphic, lateral and median leaves asymmetric, oblong, ligulate to spathulate, leaf base broadly ovate to oblong, sometimes clasping at base, distinctly to slightly auriculate, apex broadly to rounded truncate to obtuse; margins distinctly to slightly serrulate at apex, entire to slightly serrulate below, plane, except at distal margin of lateral leaves, folded from leaf insertion to mid leaf; costa single, 1/2 to 3/4 of leaf length, in cross-section with undifferentiated cells; apical cells rectangular to rhomboidal, upper median cells rhomboidal to rectangular-elongate, basal cells rectangular, pitted or unpitted, marginal cells on keeled or folded lamina linear to long-rhomboidal. Monoicous, synoicous or autoicous. Perigonia on secondary stem and branches; leaves ovate, subulate; margin entire to serrulate; costa absent; apical cells linear, upper median cells linear to irregularly rectangular, basal cells irregularly rectangular. Perichaetia on secondary stem and branches, ramenta present or absent, when absent perichaetial leaves oblong-subulate (Neckera-like), linear, apex entire to serrulate, cells mostly rectangular throughout the lamina, pitted; outer perichaetial leaves oblong, subulate, tightly appressed at base, subula reflexed; inner perichaetial leaves ovate-subulate to oblong-subulate, entire to

serrulate, costa absent or short, ending near mid-leaf; apical cells linear to rectangular, upper median cells rectangular, basal cells rectangular, pitted. Setae short, embedded in vaginulae; capsule oblong; exothecial cells mostly irregularly quadrate, thick-walled; stomata absent; operculum conic rostrate to obliquely rostrate; annulus absent; peristome double, exostome teeth mostly lanceolate, papillose, sometimes with round perforations; endostome with a low basal membrane, segments narrow lanceolate, papillose, sometimes with round perforations, sometimes trabeculate, cilia none. Spores spherical, papillose. Calyptra cucullate to campanulate hairy to smooth.

Neckeropsis is characterized by asymmetrical leaves with a narrow or wide auriculate base, and a rounded to truncate and finely crenulate apex. Also, some species have ramenta, leaf-like paraphyses along the axis or apex of the female gametoecium, as in N. undulata and N. disticha.

Three sections mentioned by Brotherus (1925) are commonly accepted in the genus. These were based on structure and maturation differences of the female gametoecium. Of these three sections only two are represented in the neotropics. They are Neckeropsis (Paraphysanthus) with two species (N. undulata and N. disticha) and Taenocladium with N. foveolata. Neckeropsis disticha and N. foveolata also occur in Africa and N. undulata is restricted to the neotropics. The genus is more diverse in Asia, where 12 species occur (Touw, 1962).

Fritsch (1982) has reported a chromosome number of 10 for two species from Japan, Neckeropsis calcicola and N. nitidula. No chromosome counts are known for the neotropical species.

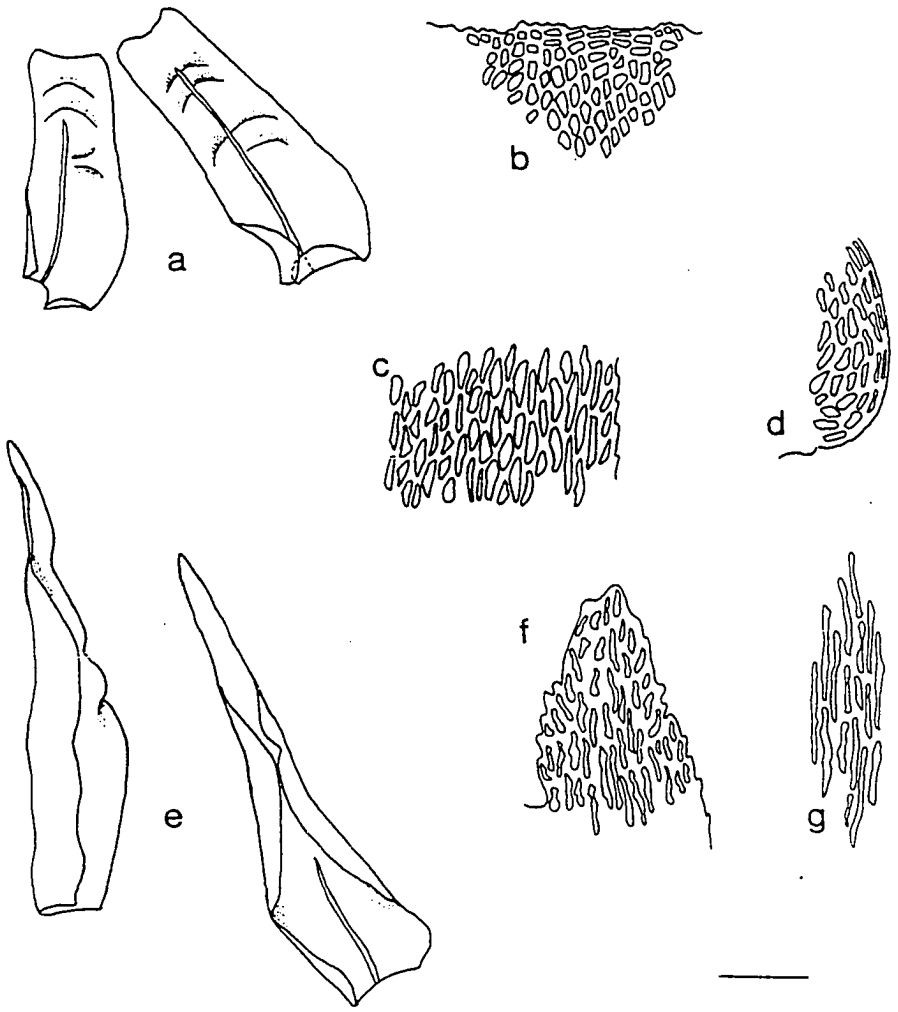
Key to the species of Neckeropsis

1. Leaves spreading to squarrose, undulate; leaf base distinctly auriculate 2.
   2. Perichaetial leaves oblong-subulate, 3.0-4.0 mm long; ramenta absent 1. N. foveolata.
   2. Perichaetial leaves ovate-subulate, 1.0 mm long, ramenta present 2. N. undulata.
1. Leaves mostly spreading, not undulate when moist; leaf base not distinctly auriculate, mostly oblong 3. N. disticha.

1. **Neckeropsis foveolata** (Mitten) Brotherus, Nat. Pfl. ed. 2, **11:** 188. 1925.
   Neckera foveolata Mitten, Trans. Linn. Soc. London **23:** 53. 1860. Type. Afrique, Beauvais in Hb. Hooker (holotype, NY!). (Fig. 16 a-g).

Plants irregularly branched; secondary stem leaves squarrose to spreading; ligulate from an ovate base, 1.70-1.80 mm long, 0.60-0.50 mm wide, undulate, truncate, auriculate; margin slightly serrulate at apex; costa 3/4 of leaf length; apical cells rectangular in 2-3 rows, 13-18 um long, subapical cells irregularly rectangular to rhomboidal, 8-10 um long, 6-8 um wide, upper median cells irregularly rhomboidal, (18)23(31) um long, 4-6 um wide, distal marginal cells 26-52 um long, 4 um wide, at base rectangular, (21)26-47(52) um long, 8 um wide, slightly pitted. Autoicous. Ramenta absent. Inner perichaetial leaves oblong, ovate, subulate, 3.5-4.0 mm long, 1.0 mm wide, apex dentate; costa ending above midleaf; apical cells linear, 26-52 um long, 4-6 um wide, upper median cells linear, 92-100 um long, 6 um wide, basal cells rectangular, 39-92 um long, 8-10 um wide. Setae 0.5

Fig. 16. Neckeropsis foveolata (Arnott s. n., NY). a, stem leaves, x40; b, stem leaf apex, showing apical cells, x400; c, stem leaf upper median cells, x400; d, stem leaf alar cells, x400; e, perichaetial leaf apex, x400; g, perichaetial leaf upper median cells, x400.



mm long; capsules immersed, oblong, 2.0 mm long; operculum conic rostrate. Spores spherical, papillose, 15-18 um in diameter.

Distribution of Ecology. (Fig. 18). Very little can be said about the ecology of this taxon since in the neotropics it is known from very few localities and label data accompanying those specimens is very scarce. It seems that it occupies the same kind of habitats as the other species of Neckeropsis known from the neotropics, that is, lowland tropical forests. It grows as an epiphyte.

Specimens examined. COSTA RICA. Alajuela: San Pedro and San Ramon hills, 8 Feb 1933, Branes 17029 (NY).

PANAMA. Veraguas: 1.7 km along road leading E just above Escuela Agrícola, Alto de Piedra, 18 May 1977, Crosby 10254 (MO).

GUYANA. Leprieur s. n. (G).

BRAZIL. Rio de Janeiro, Arnott s.n. (NY).

Discussion. As mentioned in Mitten's (1860) diagnosis of Neckeropsis foveolata, this taxon differs from N. undulata in the entirely different perichaetium. The ramenta are absent in N. foveolata, perichaetial leaves are oblong subulate and extend almost to the capsule mouth. Vegetatively, the two species are indistinguishable. Neckeropsis foveolata is not a well understood taxon since very few collections were available, for study. Limited population sampling did not allow a clear understanding fo varibility in this taxon.

This species appears to be related to N. lepineana, a widespread species in the Old World tropics. Both species share the same kind of female gametoecium structure that is, leaf like paraphysis are absent and inner perigamial leaves enlarge

after fertilization. Vegetatively N. foveolata is separated from N. lepineana by costa length. In N. foveolata the costa reaches 3/4 of the leaf length, but in N. lepineana it is shorter.

2. **Neckeropsis undulata** (Hedwig) Reichardt, Verh. Zool. Bot. Ges. Wien **18:** 192. 1868.

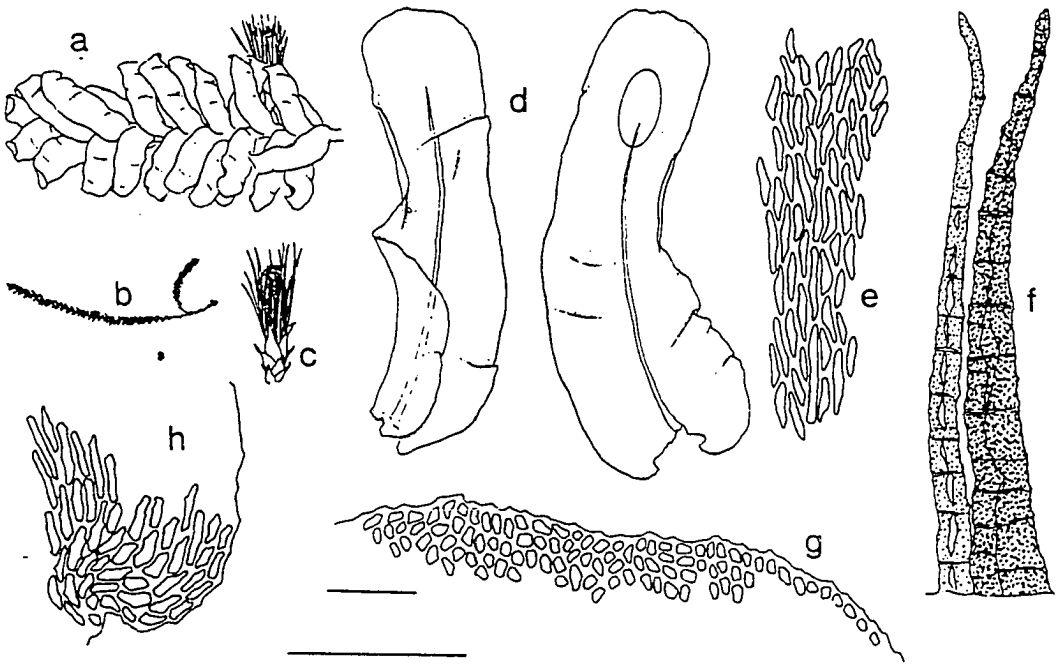
Neckera undulata Hedwig, Spec. Musc. **201.** 1801. Type. Jamaica, Swartz, s. n. (isotypes, LIV!, NY!).

Neckera amazonica Mitten, J. Linn Soc., Bot. **12:** 452. 1869; Neckeropsis amazonica (Mitten) Fleischer, Musci Fl. Buitenzorg **3:** 879. 1908, **syn. nov.** Type. Brazil. Fl. Negro ad S. Gabriel, Spruce 1336 (holotype, NY!).

(Fig. 17 a-h).

Plants small to robust, 3-7 cm tall, secondary stem unbranched to pinnate; leaves spreading to squarrose, undulate, lunate, 1.4-2.5 mm long, distal lobe 0.6-0.71 mm wide, leaf base broadly ovate-auriculate becoming oblong-ligulate, clasping at base, apex rounded truncate to truncate; margins serrate-crenulate at apex to slightly serrate below; costa single, ending 3/4 of leaf length; apical cells short rhomboidal to irregularly rectangular; 6-13 um long, 8 um wide, upper median cells irregularly rectangular, (13)18-26(34) um long, 4 um wide, distal margin cells linear, 26-52 um long, 4-6 um wide, basal cells rectangular, (31)52-62(70) um long, 6 um wide, slightly pitted. Synoicous or autoicous. Perigonial leaves ovate-subulate, 1.0 mm long, 0.3 mm wide, serrulate, margin sometimes bordered by one row of rectangular hyaline cells, apical cells irregularly linear, 21-26 um long, 6 um wide, upper median cells linear to irregularly rectangular, 39-52 um long, 6 um wide, basal cells irregularly rectangular, 39-65 um long, 6-8 um wide,

Fig. 17. Neckeropsis undulata (Clement 2, NY). a, habit showing sporophyte, x12; b, habit, x1; c, sporophyte, showing ramenta, x12; d, stem leaves, x40; e, stem leaf upper median cells, x400; f, peristome (exo-and endostome), x200; g, stem leaf apex, x400; h, stem leaf auricle showing alar cells, x400.



pitted. Ramenta inserted on vaginula, linear, 2.25-3.0 mm long, 0.10-0.28 mm wide, acute, apex serrulate; cells rectangular throughout, 52-78 um, 4 um wide, thick-walled, pitted; vaginula 0.57-1.0 mm long. Inner perichaetial leaves oblong-subulate, 1.5-2.8 mm long, 0.71 mm wide, margin entire to serrulate; costa present or absent; apical cells linear, 31-39(65) um long, 6 um wide, upper median cells linear, 52-65 um long, 6 um wide, basal cells rectangular, 78-131 um long, 6 um wide, pitted. Setae 0.70 mm long; capsule oblong; 1.0-1.5 mm long; operculum rostrate; annulus absent; exostome teeth papillose; endostome segments mostly with round perforations. Calyptra campanulate, hairy to smooth. Spores spherical, papillose, 13 um in diameter.

Distribution and Ecology. (Fig. 18). Neckeropsis undulata is widely distributed in the southern United States, Central America, the West Indies and South America. It is a common epiphyte or saxicole, from lowlands to lower montane, at elevations from sea level to 1800 m. In Mexico it has been collected on Quercus.

Representative specimens examined. MEXICO. Chiapas: Ruinas de Palenque, 180-250 m, 8 Mar 1979, Eggers et at. 837922 (NY); Quintana Roo: Ca 8 km N de Tomás Garrido, 190 m, Delgadillo 4306 (NY); San Luis Potosi: 2 mi E of Xilitla, 900 m, 28 Dec 1953, McGregor 8088(NY); Veracruz: On N side of road to Huatusco from junction with Mexico 140, ca 40 mi NW of Veracruz, 300 m, 9 Jul 1961, Pursell et al. 4924 (MO), vicinity of Mt. Orizaba, Jan & Feb 1892, Smith s. n. (NY).

GUATEMALA. Alta Verapaz: Chama, 270 m, 27 Jul 1920, Johnson 338 (NY), 350 m, Oct 1906, Türkheim 6925 (NY), Petén: La Libertad, 21 Apr 1933, Lundell 2935 (MO, NY), Laguna Petexbatum, S of Sayaxche, 50 m, 3 May 1942, Steyermark 46191 (FH, NY).

Fig. 18. Distribution maps of Neckeropsis foveolata and N. undulata.

BELIZE. Maya Mts., Hummingbird Highway, St. Margaret Creek, 405 m, 3 Sep 1961, Ropes s. n., (NY); Beaver Dam, 17 Mar, Lundell 1977 (FH); Stann Creek District, 21 Dec 1937, Gentle 2157 (NY).

HONDURAS. Atlántida: La Fragua, 20 m, 7 Feb 1928, Standley 55778 (FH); Copán: Creek Mojanales, 16 May 1919, Blake 7481 (NY).

NICARAGUA. Comarca del Cabo: 13 Jul 1972, Seymour 5878 (MO); El Recreo, 15 km W of Rama, 31 Aug 1977, Darin 2-C (MO).

COSTA RICA. Alajuela: Alto de Acosta cerca de San Ramón, 16 Feb 1935, Brenes 20406 (NY); Guanacaste: Upper slopes of Cerro San José de Libano, 1500 m, 15 Feb 1930, Dodge et al. 1917 (FH); Heredia: Vicinity of Vara Blanca, 1880 m, 26 May 1976, Croat 35534B (MO); Limón: Slopes of Cerro del Tortuguero, 3 mi inland from Green Turtle Station, 19-25 Jul 1968, Steere CR-42 (NY); Puntarenas: 5 km W of Rincón de Osa, Osa Peninsula, 5-200 m, 24-30 Mar 1973, Gentry et al. 2775 (MO).

PANAMA. Canal Zone: 6 mi N Gamboa on ridge S of Río Frijol, 6 Oct 1965, Tyson 1528 (NY), Las Cruces Trail, E of summit Garden, 133 m, 10 Aug 1961, Welch 19730 (MO); Barro Colorado Island: Along Barbour Trail, near marker 3, 9 Apr 1966, Crosby 3949A (MO); Colón: Near Peluca, on tributary to Río Boquerón, 9 Mar 1973, Kennedy 2799B (MO), near Gatun Lake, at junction of Río Aguardiente and Río Quebrada, 28 May 1923, Maxon 6558 (NY); Chiriquí: 2 mi S of Boquete, 12 Apr 1966, Crosby 3957 (MO); Darién: Pirre Base Camp, Feb 1972, Gentry M-8a (MO), on road to Yaviza, SE of Canglón, 500-800 m, 18 May 1980, Salazar 2022 (NY); Panamá: Vicinity of falls of Río Caimito, near la Chorerra, 5 Apr 1969, Crosby 4549A (MO); San José Island: Gulf of Panamá, about 55 mi SSE of Balboa, 12 Jan 1946, Johnston s. n. (NY); Veraguas: 1.7 km along road leading E just above of Escuela Agrícola, Aito de Piedra, 750 m, 18 May 1975, Crosby 10267 (MO).

BAHAMA ARCHIPIELAGO. Grand Bahama: In Fortune Hills region of Freeport, 22 Mar 1975, Correll 44749 (MO).

CUBA. Pinar del Río: Sierra del Rosario, Samek s.n. (MO), source of Río Taco-Taco, Sierra de los Organos, 400-500 m, 18 Nov 1941, Morton 4313 (FH, NY); Santiago de Cuba: Bayate, between Sabana Miranda and Sabana Risueña, 5 Jul 1915, Ekman 5897 (FH, G, NY), Finca Guadalupe de Tiguabos, 11 Apr 1935, Hioram 12869 (MO), La Gran Piedra, SE peak, 1000 m, 2 Apr 1982, Buck 7445 (NY); Santa Clara: Trinidad Mts., 400 m, 1-2 Mar 1910, Britton 4897 (NY).

JAMAICA. Clarendon: N slope of Croft Mt., 690 m, 10 Mar 1970, Hermann 22965 (MO, NY); Manchester: Marshall's Pen, 3 mi WNW of Mandeville, 690 m, 14 Apr 1981, Crosby 13813 (MO, NY); Portland: 7 mi NW of Muirton on road to Ecclesdown, along trail into John Crow Mts., 350 m, 11 Apr 1981, Buck 5661 (NY); St. Thomas: Along eastern bank of Sulphur River about 100 yards N of Bath Fountain buildings, 100 m, 29 Jul 1966, Crosby 3243 (MO), Corn Puss Gap and vicinity, ca 9 mi N of Bath on trail to Port Antonio, 550 m, 9 Apr 1981, Buck 5554 (NY).

HAIT. Artibonite: Vicinity of Ennergy, 325-900 m, 27 Jan 1926, Leonard 9256 (FH); Grand'anse: Massif de la Hotte, along small stream entering Riviére Glace, 710 m, 13 Nov 1982, Buck 9104 (NY); Nord: Vicinity of St. Louis du Nord, Morne Colombot, 30 Mar-7 Apr 1929, Leonard 14288 (FH, MO, NY), along Haitian/Dominican International Highway from Pedro Santana to Restauración 400 m, 23 Mar 1981, Reese 15379.

DOMINICAN REPUBLIC. La Altagracia: Lomo El Peñón de la Vieja Rufina, 24 km SE of Otra Banda, 41 m, 29 Mar 1981, Buck 5063 (NY); Duarte: El Jojobán, 20 km S of Nagua on road to El Abanico and Castillo, 80 m, 13 Aug 1981, Zanoni et al. 16113 (MO, NY); Independencia: 6 km NE of El Aguacate, 600 m, 21 Mar 1981, Reese 15225 (NY); Pedernales: Las Abejas, 55 km N of Cabo Rojo on Alcoa

road, 1100 m, 5 May 1982, Steere 22843 (NY); Samaná: Las Terrenas, 21 Jul 1978, Schuster RD18 (FH); Seibo: 19 km E of Sabana de la Mar on road to Miches, sea level, 28 Mar 1981, Buck 4997 (NY), W of Cañitas, 21 km W of Miches, 15 m, 28 Mar 1981, Zanoni et al. 11959X (NY); La Vega: Falconbridge Dominicana mine, N of Río Yuna, 200 m, 22 Apr 1981, Zanoni et al. 12886 (NY).

PUERTO RICO. Arecibo: Utuado, Reserva de Río Abajo, Garcia tract, Planting project, 22 Feb 1940, Steere 6631 (FH, MO, NY); Fajardo: Luquillo Mts., El Yunque recreation area, Big Tree Trail to La Mina, 500 m, 5 Mar 1981, Buck 4104 (NY); Mayagüez: Upper Río Maricao, 30 Dec 1939, Steere 5721 (MO, NY).

ST. THOMAS. On slopes of St. Peter Mountain, off Crown Mt. Rd., 400 m, 18 Feb 1981, Buck 3287 (NY).

TORTOLA. N of summit, Mt. Sage, 500 m, 9 Jun 1984, Allen 4278 (MO).

MONTSERRAT. Gages Mountains, 500 m, 2 Feb 1907, Shafer 829 (NY).

GUADELOUPE. Chemin de la Grande-Citerna, Duss 502 (NY); Basse-Terre, Deshaies, 250 m, 11 Jul 1976, De Sloover 23.520 (MO); s.l., 1877, Marie 71 (G).

DOMINICA. Lloyd 680 (NY).

MARTINIQUE. Montagne Pelée, Sep 1901, Duss 313 (NY), in forest W of Hopital de Colson, 600 m, 19 Apr 1969, Crosby 4762C (MO); Rivière Capote Hauters de l'Ajoupa Bouillon, 420 m, 10 Jun 1941, Stehlé 4005 (NY).

ST. LUCIA. Soufrière, near Quilesse, 200 m, 27 Jun 1945, Simmonds 217 (NY).

GRENADA. Grand Etang forests, 6 Jan 1960, Broadway 7870 (MO, NY).

TRINIDAD. Mount touche, 3-5 Apr 1920, Britton et al. 1542 (NY); St. George, Northern range, along LaLaja road, about 1 mi from Arima Blanchisseuse Rd turnoff, 300 m, 29 Jun 1965, Crosby 2133 (MO); vicinity of Valencia, 4 Mar 1921, N. L. & E. G. Britton 2114 (NY).

COLOMBIA. Antioquia: Tarazá, ca 5.5 km de El Doce, Finca Las Mercedes, ca 200 m, 17 Jun 1985, Sastre-De Jesús et al. 1040 (NY), Liborina, 15 km N of Liborina on road to Sabanalarga, 1100 m, 23 Jul 1986, Churchill, Sastre-De Jesús et al. 14694 (NY); Cundinamarca: San Cristobal, 20 Aug 1909, Apollinaire s.n. (G); Norte de Santander: Cerro de Cordoba above Río Cáchira, El Playón, 10 Dec 1942, Steere 7649a (NY).

VENEZUELA. Apure: Reserva Forestal San Camilo, 200 m, 6 Apr 1968, Steyermark et al. 101946 (NY); Barinas: Along Río Caparo, 100-200 m, 12 Mar 1980, Liesner et al. 9432 (MO); Bolivar: Near Las Pavas close to Salto Para, Río Caura, 230-280 m, 15-17 Jan 1977, Steyermark et al. 113033 (MO); Mérida: Colonia del Tovar, 1854-1855, Fendler 101, 861 (G); Monagas: 12.5 km NE of San Felix, 460 m, 14 Mar 1967, Pursell 8422 (NY); Sucre: Peninsula de Paria, on trail of Los Pocitos de Santa Isabel to Roma, 15-20 NW of Irapa, 700-1060 m, 12 Jul 1972, Dumont et al. VE-7639 (NY); Zulia: Sierra de Perijá, hills above the creek of Río Omira-kumá, close to frontier of Colombia and Venezuela, 1500-1800 m, 27 Mar 1972, Steyermark et al. 195675 (NY).

GUYANA. Esequibo: Rupununi, foothills of NW Kanuke Mts, near Moco-Moco, 100 m, 27 Oct 1979, Maas & Westra 3847 (G, NY), western extremity of Kanulu Mnts., in drainage of Takutu River, 200 m, 4-22 Mar 1938, Smith 3248 (G, NY).

SURINAM. Paramaribo: Agricultural garden, 13 Dec 1950, J. & P. A. Florschütz 573 (MO).

FRENCH GUYANA. Leprieur 312 (G).

ECUADOR. Esmeraldas: E of San Mateo, just below Zapallo, 500 m, 17 Sep 1982, Steere et al. 25599 (NY); Los Ríos: Hacienda Clementina, 300 m, 21 Jan 1947, Harling 2109a (NY); Napo: At Añangu, S shore of Río Napo, ca 75 Km

E of Coca, 245-325 m, 29 Jul 1985, Churchill & Sastre-De Jesús 13783, 13793 (NY); Pichincha: ca 18 km NW of San Miguel de los Bancos, forest reserve of ENDESA, 27-29 Dec 1983, Buck 10479 (NY); vicinity of Río Alambi, along road leading W from Nono toward Tandayapa, N slopes of Pichincha, 13 Jun 1975, Crosby 10733 (MO); Tungurahua: At mount Tungurahua, Spruce 1329 (NY).

PERU. Loreto: Puerto Arturo, lower Río Huallaga below Yurimaguas, 135 m, 24-25 Aug 1929, Killip et al. 27856 (NY); Madre de Dios: Tambopata, 70-80 river km SSW Puerto Maldonado at effluence Río La Torre, Tambopata Nature Preserve, 260 m, 8 May 1980, Barbour 5160a (NY); San Martín: Rioja, Moyobamba Chachapoyas km 409, 1100 m, 29 Aug 1982, Frahm et al. 498 (NY), Chachapoyas, Mattews s. n. (G); Tumbes: Zarumilla, close to Campo Verde, 600-800 m, Simpson Br-135 (MO).

BRAZIL. Acre: 15 km E of Rio Branco along the road to Abuna, 24 Feb 1978, Reese et al. 13150 (NY); Amapa: Cachoeria Tres Saltos, Rio Aiapoque, 2 Sep 1960, Irwin et al. 4762 (NY); Amazonas: Near mouth of Rio Embira (tributary of Rio Tarauca), 10 Jun 1933, Krukoff 4742 (NY); along W shore of Rio Uatumã at junction of Rio Pitinga, 24 Aug 1979, Buck 3087 (NY); Mato Grosso: Vicinity of Buriti, Chapada dos Guimarães, 720 m, 22 Oct 1973, Prance et al. 19255 (NY); Minas Gerais: Ilhue, Fazenda de Tabunha, 27 Aug 1930, Mexia 5009-A (G); Pará: Serra do Cachimbo, cataracts on rio Curuá and vicinity, 842-887 km N of Cuiabá on Cuiabá-Santarém (BR 163), 350-500 m, 208 May 1983, Reese et al, 16527 (MO, NY); Paraná: Foz do Iguacu, Parque Nacional de Iguacu, 100-200 m, 22-23 Sep 1984, Vital & Buck 12019 (NY); Rondonia: 128 km SW of Ariqueaes at Mibrasa Mining Camp, 14 May 1982, McFarland et al. 148 (NY); Roraima: Boca da Mata, vicinity of abandoned army base 216 km N of Boa Vista, ca 2 km N of Rio Surumu, 800 m, 30 Nov 1977, Buck et al 1997 (NY); Santa Catarina: Tubarão, Sep 1889, Ule 765 (MO); São Paulo: Apiai, Puiggari 191 (G).

BOLIVIA. Beni: 6 km S of Guayaramerín, 1 Feb 1978, Reese 12975 (MO, NY); Santa Cruz: Summit between San José and Tumupasa, 1500 m, 25 Aug 1902, Williams 2000 (NY); Velasco: Yotau, 300 m, Jul 1907, Herzog s. n. (NY).

PARAGUAY. Alto Paraná: Ciudad Presidente Stroessner, 21 Dec 1984, Bordas 207 (NY); Paraguari: Parque Nacional Ybycui, trail along Arroyo Mina, 200 m, 5-7 Oct 1984, Buck 11832, 11845, 11897 (NY).

ARGENTINA: Posadas: La Granja, 23 Nov 1907, Ekman 2116 (FH, NY); Corrientes: Iguazu waterfalls, 4-7 Oct 1983, Hübschmann s. n. (NY).

Discussion. Neckeropsis undulata is characterized by the undulate leaves, wet or dry, and distinctly broad auriculate base. As circumscribed by Mitten (1869), N. amazonica was distinguished from N. undulata by the purplish leaf color and synoicous sexuality. The purplish color is common in other species of Neckeropsis. Most of the studied specimens of N. undulata were autoicous, and occasionally in perichaetial buds an antheridium could be found or vice versa. This suggests that synoicous plants can be present in a population, but is at most a rare condition. Alternate sequences, starting with perigonial inflorescences, are produced, along the secondary stem or branches, followed by perichaetia. Another character used ny Mitten to segregate the two species was the calyptra. Calyptrae were observed to either be covered by segments of ramenta or smooth. Neckeropsis amazonica is considered to fall within the morphological range of N. undulata.

Of the species placed in sect. Neckeropsis (Paraphysanthus), Neckera undulata seems to be close to N. crinita (Griff.) Fleisch. from Indochina. In both species are the leaf-like paraphysis and lack the costa which are generally not present in other species of the section.

3. **Neckeropsis disticha** (Hedwig) Kindberg, Canad. Rec. Sci. **6:** 21. 1894.

Neckera disticha Hedwig, Spec. Musc. **201.** 1801. Type. Jamaica et Hispaniola. Swartz. (lectotype G!, isotype, BM!).

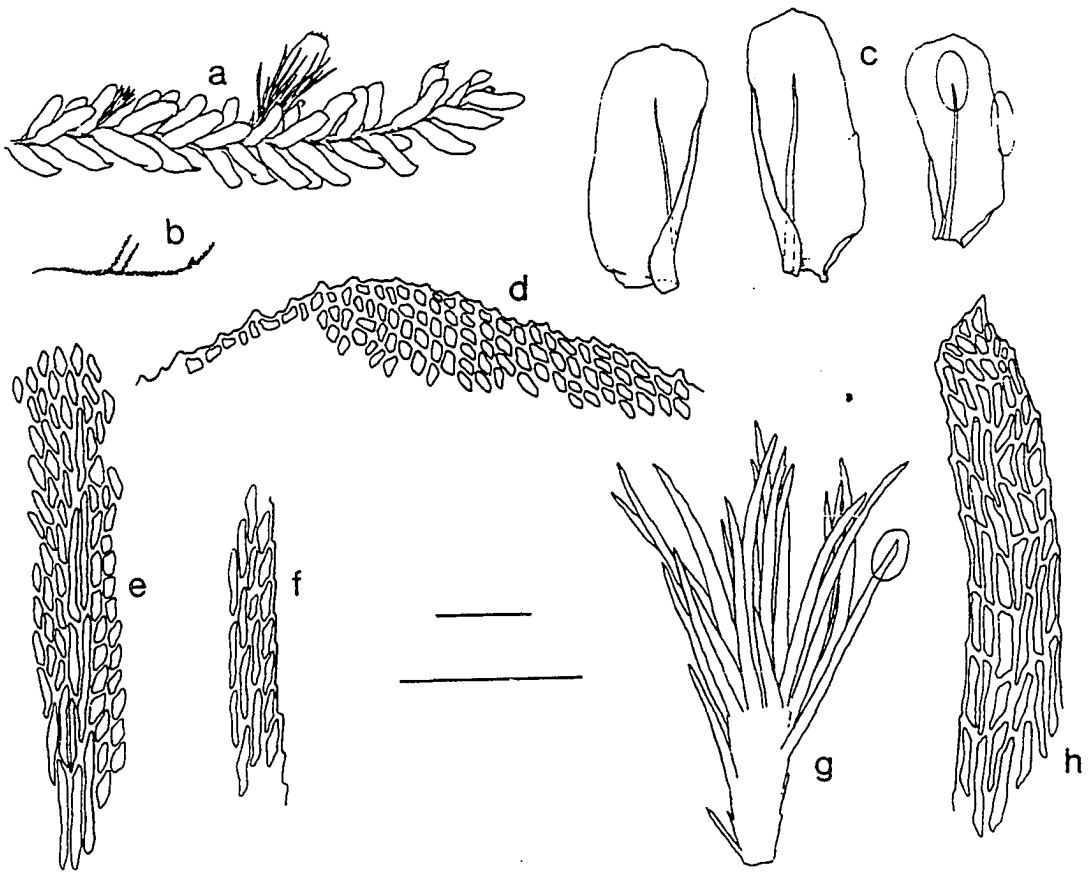
Neckera pabstiana C. Müller, Bot. Zeit, **13:** 766. 1855; Neckeropsis pabstiana (C. Müller) Brotherus, Nat. Pfl. ed. 2, **11:** 187. 1925, **syn. nov.** Type. Brazil. Sa. Catharina, Feb-Jul 1851, Pabst s. n. (lectotype H-BR!; isotype, NY!).

Neckera inundata Brotherus, Hedwigia **45:** 278. 1906; Neckeropsis inundata (Brotherus) Brotherus, Nat. Pfl. **1** (3): 1229. 1909, **syn. nov.** Type. Brazil. Amazonas [Acre]: Río Juruá, Ule 2392 (holotype H-BR!; isotypes FH!, BM!).

Neckera microtheca Herzog, Beih. Bot. Centralbl. **20**(2): 78. 16. 1910; Neckeropsis microtheca (Herzog) Brotherus, Nat. Pfl. ed. 2, **11:** 187. 1925, **syn. nov.** Type. Bolivia. La Paz: Río Blanco, 7 Aug, Herzog s. n. (isotype, NY!). (Fig. 19 a-h).

Plants small to robust, to 7.0 mm tall, irregularly branched. Stem and branch leaves spreading, smooth to crisped (not undulate), 1.4-1.7 mm long, 0.4-0.6 mm wide, base slightly ovate, mostly oblong, apex rounded truncate; margin at apex serrulate, slightly serrulate below; costa 1/2 to 3/4 of leaf lenght; cells at apex short rhomboidal, 8 um long, 8 um wide, upper median cells 15-21 um, 8 um wide, basal cells 34-44(65) um, 6 um wide, distal marginal cells mostly linear, 26-44 um long, 4-6 um wide. Synoicous. Ramenta linear, 1.7-2.0 mm long, 0.1-0.2 mm wide, acute, serrulate; apical cells rectangular, 23-26 um long, 6 um wide, upper median cells rectangular to linear 52-65 um long, 6 um wide, basal cells rectangular 70 um long, 6 um wide. Inner perichaetial leaves ovate, subulate,

Fig. 19. Neckeropsis disticha (Clement 3572, NY). a, habit, showing sporophyte, x12; b, habit, x1; c, stem leaves, x40; d, stem leaf apex, x400; e, stem leaf upper marginal cells, showing costa, x400; f, stem leaf marginal cells, x400; g, ramenta, x40; h, ramenta apex, x400.



1.0 mm long, 0.4-0.5 mm wide; margin entire to serrulate at apex; costa absent; apical cells linear, (26)39-52 um long, 6 um wide, upper median cells linear, 44-65 um long, 6-8 um wide, basal cells irregularly rectangular, 39-78 um long, 6-8 um wide. Setae 0.5-0.6 mm long; capsule cylindric, 1.5 mm long; operculum conic, rostrate. Exostome lanceolate, papillose, endostome papillose. Calyptra cucullate, glabrous to hairy. Spores spherical, papillose. 15-18 um in diameter.

Distributioon and Ecology. (Fig. 20). It has been collected mainly as an epiphyte or saxicole, from Mexico to Brazil (also known from Florida and Argentina). In Central America it is found from lowland floodplains to deciduous forests of Mexico, at elevations of 90-1800 m. It is very abundant in limestone forests of the West Indies, but is also found in lower montane forests. In South America it is commonly in shaded wet forests at low elevations to lower montane.

Representative specimens examined. MEXICO. Veracruz: Río Solosúchil, between La Escuadra y Vicente Guerrero, 25 Jan 1975, Delgadillo 3445 (MO), along Río Jaltepec at Veracruz-Oaxaca state boundary, 60 m, 4 Sep 1943, Rickett 72 (NY).

GUATEMALA. Alta Verapaz: Between Limón and Chisec, 200-230 m, 19 Mar 1942, Steyermark 45124 (FH, NY); Izabál: Vicinity of Quiriguá, 75-225 m, 15-31 May 1922, Standley 24449a (FH, MO, NY); Petén: Along Río Machaquila, north of El Cambio, 75 m, 24 Apr 1942, Steyermark 45914 (FH).

BELIZE. Cayo: Tea Kettle, 12 May 1931, Bartlett 13146 (FH, MO, NY), Mount Hope, 18 Mar 1933, Lundell 2002 (FH, NY).

HONDURAS. Highland Creek, Bradley's Plantation, 3 Feb 1903, Wilson 292 (NY).

Fig. 20. Distribution map of Neckeropsis disticha.

NICARAGUA. Bluefields: Base camp 3.6 km SE Cerro San Isidro, Río Kama, Río Escondido, 65 m, 7 Mar 1966, Proctor et al. 27053 (MO, NY), Comarca del Cabo, 13 Jul 1972, Seymour s. n. (MO).

COSTA RICA. Alajuela: Vicinity of Guatuso de San Rafael, 80-100 m, 4 Aug 1949, Holm et al. 1306 (G); Cartago: Turrialba, E of Instituto Interamericano de Ciencias Agrícolas, 17 Feb 1966, Crosby 3654 (MO); Limón: Along Río Tortuguero ca 2 mi SW of Tortuguero village, 19-25 Jul 1968, Steere CR-50 (NY).

PANAMA. Bocas del Toro: United Fruit Co. Farm 8, 29 Aug 1925, Dodge et al. 4149 (FH, NY); Canal Zone: Río Boquerón and about the Peluca hydrographic station, 70 m, 29, 31 Dec 1934, Steyermark et al. 17260 (MO); Colón: Left bank of Río Guanche where it meets the sea, 7 km SW of Portobelo, 3 Jun 1975, Crosby 10711 (MO); Panamá: Around Alhajuela, 30-100 m, 11-12 Jan 1911, Pittier 2350 (NY).

CUBA: Pinar del Río: Baños de San Vicente, 26 Aug - 17 Sep 1910, E. G. Britton 7371 (NY); Santa Clara: Arroyo de Monoca, 1-12 Mar 1910, E. G. Britton 5026 (NY); Santiago de Cuba: Caney, Alto Vialón, arroyo Ramona, 500 m, 9 Apr 1982, Shaw 5387 (NY).

JAMAICA. Manchester: Marshall's Pen, 3 mi WNW of Mandeville, 690 m, 14 Apr. 1981, Buck 5769 (NY); St. Andrew: Hardwar Gap, 12 Apr 1981, Crosby 13735 (NY); St. Elizabeth: Vicinity of Elim Whark, 10 Mar 1975, Proctor 34912 (NY); St. James: 4 mi NE of Maroon Town on road to Spring Vale, 150 m, 22 Apr 1981, Crosby 13949 (NY); Saint Thomas: Bath, trail N from Bath Fountain Hotel, along Sulphur River, 300 m, 8 Apr 1981, Buck 5521 (NY); Trelawny: Vicinity of Windsor Cave, 140 m, 21 Apr 1981, Crosby 13929 (MO, NY).

HAITI. Grand'anse: Massif de la Hotte, La Vie, at edge of Plaine de Cayes, south Camp Perrin, 13 May 1941, Bartlett 17678 (G); Nord: Vicinity of St. Louis du Nord, 30 Mar-7 Apr 1929, Leonard et al. 14198 (FH, NY).

DOMINICAN REPUBLIC. La Altagracia: 0.5 km from Otra Banda on road to Cruce de los Isleños y Nisibón, 90 m, 27 Jan 1982, Zanoni et al. 18977PX (MO); Barahona: Along floodplain of Río Nizao, 1 to 3 km upstream from Villa Nizao, 100 m, 21 May 1981, Zanoni et al. 13542 (NY); Dajabon: Cañada Tirolis, 1 km S of Villa Anacaona, 1300 m, 23 Mar 1981, Buck 4833 (NY); Sánchez Ramírez: Río Cevicos, W of Cevicos town, 80 m, 22 Sep 1982, Zanoni et al. 23425 (MO); El Seibo: 7 km S of Sabana de la Mar on road from El Valle, 10 m, 28 Mar 1981; Buck 4985 (NY); La Vega: Entrance to Falconbridge Dominicana mine operation, Loma Le Peguera ESE of Bonao, 180 m, 30 Jul 1981, Zanoni et al. 15789 (MO, NY).

PUERTO RICO. Cayey: Road to Salinas, 16 Dec 1939, Steere 5291 (MO), NY); Arecibo: Between Arecibo and Utuado, 4 Mar 1914, E. G. Britton 2078 (NY), along Hwy 140 ca 4 mi SSW of Florida, S of junction of Río Yunes, 26 Feb 1981, Buck 3647 (NY); Fajardo: Luquillo Mts., N slope, 8 Mar 1899, Heller et al. 795 (FH, NY), Aguas Buenas, 11 Nov 1939, Steere 4881 (MO).

ST. THOMAS. On slopes of St. Peter Mt., just off Crown Mt. Rd., 400 m, 18 Feb 1981, Buck 3283 (NY).

TORTOLA. Tortola, 375 m, 13-17 Feb 1913, Britton et al. 841 (NY).

GUADALOUPE. No locality, 20 Mar 1902, Duss 1011 (NY).

TRINIDAD. Caura river valley, 1 Apr 1920, E. G. Britton et al. 1208 (FH, NY); St. George: Las Tapas Trace from summit of Arima-Blanchisseuse Road, 2 Jul 1965, Crosby 21779 (MO).

COLOMBIA. Antioquia: Puerto Triunfo, Rio Claro, Reserva forestal El Refugio. 130 m, 12 Jun 1985, Sastre-de Jesús et al. 1415 (NY); Boyacá: Sogamoso, Weir 167 (NY); Choco: Bank of Río San Juan, near Andagoya, 60 m, 27 Apr 1939, Killip 35381 (FH); Cundinamarca: Río Chico, Apollinaire s. n. (G); Vaupes: Río Apaporis, Raudal de Jerijerimo, Mar 1951, Schultes 11755 (FH, NY).

VENEZUELA. Barinas: Along Río Caparo, 2-4 km up river, 100-200 m, Liesner 9435 (MO); Bolivar: Salto Para, Río Caura, 200 m, 15 Jan 1977, Steyermark et al. 113025 (MO); Sucre: Río Sabacual-Guarauno, 8 Oct 1970, Bermudez A-00023 (MO).

GUYANA. Esequibo: Camria Fall, River Cuyuni, Richards 848 (NY).

ECUADOR. Esmeraldas: 15 km NE of Muisine, SW of Esmeraldas, 130 m, 16 Sep 1982, Steere et al. 25582 (G, NY); Morona Santiago: Misión Bomboiza, 800 m, 23 Apr 1973, Holm-Nielsen 4179 (MO); Napo: At Añangu, S shore of Río Napo (ca 75 km E of Puerto Francisco de Orellana - "Coca"), 245-325 m, 29 Jul 1985, Churchill & Sastre 13789 (NY), Hotel Jaguar, ca 50 km below Puerto Mishahualli, 400 m, 11 Jan 1981, Steere E105 (NY); Los Ríos: Río Palenque Science Center, 47 km S, by rd., of Sto. Domingo, 8 Jul 1984, Crosby 14743 (MO, NY), Hacienda Clementina, Mumbe, 130 m, 27 Jan 1947, Harling 2117 (NY).

PERU. Amazonas: Chacapoyas, Mathews s. n. (G); Huanuco: Cuevas de las Lechuzas, Tingo María, 700 m, 6 Jun 1977, P. & E. Hegewald 8288 (NY); San Martín: Tarapoto, Spruce 1333 (G, NY).

BRAZIL. Acre: Serra da Moa, 30 Apr 1971, Maas et al. P12660 (FH, MO, NY); Amazonas: Vicinity of Manaus, IgarapéIpixuna, Lower Rio Negro opposite Manaus, igapó, 1 Apr 1971, Prance et al. 11266 (FH, MO, NY); Bahia: Itabuná plantations of CEPLAC, 24 Jan 1980, Vital 8653 (MO); Minas Gerais: Ilheu, 200 m, 27 Aug 1930, Mexia 5003-A (G, MO); Pará: Rio Mojú, 20 Jul 1965, Pires 9929

(NY); Paraná: Foz do Iguacu, Parque Nacional do Iguacu, 100-200 m, 22-23 Sep 1984, Vital & Buck 12011 (NY); Santa Catarina: Tubarão, Sep 1890, Ule 83 (NY), Morretes, Rio Sapitanduva, 50 m, 25 Aug 1976, Hatschbach 38857 (MO); São Paulo: Biological Station Mogi Guacu, 25 Jan 1977, Vital 6917 (MO).

BOLIVIA. Beni: Along low banks of the Río Yata ca 40 km WSW of Guayatamerin, 5 Feb 1978, Reese 13021 (NY); Pando: Río Mapiri, 450 m, 1 Oct 1901, Williams 1999 (NY).

PARAGUAY. Caaguazu: Coronel Oviedo, 16 Oct 1984, Bordas 131 (NY); El Chaco: Río Paraguay, 13 Sep 1893, Lindmann B332 (NY); Paraguari: Parque Nacional Ybycui, along trail to mirador, above administration area, 200 m, 4 Oct 1984, Buck 11821 (NY).

Discussion. Neckeropsis disticha is recognized by the smooth or crisped leaves, not undulate, and oblong or slightly ovate leaf base. In populations of Neckeropsis disticha two growth forms can occasionally be observed, those with flat, smooth leaves and those with crisped, twisted leaves. Neckeropsis inundata is considered an aquatic form of N. disticha, since specimens collected in water or in very wet conditions tend to have very spaced leaves as is observed the type of N. inundata. Herzog characterized Neckeropsis microtheca by a smaller capsule and reduced peristome. Examination of the type showed that the plant material studied by Herzog was a poorly developed specimen. Therefore it is considered conspecific with N. disticha.

Within the section Neckeropsis, N. disticha might be related to two other species that also lack auricles. Those are N. fleischeri (Dixon) Touw and N. semperiana (Hampe ex C. Müller) Touw from Southeast Asia.

Descriptive morphology of the Thamnobryaceae

1. Growth form and ramification. The plants of the genera in the Thamnobryaceae are differentiated into plagiotropic and orthotropic shoots (Fig. 21). The plagiottropic shoot is mostly covered by scale-like leaves which seem to lack chlorophyll. The orthotropic shoot, which is usually produced sympodially, has an unbranched basal part and branched distal part. The unbranched part is commonly referred to as stipe. The branched part is known as the secondary stem. The branches and leaves are placed in one plane of orientation, at a right angle to the direction of incident light. According to Richard's (1984) classification of growth-forms of tropical bryophytes, the Thamnobryaceae falls into feather-forms. In this category the primary stem or plagiotropic shoot (Fig. 21 a) adheres to a substrate (tree trunks, rock-faces and other sloping surfaces) and the secondary stem (Fig. 21 c-f) is dorsiventrally pinnately branched.

Touw (1971) characterized the ramification pattern of the Hypnodendraceae into three categories, pinnate, palmate and umbellate (Fig. 22). In pinnate ramification, the stipe and branches are in the same plane. Branches oriented at a right angle to the erect stipe and with a stronger development toward the base are characterized as palmate. Umbellate ramification is that one in which all the branches are of equal strength and point in all directions. Pinnate ramification is observed in all the genera of the Thamnobryaceae but is less frequent in Thamnobryum. Homalia, Homaliodendron and Pinnatella show only pinnate ramification. Palmate and umbellate are found in Porotrichum and Thamnobryum (Fig. 22 b-c). In Porotrichum palmate and pinnate ramifications are more frequent than the umbellate type.

Fig. 21. Growth habit in Thamnobryaceae. a, plagiotropic shoot; b, orthotropic shoot; c, branches of 3rd degree; d; branches of 4th degree; e, flagelliform branches from apex; f, axillary flagelliform branch.

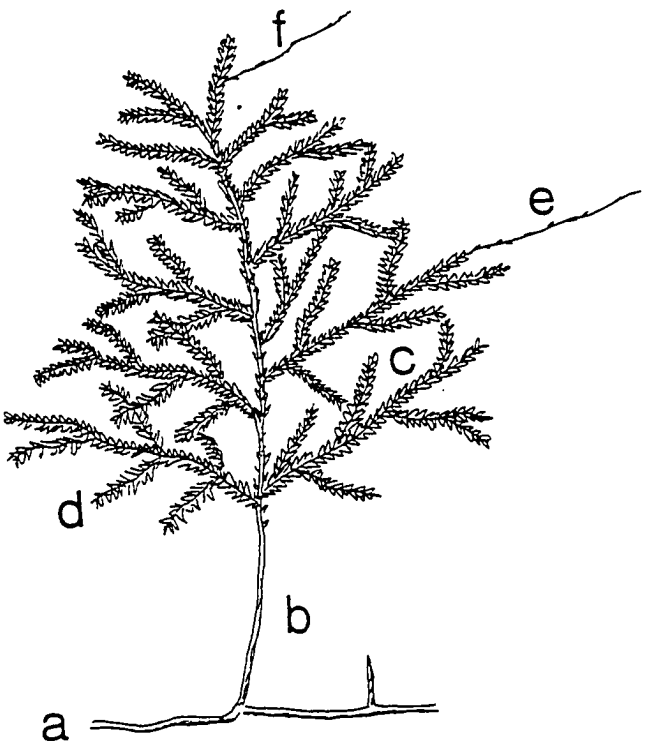
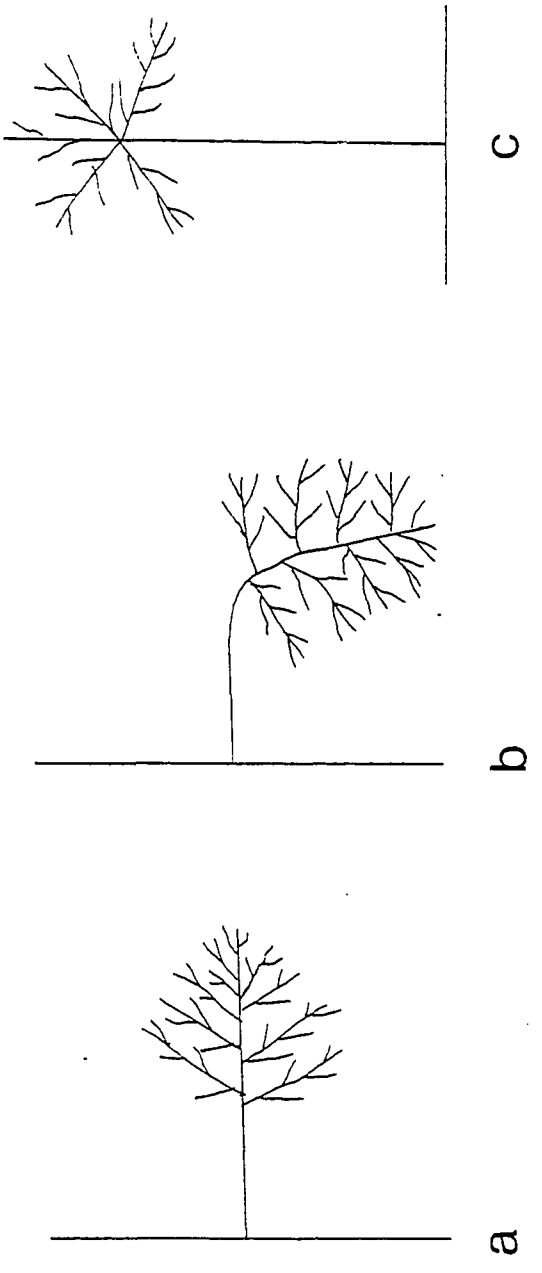


Fig. 22. Branching pattern in the Thamnobryaceae. a, pinnate; b, palmate; c, umbellate.



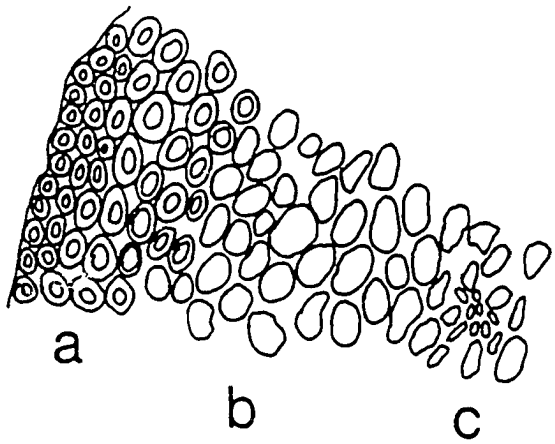
Flagelliform branches are commonly present in all the genera of the family (Fig. 21 e-f). These may be produced at the tips of the branches or axillary. No morphological differences are observed between the two. Both kinds bear reduced leaves. Rhizoids may be produced upon contact with a substrate. The leaves on these branches do not resemble any other leaves on the plant. In other mosses the leaves of the flagelliform branches may be equal to those borne by the primary stem, e.g., in Squamidium (Allen & Crosby, 1986).

2. Stipe anatomy. In the Thamnobryaceae the stipe is circular to elliptic in cross-section (Fig. 23). It consists of a small central strand, a cortical zone and peripheral cells. The central strand is formed by small irregularly hexagonal cells. A many layered cortical zone composed of large parenchymatous cells surrounds the central strand. The cortical zone abruptly changes into several layers of small extremely incrassate cells which form the outer layers of the stem. Throughout the family the stipe morphology is fairly uniform with the exception of Homalia and Homaliodendron that do not have a central strand. Variation otherwise resides in the number of cells that compose each layer. This type of stipe anatomy is found also in some genera of supposedly related families, such as the Hypnodendraceae (Touw, 1971).

3. Branch primordia. These are very rare or absent along the stipe, but common along the upper part of the stem. The branch primordia are covered by foliose pseudoparaphyllia. These are mostly spreading but very rarely tightly appressed.

4. Leaves. The leaves are differentiated into stipe and stem leaves in Homaliodendron, Pinnatella, Porotrichum and Thamnobryum. Homalia is an exception since the stipe is not developed; only juvenile leaves are observed at the base of the stem. Two kinds of stipe leaves, appressed and spreading are present

Fig. 23. Stem cross-section of Thamnobryum fasciculatum (Maxon 767, FH), x400. a, epidermal cells; b, cortical cells; c, central strand.



in the family. The appressed stipe leaves are mostly obovate, abruptly apiculate and have a straight insertion line. These are found in Homoliodendron and some species of Porotrichum. Spreading stipe leaves display greater diversity in shape and orientation. In shape they may range from triangular, triangular-ovate to deltoid-subulate. The insertation line is V-shaped and leaf margins are recurved. In orientation they may range from spreading to squarrose. Pinnatella and some species of Porotrichum have this kind. In Thamnobryum and some species of Porotrichum the stipe leaves are spreading but from and erect base. In this case the insertation line is straight. Size of stipe leaves increases from the base of the stipe upwards, a gradual transition occurs from stipe to upper leaves. In many cases the transition is not gradual and a rather abrupt change in the leaf shape is observed at the area where branching starts. Secondary stem leaves exhibit mostly broader leaf bases at this area of transition.

Branch leaves are smaller than stem leaves. Size of branch leaves decreases toward the branch tip and side branches have even smaller leaves. In weekly ramified plants the branch leaves are larger than in those with a strong ramification. Stem and branch leaf shape is an important criteria for specific distincitions in most genera of this family.

5. Margins. Leaf margins in the family are plane with the exception of some species of Porotrichum which have recurved margins at the leaf base. Serrated margins are common in many species of all genera in the Thamnobryaceae.

6. Costa. In cross-section the costa is not internally differentiated in the members of this family. Costa width is a reliable criteria to separate the genera. For example, Pinnatella and Thamnobryum are characterized by a broad and stout costa. A slender costa is typical of Porotrichum and Homaliodendron. Homalia exhibits a short-double or single costa.

7. Cells. Leaf cells have a small papilla at their ends in many species of Porotrichum and Thamnobryum. In Pinnetella the leaf cells bear 1-2 small papilla over the lumina. Differences in cell shape are important generic distinctions in this group. In all species of Porotrichum cells from apex to leaf base grade from rhomboidal, long-hexagonal to rectangular. Thamnobryum and Homaliodendron exhibit shorter apical cells than Porotrichum. Rounded to hexagonal cells are typical of Pinnatella. Alar cells may be differentiated in some species of Porotrichum.

8. Gametangia. The genera in the Thamnobryaceae are dioicous and no sexual dimorphism was observed. Both perigonia and perichaetia develop along the main stem and branches, never on the stipe. Unfertilized perichaetia have fairly small leaves, but after fertilization perichaetial leaves expand.

9. Sporophytes. Long exserted capsules are characteristic of all the genera in the family. The peristome is considered a hypnoid-peristome. Two basic peristome morphologies are observed in the family. In Thamnobryum fasciculatum, as in some species of Porotrichum and Homalia, the exostome teeth are broadly lanceolate abruptly tapering toward the apex (Fig. 24). The apical section of the teeth tends to be hyaline or of a lighter color than the base. Exostome teeth are cross striate or cross striate with overlying papillae at the base. At the apex, teeth are only papillose. In this type the endostome segments are papillose and perforate, cilia are well developed (Fig. 25). In some species of Porotrichum, as in P. longirostre, the exostome teeth are lanceolate and striate with overlying papillae (Fig. 26). Endostome segments are also papillose and perforate, but cilia may be rudimentary. In both types the papillae may be simple or branched. Homaliodendron also exhibits this type of peristome. The back of the exostome has the characteristic large trabecula of a hypnoid peristome.

Fig. 24. Scanning electron micrograph of peristome of Thamnobryum fasciculatum (Williams 1980, H). A, general view of exostome, x200; B, detail of upper region of exostome region, x800; C, detail of base of exostome, x800; D, detail of mid-portion of exostome, x800.

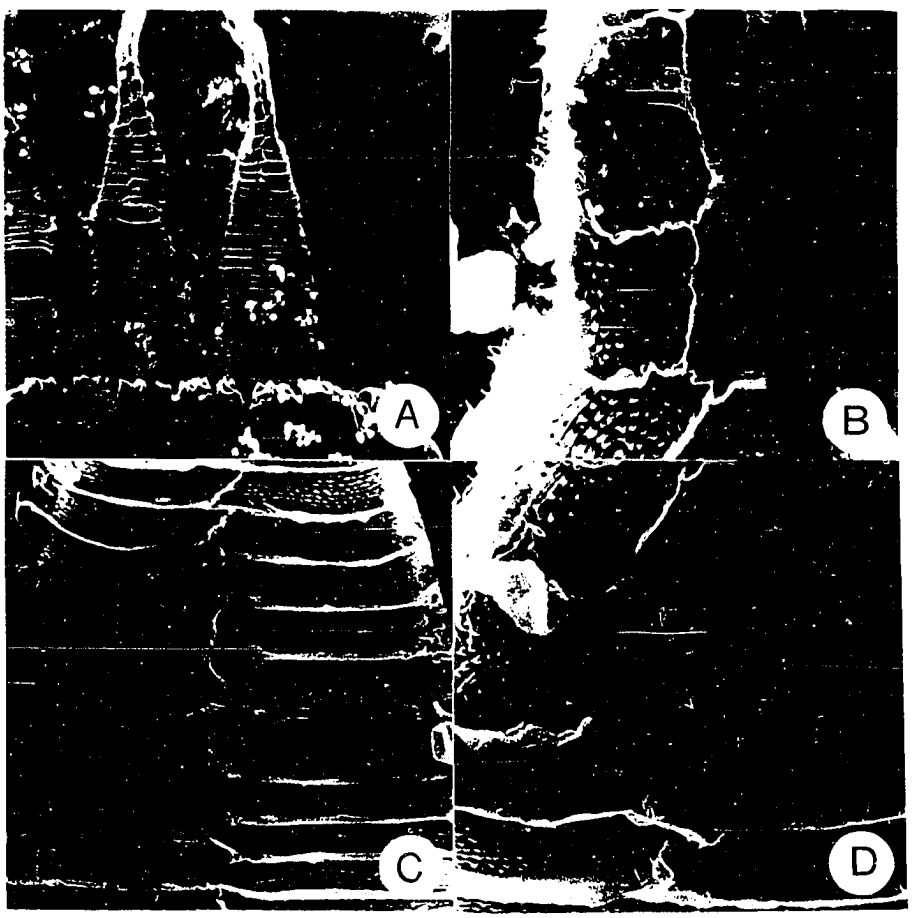


Fig. 25. Scanning electron micrograph of peristome of Porotrichum lancifrons. A, general view of exostome and endostome, x300; B, detail ventral view of exostome, x650; C, exostome toward base, x650: d, upper area of exostome, x650.

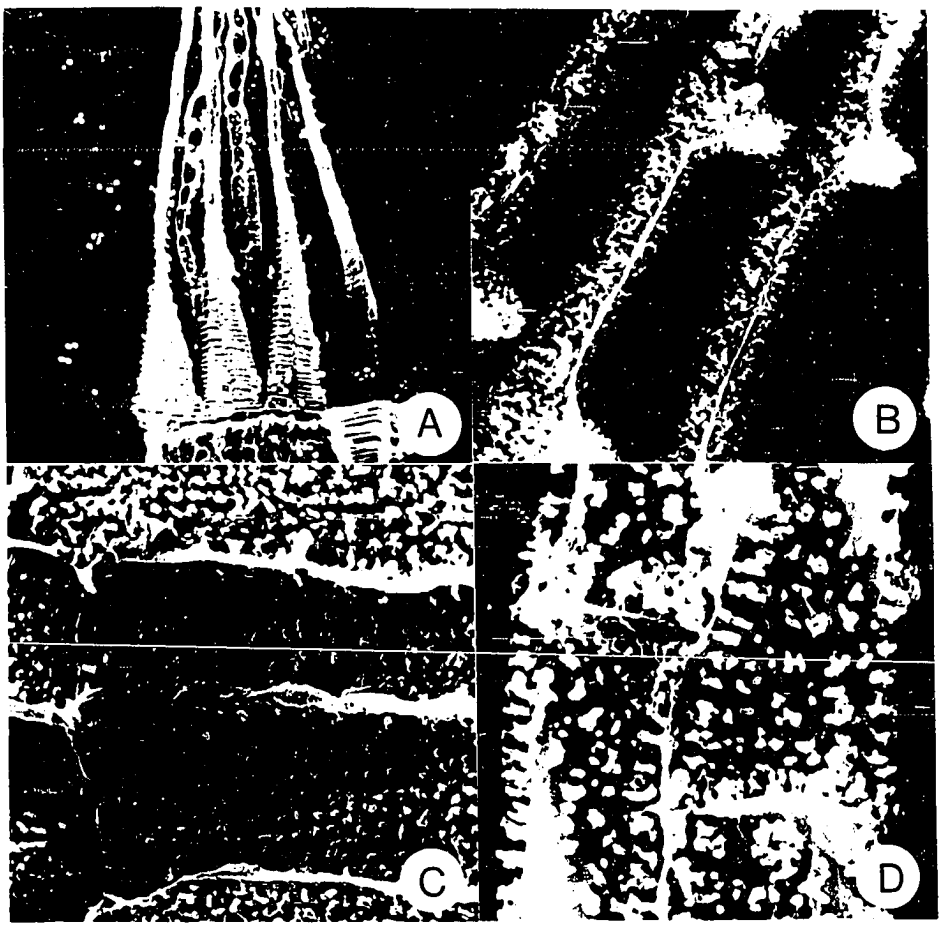
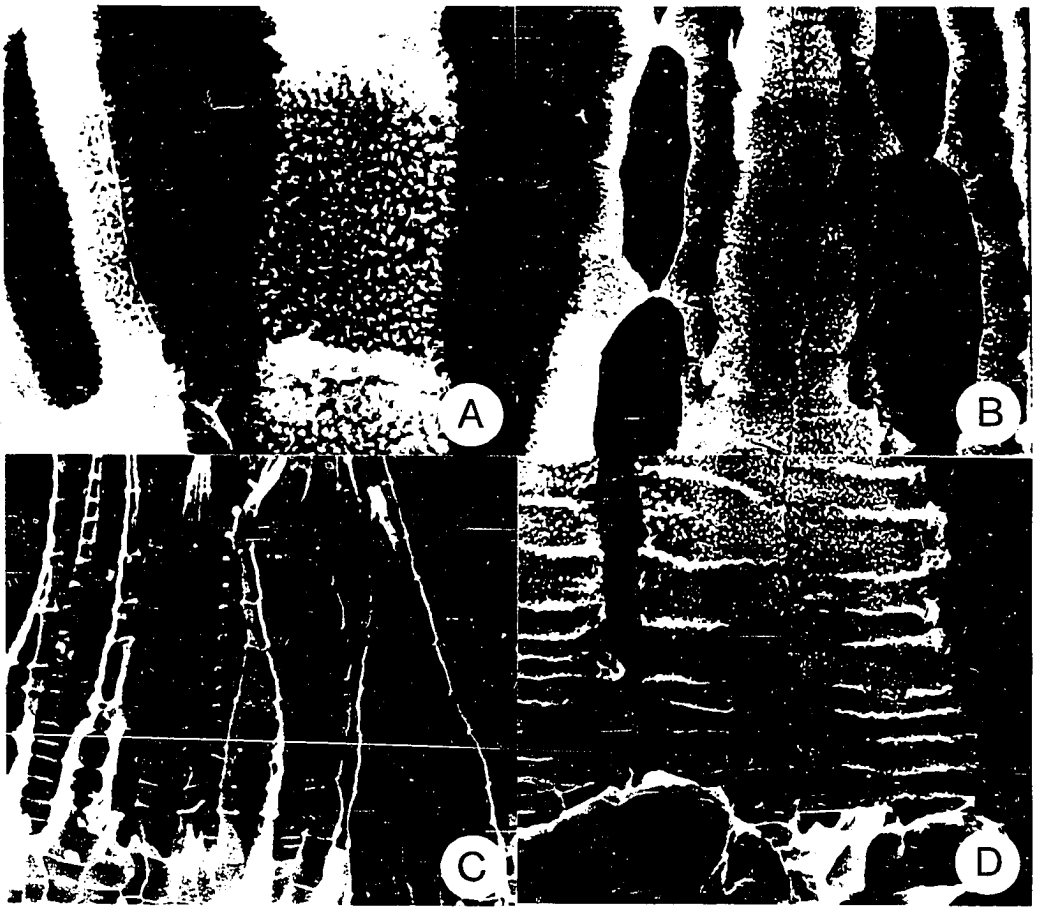


Fig. 26. Scanning electron micrograph of peristome of Porotrichum longirostre (Allioni 568, H). A, back of exostome, x650; b, exostome, detail of upper region, x650; c, general view of exostome and endostome, x100; d, exostome, detail of basal area, x650.



Phylogenetic considerations

In Buck and Vitt's (1986) familial classification for pleurocarpous mosses, the order Hypnales includes six superfamilies. In this classification the Thamnobryaceae, Hypnodendraceae, Pleuroziopsidaceae and Pterobryellaceae were grouped into the suborder Hypnodendrineae. All these families are characterized by a dendroid (stipitate) habit and coarsely serrate margins of stem leaves. They are placed in the Hypnales by their exostome teeth exhibiting shoulders and cross-striate ornamention which are defining features for the Hypnales. As the Hypnodendraceae and Pterobryellaceae share the same dendroid habit and serrate leaf margins they are considered the sister groups for the Thamnobryaceae.

Character analysis

1. Growth form and habit. The Thamnobryaceae are characterized by a primary creeping stem, a stipe and a distal branched part. The stipitate dendroid habit is typical of the members of the Hypnodendrineae, but the primary creeping stem is a unique feature for the Thamnobryaceae. Homalia is the only member of the family that does not have a stipe, however, it could be interpreted that it was lost. The position of Homalia in the family should receive further attention since present placement is based on material studied from the neotropics.

2. Complanate stem and leaves. Complanate stems with flat, spreading leaves is characteristic of Pinnatella, Porotrichum, Homaliodendron and Homalia. Thamnobryum and Handeliobryum as well as the other families in the Hypnodendrineae do not exhibit complanate stems, but instead show spreading leaves. Therefore complanate stems and erect-spreading leaves are a derived condition within the Thamnobryaceae.

3. Costa. In Thamnobryum, Handeliobryum and Pinnatella the costa is stout and broad. The Hypnodendraceae and Pterobryellaceae exhibit the same pattern. A slender costa observed in Porotrichum and Homaliodendron is derived within the family.

4. Lamina. A bistratose lamina is present only in the genus Handeliobryum, and this considered derived.

5. Cell pattern. Except Pinnatella that has papillae over the lumina, other genera in the family are papillose by projecting angles. The Hypnodendraceae and Pterobryellaceae are characterized by the latter feature also. Therefore papillae over the lumina are the derived feature.

6. Intramarginal bands. Linear cells forming an intramarginal band is a unique feature for Pinnatella.

7. Peristome. Exostome teeth of Thamnobryum and Homalia have shoulders, which is also present in Hynodendron and Pterobryella. Therefore the presence of lanceolate exostome teeth is considered a derived condition. This character is observed in Homaliodendron, Pinnatella and Porotrichum. No sporophyte is known for Handeliobryum. Its placement in the family is based only on vegetative characters. The costa and cell pattern is that of Thamnobryum. The only feature that separates the two genera is the bistratose lamina in Handeliobryum. In Porotrichum, Homaliodendron and Pinnatella the exostome teeth are papillose. This character is considered derived within the family since in the outgroup the exostome teeth are cross-striate.

Thamnobryaceae Margadant & During, Beknopte Fl. Ned. Blad- en Levermossen 443. 1982. Type. Thamnobryum Niewland, Am. Midl. Naturalist. **5**: 50. 1917.

Robust to small plants, dull or shiny, mostly dendroid, complanate, often with flagelliform branches. Axillary hairs with short-quadrate stalk cell and long rectangular apical cells; paraphyllia absent; pseudoparaphyllia filamentose to foliose. Primary stem creeping, sparsely or abundantly covered by reddish rhizoids; in cross-section with mostly elliptic to irregularly round, small, incrassate outer cells surrounding large, thick-walled cells, central strand absent or present; leaves erect-appressed to erect spreading, deltoid, lanceolate, obovate-subulate to oblong-ligulate, acute to broadly acute; margins entire to slightly serrate; costa absent or present; upper medial cells fusiform, rhomboidal, linear to rectangular, smooth to papillose. Secondary stem mostly perpendicular to substrate, in cross-section with irregularly round to elliptic, small, incrassate cells surrounding large, hexagonal cells, central strand usually present; stipe leaves erect, appressed, erect-spreading, spreading to squarrose, obovate, deltoid to lanceolate, acute; margins mostly entire, plane to recurved; costa single; upper median cells fusiform, linear to rectangular; stem leaves erect, erect-spreading to spreading, smooth or slightly plicate, oval, ovate, ovate-ligulate or oblong-ligulate, acute, broadly acute to obtuse; margins entire to serrate; costa single, slender to broad; apical cells round, oval, rhombic to fusiform, upper median cells rhomboidal, fusiform to linear, basal cells linear to rectangular, smooth or papillose at projecting angles or over lumina, sometimes pitted; branch leaves mostly smaller than stem. Dioicous. Perigonial leaves lanceolate, ovate-subulate, somewhat concave, acute; margins entire; costa absent; upper median cells fusiform to rectangular. Perichaetial leaves ovate to oblong-subulate, acute; margins entire to slightly serrate; costa absent or present, single; upper median cells fusiform to linear,

smooth or papillose by projecting angles, pitted or unpitted. Seta short to long, smooth; capsules oblong, cylindric to ovoid; exothecial cells short-quadrate to rectangular; stomata present; annulus absent or present; operculum conic; peristome double; exostome teeth lanceolate to broadly lanceolate, abruptly tapering toward apex, striate, papillose or striate with overlying papillae; endostome with a high basal membrane, segments lanceolate, smooth to papillose, perforate, cilia usually present or rudimentary. Spores spherical, papillose. Calyptra mostly cucullate.

The Thamnobryaceae are characterized by a primary creeping and an erect to pendent secondary stem. The basal part of the secondary stem is unbranched. Genera in this family have a hypnoid peristome. Exostome teeth may exhibit distinct shoulders like in Thamnobryum or be lanceolate like in most species of Porotrichum.

In this treatment five genera are include in the family. Handeliobryum, placed also in this family, does not occur in the area of study.

Key to the genera

1. Leaf margins deeply serrate at apex

1. Homaliodendron

1. Leaf margins not deeply serrate

2.

2. Apical cells of leaves usually round with 1-2 papillae over the lumina

2. Pinnatella.

2. Apical cells of leaves rhombic to fusiform, smooth or if papillose by projecting angles

3.

3. Stem leaves mostly asymmetric, costa short-double

3. Homalia.

3. Stem leaves mostly symmetric, costa single, well developed

4.

4. Plants usually dull; costa strong, mostly subpercurrent; apical cells mostly short-rhombic

4. Thamnobryum.

4. Plants usually shiny; costa slender, mostly 1/2 to 3/4 of the leaf length; apical cells fusiform to long-rhomboidal

5. Porotrichum.

1. **Homaliodendron** Fleischer, Hedwigia **45:** 74. 1906. Type. Homaliodendron flabellatum (Smith) Fleischer

Plants dendroid, mostly irregularly branched, flagellate branches present, light to dark green, slightly glossy. Primary stem creeping, in cross-section with small, thick-walled outer cells surrounding large inner cells, central strand absent; leaves triangular, acute; margins entire; costa single, 1/2 to 1/4 of leaf length; apical cells fusiform, upper median cells irregularly rectangular, pitted; basal cells rectangular, pitted. Secondary stem erect to perpendicular to substrate, stipitate, upper part irregularly branched to pinnate; axillary hairs 4-5 cells long, stalk cell quadrate, short, golden; paraphyllia absent; pseudoparaphyllia foliose. Stipe leaves distally triangular to lanceolate, erect-appressed; secondary stem leaves and branch leaves ovate-oblong, stem leaves 2-3 times larger than branch leaves, erect-spreading to spreading, apex dentate, teeth mostly multicellular, leaf insertation V-shapped or straight; margin plane, slightly folded at distal base;

costa single; 1/2 to 3/4 of the leaf length, in cross-section with undifferentiated cells; apical cells rhombic, upper median cells long rhomboidal, pitted, basal cells rectangular, pitted. Dioicous. Perigonial leaves oval, concave. Outer perichaetial leaves oval, short acuminate; inner ones ovate to oblong, gradually or abruptly subulate; margins entire to serrate. Setae mostly short, capsule ovoid to cylindric; exothecial cells short-rectangular, rectangular to hexagonal; stomata present, phaneropore; operculum conic; annulus absent; peristome double, exostome teeth lanceolate, faintly striate; endostome with a low basal membrane, segments lanceolate, papillose, cilia absent. Spores spherical, papillose.

The name refers to the flat dendroid habit, typically present in most species of this genus. Homaliodendron is also characterized by asymmetrical leaves with deeply serrate apices. It is placed in the Thamnobryaceae by the stipitate dendroid habit and the exostome teeth with distinct trabeculae at back. The exostome teeth are similar to the papillose teeth of some Porotrichum species.

Homaliodendron scalpellifolium which is known from Southeast Asia exhibits chromosome counts of 10 (Fritsch, 1982). This is the only chromosome count reported for the genus. Homaliodendron is more diverse in Southeast Asia.

1. **Homaliodendron flabellatum** (Smith) Fleischer, Hedwigia **45:** 74. 1906.

   Hookeria flabellata Smith, Trans. Linn, Soc. **9:** 280, pl. 23, f. 2. 1808; Neckera flabellata (Smith) Mitten, J. Linn. Soc., Bot. suppl, **1:** 118. 1859. Type. India occidentali.

   Pterogophyllum decompositum Bridel, Bryol. Univ. **2:** 764. 1827; Homaliodendron decompositum (Bridel) Wagner, Bryologist **55:** 144. 1952, **syn. nov.** Type. Hispaniola. Desvaux s. n. (holotype, B; isotype, slide in NY!).

Neckera mohriana C. Müller, Linnaea **38:** 646. 1874; Homaliodendron mohrianum (C. Müller) Fleischer, Hedwigia **45:** 77. 1906. Type. Mexico. Mirador, Mohr s.n. (isotype, NY!).

Porotrichum grandidens C. Müller, Hedwigia **37:** 243. 1898; Homaliodendron grandidens (C. Müller) Brotherus, Nat. Pfl. **1**(3): 851. 1906. Type. Haiti. Bois de Furcy, 1515 m, Aug 1891, Picarda s. n. (n. v.) (Fig. 27 a-f).

Plants 4-10 cm tall, dendroid; primary stem leaves triangular, 1.0 mm long, apical cells 26 um long, 8 um wide, upper median cells 26-39 um long, 8 um wide, basal cells 26-52 um long, 8 um wide. Secondary stem leaves oblong-ligulate, 3.0-4.0 mm long, 1.0-1.5 mm wide; apical cells 21-26 um long, 8-13 um wide, 39-65 um long, 8-10 um wide, basal cells 52-92 um long, 6-10 um wide. Sporophytes not seen.

Distribution and Ecology. (Fig. 28). Homaliodendron flabellatum is a widespread species in Southeast Asia. In the neotropics it is known from Mexico, Guatemala, Costa Rica, Cuba, Jamaica and Dominican Republic. It occurs in montane forests from 1000-3600 m.

Representative specimens examined. MEXICO. Oaxaca: Juárez Mountains, 21 Dec 1962, Sharp s. n. (NY); Veracruz: Near Jalapa, 28 Jun 1908, Pringle 15152 (FH), Jalapa, Deepe et al. s. n. (NY).

GUATEMALA. Zacapa: Upper reaches of Río Sitio Nuevo, 1500-1800 m, 25 Jun 1942, Steyermark 43229 (FH, NY).

Fig. 27. Homaliodendron flabellatum. a, growth habit, showing flagelliform branches, x1; b, branch, x12; c, stem leaf, x40; d, stem leaf upper median cells, x400; e, stem leaf upper margin, x400.

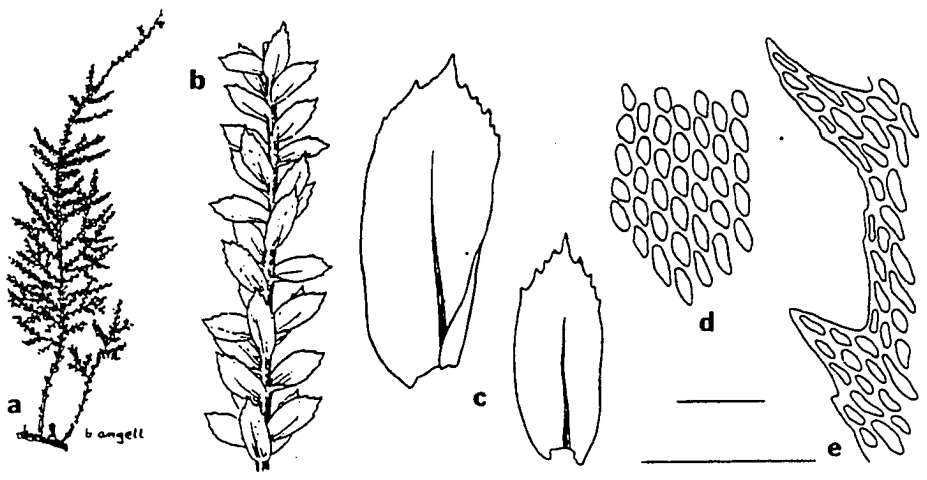
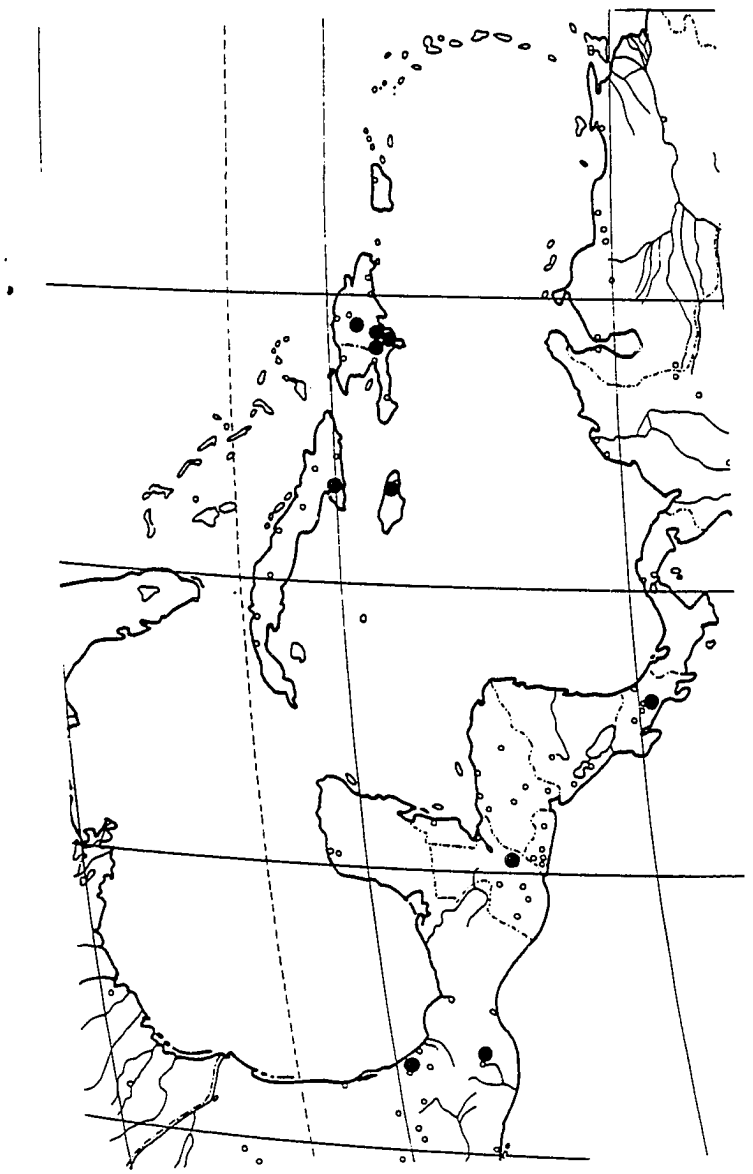


Fig. 28. Map of neotropical distribution Homaliodendron flabellatum.



COSTA RICA. San José: Copey valley, ca 30 km S of Cartago, 2000 m, 4 Feb 1979, Griffin et al. B 107 (NY).

CUBA. Santiago de Cuba: Sierra Maestra, northern spur of Pico Turquiño, 1850 m, 16 Apr 1915, Ekman 5468 (FH, NY).

JAMAICA. Portland: Lower eastern ridge of Mossman's Peak, 1600-1700 m, 30 Jun 1926, Maxon 9651 (FH, NY), in forest N of Portland Gap, 1727 m, 10 Aug 1966, Crosby 3522, 3532 (MO).

DOMINICAN REPUBLIC. Independencia: 4 km S of El Aguacate on road to Pedernales, 1300 m, 21 Mar 1981, Buck 4699 (NY); Pedernales: Las Abejas, 52 km N of port of Cabo Rojo on Alcoa road, 3600 m, 7 May 1982, Buck 8347 (NY); Vega: S bank of Río Los Guanos, just above confluence with Río de la Izquierda, 1100-1200 m, Jul 1967, Norris et. al. 5137 (NY).

Discussion. In the neotropics Homaliodenron flabellatum occurs in lower montane and montane forest ranging from 1400-1900(3000) m in Central America and the West Indies. It seems not to be widespread in the West Indies, since there is no record of material from Puerto Rico or the Lesser Antilles. It has commonly been mistaken with Porotrichum lancifrons and other species of Porotrichum, from which it can be distinguished by the oblong-ligulate leaf shape, short apical cells, and mostly erect-spreading leaves. This taxon has not been found with sporophytes in the New World but in Asia, where the genus is more diverse, it is frequently found bearing sporophytes. Flagelliform branches were commonly found in the material studied.

2. **Pinnatella** Fleischer, Hedwigia, Hedwigia **45:** 79. 1906. Type (chosen here). Pinnatella rotundifrondea (C. Müller) Fleischer

Mostly slender to medium-sized plants, yellow green to dark green, usually dull, unbranched to regularly pinnate, dendroid. Axillary hairs with a short-quadrate stalk cell and long rectangular apical cells; paraphyllia absent; pseudoparaphyllia foliose. Primary stem creeping, in cross-section with mostly elliptic, rounded to oval incrassate cells surrounding large irregularly hexagonal cells, central strand absent; primary stem leaves erect-appressed to spreading, deltoid to lanceolate, acute to broadly acute; margins entire, crenulate to serrate; costa ending below apex to 3/4 of leaf length; upper median cells long rhomboidal to irregularly hexagonal. Secondary stem erect to perpendicular from substrate, leaves erect to slightly erect-spreading, oval, ovate, ovate-ligulate to ligulate, somewhat concave, acute, broadly acute to obtuse; margins entire, crenulate to serrate; costa strong, ending below apex to 3/4 of leaf length; apical cells oval, rounded to hexagonal, incrassate, upper median cells irregularly long rhomboidal to hexagonal, marginal cells irregularly short quadrate, transversely inserted with some bands of linear to rectangular intramarginal cells, basal cells irregularly rectangular, uni- to pluripapillose; branch leaves smaller, oval, ovate to ligulate, areolation same as stem leaves. Dioicous. Perichaetial leaves ovate-lanceolate. Seta short; capsule ovoid; stomata present; annulus somewhat differentiated; operculum conic short-rostrate; peristome double, exostome teeth lanceolate, gradually acute, papillose; endostome with a low basal membrane, segments papillose, cilia absent. Spores papillose.

As indicated in the name Pinnatella, this genus is characterized by a very small dendroid habit. Plants are typically dull and leaves slightly concave with

one or two papillae over the cell lumina. The cell pattern and strong costa places it close to Thamnobryum.

No chromosome counts are known for this genus. The greatest number of species known for this genus occurs otuside of the neotropics.

Key to species

1. Plants mostly regularly branched, dendroid; leaf apex broadly acute to obtuse
   1. P. minuta
1. Plants mostly irregularly branched, forming irregular strands; leaf apex acute
   2. P. callicostelloides

1. **Pinnatella minuta** (Mitten) Brotherus, Nat. Pfl. **1**(3): 857. 1906.

   Porotrichum minutum Mitten, J. Linn. Soc., Bot. **12**: 465. 1869. Type. Cuba. Wright 85 (holotype, NY!).

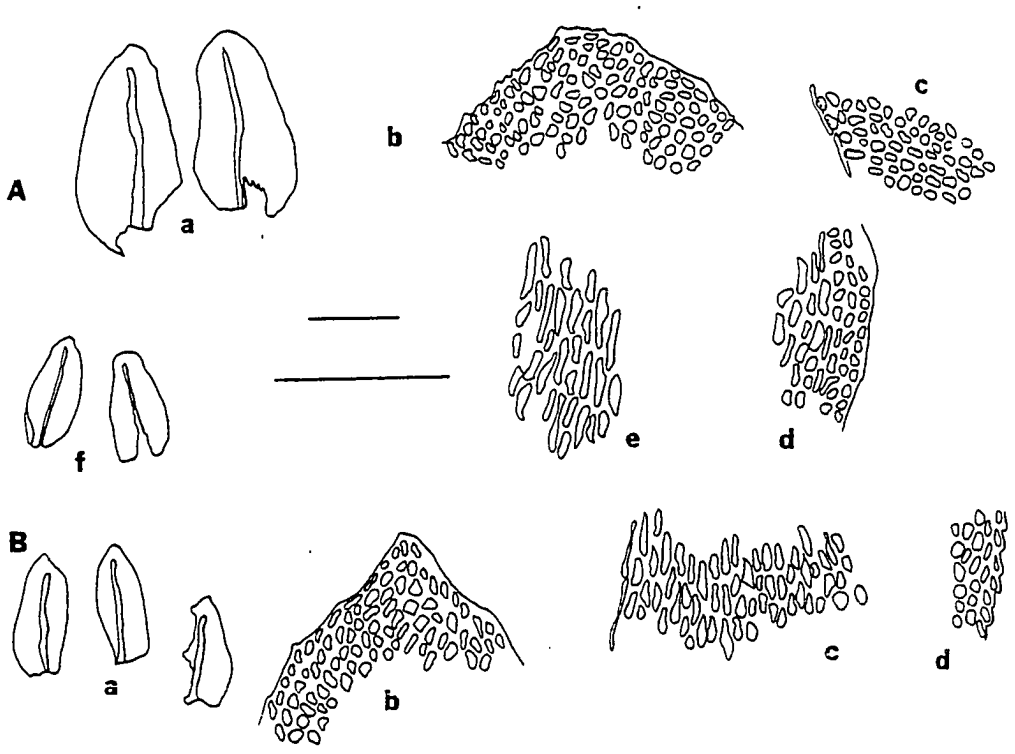
   Pinnatella jamaicensis Bartram in Orcutt, Jamaica Naturalist **1**: 17. 1928, **syn. nov.** Type. Jamaica. St. Elizabeth: Vicinity of Balaclava, 5 Aug 1927, Orcutt 2352 (holotype, FH!).

   Porotrichum paraguayense Brotherus, Bih. K. Svenska Vet. Ak. Handl. 26 Afd. **3(7)**: 42. 1900, **syn. nov.** Type. Paraguay. Pirapö, 4 Aug 1893, Lindman 271 (isotype, NY!).

   (Fig. 29A a-f).

Small, inconspicuous plants, to 3.0-4.0 cm tall, light green to yellowish, dull to slightly shiny, frondose. Flagelliform branches present, axillary or at shoot apex, very slender and thin. Axillary hairs (3)4-5 cells long, stalk cell

Fig. 29. A, Pinnatella minuta (Reese 15569, NY). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaf upper median cells, showing costa, x400; d, stem leaf basal cells, x400; e, stem leaf margin and alar cells, x400; f, branch leaves, x40; B, Pinnatella callicostelloides (Skottsberg 271, H-BR). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaf upper median cells, x400; d, stem leaf upper marginal cells, x400.



short-quadrate; paraphyllia absent; pseudoparaphyllia foliose. Primary stem creeping, in cross-section elliptic, with 4-5 outer layers of rounded to elliptic, incrassate cells surrounding 5-6 layers of inner large, thin-walled cells; leaves ovate tc ovate-lanceolate, 0.8 mm long, decurrent, acute; margins crenulate; costa single, 3/4 of leaf length; upper median cells irregularly rounded to irregularly rectangular; 10 um in diameter, uni- to pluripapillose, marginal cells transversely inserted, rectangular, cells toward base becoming elongate to rectangular, 15-34 um long. Secondary stem leaves erect-spreading, oval to ovate-ligulate, 1.0-1.4 mm long, symmetric to slightly asymmetric, slightly concave, somewhat twisted when dry, broadly acute to obtuse; margins crenulate; costa single, 3/4 of leaf length, one or two rows of cells extending over costa; apical cells oval to irregularly rounded, 10 um in diameter, marginal cells transversely inserted, upper median cells irregularly rounded to hexagonal , 13 um in diameter, thick-walled, uni- to pluripapillose, basal cells rectangular, 18-39 um long, 6 um wide; branch leaves ligulate; leaves on flagelliform branches erect, ligulate, size variable, obtuse. Sporophyte unknown.

Distribution and Ecology. (Fig. 30). This species is known from the West Indies, Central and South America. It grows on three trunks and rocks in lowland forests.

Specimens examined. CUBA. S. d., Wright 85 (NY).

JAMAICA. Trelawny: Vicinity of Windsor Cave, 140 m, 21 Apr 1981, Crosby 13905 (NY), Cockpit country, near St. Paul's, 13-18 Sep 1906, Britton 311 (NY), vicinity of Balaclava, 5 Aug 1927, Orcutt 2352 (FH).

DOMINICAN REPUBLIC. La Altagracia: Hill el Peñón de la Vieja Rufina, 24 km SE of Otra Banda on road to Punta Cana, 41 m, 29 Mar 1981, Reese 15569

(NY), 3 km of Boca de Yuma, along trail to Río Dulce, 30 Mar 1981, Reese 15593 (NY).

PARAGUAY. Itapúa: Pirapó, 4 Aug 1893, Lindman 271 (NY), Municipio Domingo Robledo, Salto Tembey on Río Tembey, near Yatytay, 200 m, 12 Oct 1984, Buck 12262A (NY).

Discussion. This is an easily overlooked species since it is so small and grows among other corticolous bryophytes. As pointed by Bartram (1949) this species may be less localized than the few collections of it indicate. Pinnatella jamaicensis is considered conspecific with P. minuta since the only difference noted was that of size. A character used by Bartram (1928) to separate the species was the presence of flagelliferous branches. I have found this feature to be variable and not satisfactory to segregate the two. Wagner (1951) also noted the difficulty in separating the two taxa but still kept them separate. The type of Pinnatella geheebii was not studied, but material from Africa assigned to that taxon was found to be similar to P. minuta.

2. **Pinnatella callicosteloides.** (Thériot) Brotherus, Nat. Pfl. ed. 2, **11:** 196. 1925.

Porotrichum callicostelloides Brotherus ex Thériot, Rev. Chil. Hist. Nat. **21:** 176. 1917. Type. Chile. Los Perales de Marga-Marga, Quebrada de los Canelos, Dusén 195 (isotype, H-BR!).

Pinnatella macrostica Brotherus in Skottsberg, Nat. Hist. Juan Fernandez **2:** 433. 1924, **syn. nov.** Type. Juan Fernandez. Quebrada de las Casas, 11 Feb 1917, Skottsberg 271 (holotype, H-BR!).

(Fig. 29B a-d).

Pale, green small plants, 2.0 cm tall, forming loose, irregular strands to sometimes slightly dendroid. Axillary hairs 2-3 cells long, stalk cell short-quadrate; paraphyllia absent; pseudoparaphyllia filamentose to foliose. Primary stem creeping, in cross-section with 3-4 layers of small incrassate cells surrounding 2-3 layers of large hexagonal cells, central strand absent; leaves spreading, deltoid, 0.5 mm long, acute; margins crenulate; costa ending below apex; upper median cells long fusiform 10-15 um long, papillose. Stipe leaves erect-spreading, deltoid, 1.0-1.5 mm long, acute; margins crenulate; costa strong, 3/4 of leaf length; apical cells rhombic, 10-15 um long, 4 um wide, upper median cells rhomboidal to fusiform, 15-30 um long, basal cells rectangular, 20-30 um long, papillose; stem leaves erect-spreading, oblong-lanceolate, 0.9-1.0 mm long, acute; margins plane, serrate; costa stout, 2/3-3/4 of leaf length; apical and upper median cells irregularly rhomboidal to irregularly rounded, 8 um in diameter, basal cells rectangular, 10-15 um long, alar cells irregularly short-rectangular, 1-2 buiging papillae over lumina. Sporophyte not observed.

Distribution. (Fig. 30). Pinnatella callicostelloides is known from Chile and Juan Fernández. It grows on rocks and tree trunks.

Specimens examined. CHILE. Los Perales de Marga-Marga, Dusén 195 (H-BR).

JUAN FERNANDEZ. Quebrada de las Casas, 11 Feb 1917, Skottsberg (H-BR).

Discussion. This species is recognized by the oblong lanceolate leaves with acute apices. The growth habit seems to be different from that of P. minuta. In P. callicostelloides plants form irregularly branched strands and P. minuta has a distinct dendroid habit.

Fig. 30. Distribution map of Pinnatella minuta and P. callicostelloides.

3. **Homalia** (Bridel) Bruch, Schimper & Gümbel, Bryol. Eur. **5**: 53. 1850 (facs. 44-45, Mon. 1), "Omalia" corr. Schimper, Syn. **471**, 1860. Type. Homalia trichomanoides (Hedwig) Bruch, Schimper & Gümbel.

Plants unbranched, irregularly branched to dendroid, mostly light green to dark green, very shiny. Primary stem creeping; leaves oblong-ligulate, asymmetric; margin slightly serrulate at apex, entire below; costa single, or double; apical cells irregularly rhombic, upper median cells linear, basal cells rectangular. Secondary stem mostly perpendicular from substrate, unbranched, irregularly branched to dendroid, sometimes short stipitate, complanate; axillary hairs 5-7 cells, stalk cell differentiated, golden; paraphyllia absent; pseudoparaphyllia filamentous. Secondary stem leaves erect-spreading, plane, asymmetric, oblong-ligulate, broadly acute, sometimes nearly obtuse to acute, ending in a short point; margins serrate to serrulate at apex, plane, distal margin sometimes slightly folded; costa single to short and double, 1/4 of leaf length, in cross section with undifferentiated cells; apical cells irregularly rhomboidal to rhombic, upper median cells linear, basal cells rectangular, pitted to slightly pitted. Dioicous. Perigonia on secondary stem amd branches; leaves lanceolate; margins entire, bordered by one row of rectangular cells; costa absent; apical cells rhomboidal, pitted, upper median cells rhomboidal, pitted, basal cells irregularly rectangular, sometimes inflated, thin-walled. Perichaetia on secondary stem and branches; leaves broadly ovate, abruptly subulate, margin serrate at apex; costa present; apical cells linear, upper median cells linear, basal cells rectangular, pitted throughout, thick-walled. Setae long; capsule oblong, neck narrow; exothecial cells mostly irregularly quadrate; stomata present, phaneropore; operculum conic; annulus not observed; peristome double, exostome teeth densely cross-striate,

hyaline and papillose above, trabeculate at back; endostome segments lanceolate from a high basal membrane, papillose above, keeled, perforate, cilia present. Spores spherical, smooth. Calyptra cucullate.

The name Homalia indicates a strongly flattened plant with branches in the same plane. The neotropical species may be recognized by a beautiful iridescent green color. Of the 13 species presently assigned to the genus only one occurs in the neotropics. The hypnoid peristome present in this genus suggests that if does not belong to the Neckeraceae. The placement of Homalia in the Thamnobryaceae is based mainly on peristome morphology.

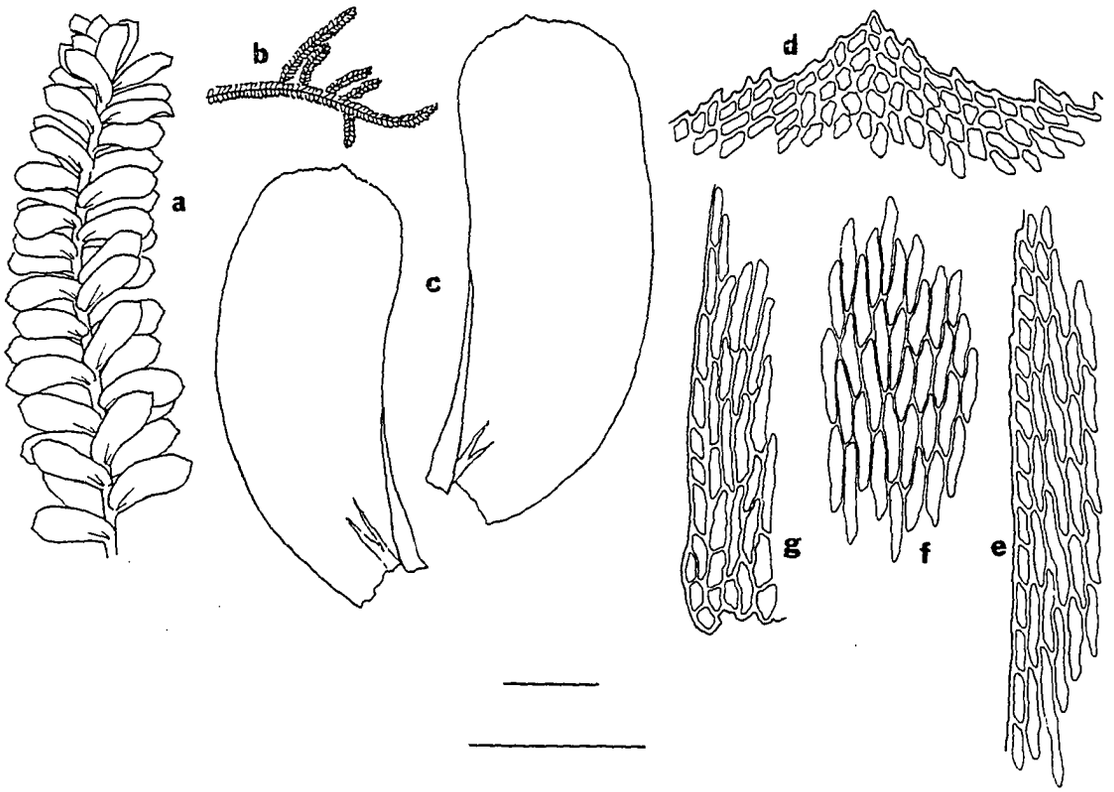
A chromosome count of 11 has been reported for H. japonica (Fritsch, 1982) and H. trichomanoides (Fritsch, 1982).

1. **Homalia glabella** (Hegwig) Bruch, Schimper & Gümbel, Bryol. Eur. **5:** 54. 1850 (facs, 44-45 Mon, 2).

Neckera glabella Hedwig, Spec, Musc. **231,** 1801; Neckera glabella (Hedwig) Weber & Mohr, Ind. Musc. Pl. Crypt. **3.** 1803. Type. Jamaica, Swartz (isotype, BM!). (Fig. 31 a-g).

Plants mostly 3.0-15 cm tall, secondary stem unbranched to pinnate; primary stem leaves 1.0-1.5 mm long; apical cells 18 um long, 8 um wide, upper median cells 52-70 um long, 6-8 um wide, basal cells 39-78 um long, 6 um wide. Secondary stem leaves oblong-cultriform, 2.5-3.5 mm long, 1.0-1.5 mm wide, apical cells rhomboidal, 52-65 um long, 21-26 um wide, upper median cells long hexagonal to long fusiform, 60-92 um long, 15 um wide, basal cells long hexagonal to linear, 78-100 um long, 15-21 um wide, slightly pitted. Perigonial leaves 1.1 mm long, 0.57 mm wide, apical cells 26 um long, 8-13 um wide, upper median cells 39-78

Fig. 31. Homalia glabella (Steere 5650, NY). a, branch, x12; b, habit, x1; c, stem leaves, x40; d, stem leaf apex, x400; e, stem leaf marginal cells, x400; f, stem leaf upper median cells, x400; g, stem leaf basal cells, x400.



um long, 6-8 um wide, basal cells 26-52 um long, 13 um wide, thin walled, inflated. Perichaetial leaves 2.2-2.4 mm long, 0.9 mm wide, apical cells 26-29 um long, 6-8 um wide, upper median cells 52-100 um long, 8 um wide, basal cells 52-92 um long, 8-10 um wide. Setae 1.5-2.0 cm long; capsule 2.0 mm long. Spores 13 um wide.

Distribution and Ecology. (Fig. 32). This species is known from Central America, the Caribbean and one locality in Venezuela. In the West Indies it has not been found in the Dominican Republic. The elevational range is from 20-2500 m, from the lowlands to cloud forests. It mostly occurs on shaded, wet limestone boulders; roots, and bark.

Representative specimens examined. MEXICO. Chiapas: Municipio de Cintalapa, SE of Cerro Baul on the border of the state of Oaxaca, 16 km NW of colonia Figaroa, 27 Apr 1972, Breedlove 24874 (MO); Puebla: Near Villa Juárez, 1180 m, 28 Mar 1945, Sharp 3181 (MO, NY); San Luis Potosi: 2 mi E of Xilitla, 900 m, 28 Dec 1953, McGregor 8067 (NY), Veracruz: Zacuapán, Apr 1908, Purpus 4302 (FH, MO, NY), Sierra de Chiconquiaco, between Santa Rita and Bella Luz, ca 40 km NW, 1750 m, 26 Jul 1979, Hermann 28839 (NY), 9 km NE of Huayacocotla, road to Zilacatipán, 1700 m, 13 Mar 1980, Juárez 1420 (MO).

GUATEMALA. Alta de Verapaz: Mountains along road between Tactic and the divide on road to Tamahú, 1500-1600 m, 1-7 Apr 1941, Standley 91483 (NY); Izabal: Along trail beginning from mile 33.23 between Dartmouth and Morales towards Lago Izabal, Mico Mt., 35-150 m, 7 Apr 1940, Steyermark 39056 (NY); Zacapa: Ravine bordering Quebrada Alejandria, summit of Sierra de las Minas, vicinity of finca Alejandría, 2500 m, 13 Oct 1939, Steyermark 29931 (FH).

Fig. 32. Distribution map of Homalia glabella.

HONDURAS. Atalántida: Lancetilla valley, near Tela, 20-66 m, 6 Dec 1927-20 Mar 1928, Standley 54597 (FH, NY); Francisco Morazán: Along abandoned silver mine road on Cerro El Tigre, SW of San Juancito, 1800 m, 29 Nov 1975, Richard et al. 3569 (MO, NY); Santa Barbara: Near El Mochito Mines, ca 3 km up trail leading N from Estadio San Juan, NW of El Mochito, 1330 m, 9 May 1966, Crosby 2786 (MO).

NICARAGUA. Jinotega: About 6 km N of Santa María Ostuma, just off Ruta Nacional, 3 km along road to Aranjuez, 1450 m, 6 May 1966, Crosby 2741 (MO).

COSTA RICA. Alajuela: Along the upper Río Sarapiqui, near Cariblanco and along the road to colonia Virgen del Socorro, 800 m, 21 Feb 1982, Burger et al. 11910A (NY), Santa María National Park, 1 km W of E end of Park, 7 km E of colored house at junction of road to Hacienda Santa María, 600 m, 8 Fe b 1978, Liesner 5203 (MO); Cartago: Valley of Río Reventazón, 9 km ENE of Turrialba near Pavones, 650 m, 30 Jan 1949, Holm et al, 1266 (G); Guanacaste: El Silencio, near Tilarán, 750 m, 13 Jan 1926, Standley et al. 44737 (FH, NY); Heredia: S slope Volcán Barba, ca 1 km WNW of Río Ciruelas, near where road 114 crosses stream and 8.2 km from San José de la Montaña, 1900 m, 3 May 1975, Crosby 9915 (MO); Puntarenas: Vicinity of The Inn at Quaker settlement of Monte Verde, 1200 m, 2 Feb 1966, Crosby 2479 (MO, NY); San José: SE slopes of Cerros de Zurqui, N of village of San Luis Norte, 17 NNE of city center of San José, 1840 m, 28 Mar 1973, Crosby et al. 6392 (MO).

PANAMA. Coclé: Alto Calvario, 7 km N of El Copé, 850 m, 19 May 1977, Folsom et al. 3310 (MO); Veraguas: 1.7 km along road leading E just above Escuela Agrícola, Alto de Piedras, 750 m, 18 May 1975, Crosby 10246 (MO).

CUBA. Santiago de Cuba: Yunque de Baracoa, Jul 1936, Carabia s. n. (FH), La Gran Piedra, 1.5 km SE of peak, 1000 m, 3 Apr 1982, Buck 7601 (NY).

JAMAICA. Manchester: Fairfield, 4-6 Sep 1908, Britton 860 (NY), Moy Hall, Nov 1928, Orcutt 6832 (MO, NY); St. Thomas: Vicinity of House Hill, Sulphur River, 450-500 m, Maxon 9402 (FH, NY); Corn Puss Gap and vicinity, ca 9 mi N of Bath, on trail to Port Antonio, 550 m, 9 Apr 1981, Crosby 13647 (MO, NY).

PUERTO RICO. Arecibo: Utuado, 12 Mar 1887, Sintenis F123 (G); Fajardo: NW side of Sierra de Liquillo, above El Verde, 26 Jan 1940, Steere 6312 (MO, NY), Caribbean National Forest, Luquillo Division, El Yunque recreational area, Big Tree Trail to La Mina Falls, 500 m, 5 Mar 1981, Buck 4089 (NY); Mayagüez: Old trail above upper Río Maricao, 30 Dec 1939, Steere 5650 (FH, MO, NY); Ponce: Ridge N of Río Doña Juana, N of Villalba, 18 Jan 1940, Steere 6013 (FH, MO, NY).

WINDWARD ISLANDS. Guadeloupe: no locality, Duss 55109 (NY).

VENEZUELA. Caracas: 1200 m, Jan 1846, Funck et al. 370 (NY).

Discussion. Homalia glabella is very easily recognized by the glossy green color, and broadly acute apex. It has been confused with Neckera villae-ricae Besch., but Homalia lacks a distinct folded distal margin, and it is dioicous. In Central America, 52% of the plants studied were female, 22% male and only 9% had mature sporophytes. Sterile plants were very rare with only 11%. In the Caribbean female plants also were more common (47%) but were followed by sterile plants (39%). Plants with sporophytes were not found among the sampled material in the Caribbean.

4. **Thamnobryum** Nieuwland, Am. Midl, Naturalist **5:** 50. 1971.

Thamnium Bruch, Schimper & Gümbel, Bryol. Eur. **5:** 211. 1852 (fasc. 49-51 Mon. 1), hom, illeg. Type. Thamnobryum alopecurum (Hedwig) Gangulee, Mosses of Eastern India and Adjacent Regions **5:** 1452. 1976.

Plants medium-sized to robust, dendroid, pinnate to sparsely branched, dark green to yellow-green, slightly shiny to dull. Primary stem creeping, in cross-section elliptic, with small, rounded incrassate cells surrounding large hexagonal cells, central strand present; leaves erect-spreading, deltoid to obovate-subulate; acute; margins entire; costa absent or present, short-double to single; upper median cells fusiform, linear to rectangular. Stipe mostly dark brown, in cross-section elliptic, with outer small cells surrounding thick-walled hexagonal cells, central strand present; leaves appressed with squarrose to spreading apices, or erect-spreading to spreading, broadly triangular to triangular-subulate, acute; margins entire; costa single; upper median cells linear, smooth to papillose at projecting angles, pitted to unpitted. Stem and branch leaves erect-spreading, slightly plicate when dry to smooth, ovate, ovate-lanceolate, ovate-oblong to oblong-ligulate, acute, broadly acute to obtuse; margins slightly serrate to serrate at apex, entire below; costa strong, subpercurrent, in cross-section undifferentiated; apical cells hexagonal, rhombic to rhomboidal, upper median cells linear to rectangular, basal cells linear to rectangular, smooth to papillose by projecting angles, pitted or unpitted. Dioicous. Perigonia leaves obovate-subulate, acute; margins entire; costa absent; upper median cells linear. Perichaetial leaves lanceolate to ovate-subulate, acute; margins entire; costa absent; upper median cells linear to rectangular. Setae long; capsule horizontal, cylindric, smooth;

exothecial cells quadrate to rectangular; stomata present, phaneropore; annulus present; peristome double, exostome teeth lanceolate, tapering toward apex, striate at base, becoming striate with overlying papillae, papillose at apex, trabeculate; endostome segments from a high basal membrane, papillose, perforate, cilia present. Operculum conic. Calyptra not seen. Mature spores not observed.

In the neotropics this genus is represented by two species. I am in agreement with the concept proposed by Robinson (1975) in his Mosses of Juan Fernandez Islands. This concept includes in Thamnobryum dull plants with strong costa and short leaf cells (i.e., hexagonal to rhombic in the apical region). Thus, Porotrichum fasciculatum is considered here to fit within the concept of Thamnobryum.

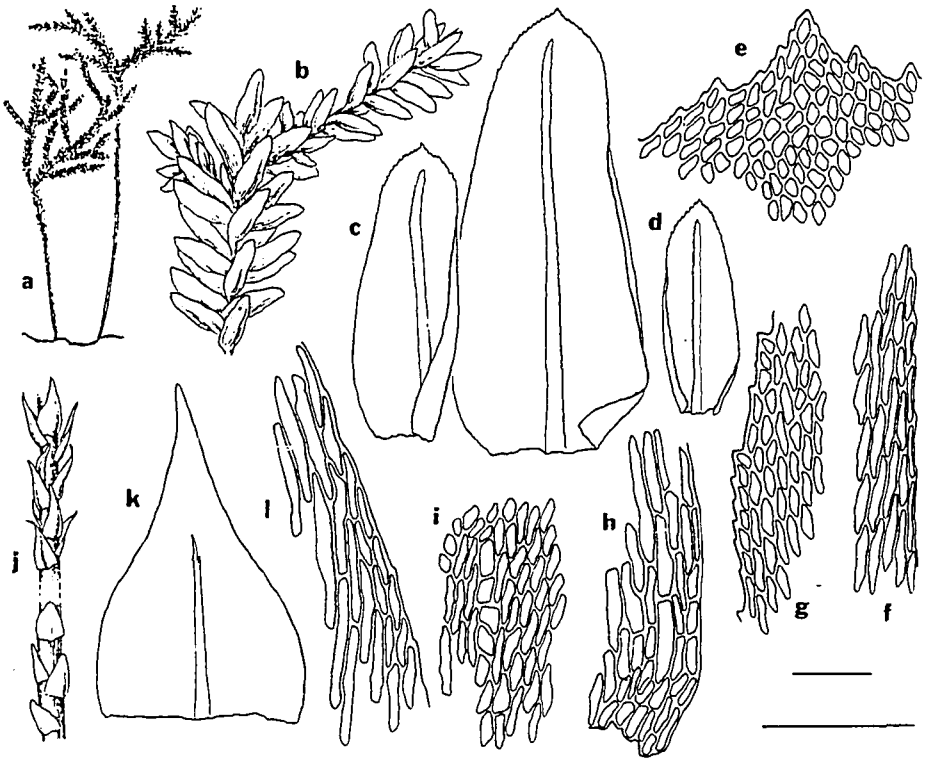
A chromosome count of 11 in Thamnobryum alopecurum is known for the genus (Fritsch, 1982).

Key to species

1. Plants robust; leaves when dry slightly plicate, complanate, ligulate to oblong-ligulate; apical cells mostly rhombic to rhomboidal
   1. T. fasciculatum
1. Plants small to medium-sized; leaves when dry smooth, somewhat concave, ovate to ovate-lanceolate; apical cells mostly hexagonal
   2. T. tumidicaule

1. **Thamnobryum fasciculatum** (Hedwig) Sastre, **comb. nov.** Hypnum fasciculatum Swartz ex Hedwig, Spec. Musc. 245. 1801; Thamnium fasciculatum (Hedwig) C. Müller, Hedwigia **37:** 260. 1898; Porothamnium fasciculatum (Hedwig) Fleischer, Musci Fl. Buitenzorg **3:** 927. 1908. Type. Jamaica, Swartz s.n. (isotypes, G!, H!, NY!). (Fig. 33 a-l).

Fig. 33. Thamnobryum fasciculatum (E. G. Britton, 80, NY). a, habit, dry, x1; b, stem and branch, x12; c, stem leaves, x40; d, stem leaf upper marginal cells, x400; e, branch leaf marginal cells, x400; f, stem leaf alar and basal cells, x400; g, stem leaf upper median cells, x400; h, stipe, showing leaves, x12; i, stipe leaf, x40; j, stipe leaf upper marginal cells, x400.



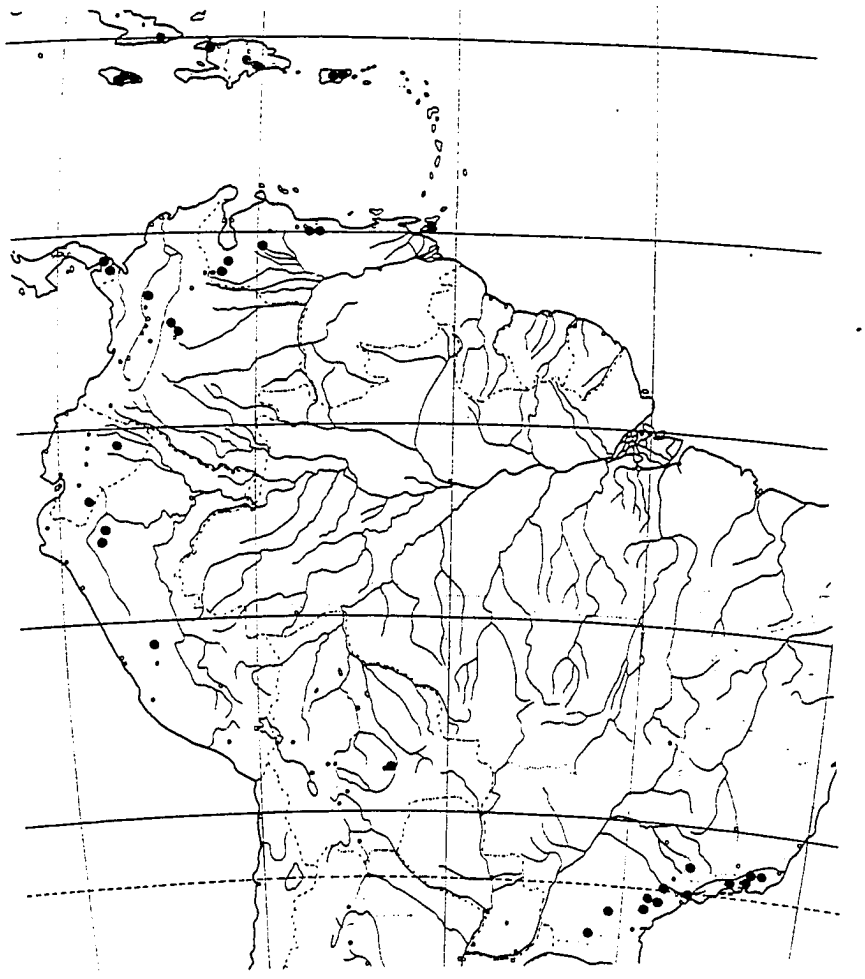
Plants robust, 5-15 (20) cm tall, dendroid, dark green to yellow green, slightly shiny, pinnately to irregularly branched. Axillary hairs 2-3 cells long, stalk cell short-quadrate; paraphyllia absent; pseudoparaphyllia small, foliose. Primary stem creeping, in cross-section elliptic, wiht 5-6 layers of small, thick-walled cells and 3-6 layers of inner large, hexagonal, thin-walled cells; leaves erect-spreading. obovate-subulate, 1.8-2.0 mm long, acute; margins entire; costa absent or present, short-double or single, 1/2-2/3 of leaf length; upper median cells fusiform to linear, 39-78 um long, 6 um wide. Stipe mostly pendant to perpendicular from substrate, dark brown; elliptic in cross-section, with 5-6 layers of small, thick-walled cells and 15-20 inner layers of thin-walled hexagonal cells, central strand present; base of stipe leaves erect-appressed when dry, erect-spreading when moist. broadly-triangular, becoming subulate on more distal stipe leaves, 2.0-2.5(3.0) mm long, apiculate to filiform; margins entire; costa single, 2/3 to 3/4 the leaf length; upper median cells linear, 57 um long, 6 um wide, slightly to distinctly popillose at projecting angles, pitted. Stem and branch leaves erect-spreading, slightly plicate when dry, ovate-oblong to oblong-ligulate, (2.5)3.4-4.0 mm long, 1.0-1.5 mm wide, obtuse, broadly acute to acute, apiculate; margin slightly serrate to serrate at apex, sometimes extending below apex; costa strong, mostly ending below apex, to sometimes 3/4 of leaf length, smooth at back, in cross-section undifferentiated; apical cells rhombic to rhomboidal, 21-26 um long, 8 um wide, upper median cells linear, 39-57 um long, 6 um wide, 2-3 rows of linear marginal cells, sometimes not clearly distinct, mostly longer than upper median cells, 60-100 um long, 4-6 um wide, basal cells linear, 60-92 um long, 4 um wide, slightly to distinctly papillose by projecting angles, slightly pitted. Dioicous. Perigonial leaves obovate-subulate, 1.5-1.7 mm long, acute; margin entire; costa absent; apical cells linear, 52-78 um long, 6 um wide, upper median

cells linear, 65-78 um long, 6 um wide. Perichaetia usually on branches, outer leaves triangular, 1.2-1.4 mm long, inner leaves ovate-subulate, 1.6-2.0 mm long, acuminate; margin entire; costa absent; apical cells rectangular, 52-100 um long, 6-8 um wide, upper median cells rectangular, 52-81 um long, 6-8 um wide, basal cells lax, irregularly rectangular, 39 um long, 8 um wide. Setae long, 2.0 cm, reddish-brown; capsule mostly horizontal, cylindric, 3.0 mm long, neck somewhat narrow and constricted; exothecial cells quadrate to hexagonal, becoming rectangular toward base; stomata present; annulus present, 2-tiered, reddish, thick-walled; operculum conic, long rostrate; exostome teeth dark orange, becoming hyaline toward the apex, lanceolate from a broad base, abruptly tapered toward apex, striate from base to 3/4 of length, upper part papillose; endostome pale, segments from a high basal membrane, keeled, perforate, papillose, cilia present. Calyptra not observed. Spores spherical, mature spores not observed.

Distribution and Ecology. (Fig. 34). This species grows mostly in very wet and shaded habitats, like on rock walls near cascades, or on rocks and soil by stream. The "frond" points down when growing on vertical surfaces, but on a flat surface this tends to be parallel to it. The species occurs at mid to low elevations in the West Indies and South America. In Central America it is only known from the Panama-Colombian border in the Serranía del Darién

Representative specimens examined. PANAMA. Serranía del Darién, Cerro Mali, 1200 m, 16 Jan 1975, Mori et al. 4310 (H, MO), West ridge of Cerro Tacarcuna massif, 1700 m, 1 Feb 1975, Mori et al. 4496 (MO).

Fig. 34. Distribution map of Thamnobryum fasciculatum.



JAMAICA. St. Andrew: Gully 1/4 mi SE of Morce's Gap, 1800 m, 14 Jul 1966, Crosby 3017 (MO), New Haven Gap, vicinity of Cinchona, 2-10 Sep 1906, Britton 80 (NY); John Crow Peak, 1700-1800 m, 2 Feb 1903, Underwood 719 (H, NY); Portland: Valley of Trafalgar River, near Jumbe Spring, 800 m, 6 Mar 1920, Maxon et al. 767 (BM, FH, NY), Trail from Morces Gap to Vinegar Hill, 1175-1500 m, 6 Mar 1920, Maxon et al. 729 (BM, FH, NY).

HAITI. Massif du Nord: Port-de-Paix, Haut-Piton, 1150 m, 20 Sep 1925, Ekman 4865 (FH, NY).

DOMINICAN REPUBLIC. La Vega: Trail from Tablones to Lagunita, west of La Ciénaga, 1200-1800 m, Jul 1967, Norris et al. 5845 (NY), Hill La Campana, Río Los Plátanos, 1036 m, 2 Jan 1948, Allard 18375h (NY), Vicinity of Pyramids, 13.8 km of Valle Nuevo, 2200 m, 30 Apr 1982, Buck 8017 (H, NY), Shaw 5683 (H, NY).

PUERTO RICO. Arecibo: Cordillera Central, Cerro Punta, S of Jayuya, 20 Jan 1940, Steere 6194 (FH, NY), Utuado, Sintenis s. n. (BM, H, NY), Reserva Forestal Toro Negro, Salto Inabón, 2 Jan 1985, Acevedo s. n. (NY); Fajardo: Sierra de Luquillo, La Coca Waterfall, 3 May 1940, Steere 7040 (FH), Fajardo: Sierra de Naguabo, Summit of Loma La Mina to Río Blanco, 360-945 m, 21 Jul 1914, Shafer 3354 (BM, H, NY); Ponce: Doña Juana, N of Villalba, 18 Jan 1940, Steere 6067 (FH, NY), Britton et al. 7484 (NY), Doña Juana River, above Swimming Pool, 19 Jan 1940, Pagán 6158 (FH), Adjuntas, Monte Cerrote, 900-1050 m, 15 Mar 1915, Britton et al. 5464 (NY); between Adjuntas and Jayuya, Creek Los Corchos, 800-900 m, 13 Mar 1915, Britton 5335 (FH, NY).

COLOMBIA. Antioquia: Campamento, area between km 6.6 to 14.6 of Campamento on road to las Brisas, 1430-1830 m, 2 Aug 1986, Churchill et al. 15046 (NY); Boyacá: La Vega, Bogotá, Feb 1917, Apollinare 427 (H), Pacho, 1800 m, Weir 259 (BM, H), Tacarema, 2200 m, Lindig 2034 (BM).

VENEZUELA. Caracas: 1500 m, Funck et al. 255 (BM, H), Colonia del Tovar, Fendler 142 (BM, H, NY): Portuguesa: Cloud forest, 15 km E of Chabasquén, 67 km NNW of Guanare, 1450-1520 m, 29-31 Oct 1982, Steyermark et al. 126718 (MO); Tachira: Slopes along Quebrada Agua Azul, south of El Reposo, 14 km SE of Delicias, 2150-2300 m, 22-23 Jul 1979, Steyermark et al. 118445 (NY).

TRINIDAD. Crüger s. n. (NY).

ECUADOR. Azuay: Gualaquiza, San Francisco River, 20 Jun 1909, Allioni 8348 (H); Napo: La Fama, valley of Río Chingual east of El Pun, 2000-2100 m, 1 Aug 1943, Steere 8440 (NY).

PERU. Amazonas: Bagua, ca 20 km E of La Peca, 1900 m, 22 Jul 1978, Barbour 2822 (MO); Cuzco: La Convención, 1800 m, Oct 1919, Bües s. n. (NY); Junin: Tarma, Chanchamayo valley, above La Merced, at Cumbre Yacunay, 2000 m, 15 Aug 1957, Hutchinson 1915 (NY), Valley Chanchamayo, Schunke 198 (MO).

BRAZIL: Minas Gerais: Caldas, Regnell 84 (FH, H); Paraná: Desvio Ypiranga, 6 Sep 1911, Dusén 13343 (BM, FH, H, NY); Río de Janeiro: Serra do Itatiaia, Mont Serrat, 900 m, 11 May 1902, Dusén 416 (H, NY), Serra de Fribergo, 5 May 1927, Bandeira 692 (H), Serra dos Orgãos, 15 Feb 1887, Schenck 4806 (H), Petropolis, Pedreira da Quintandinha, 16 Feb 1924, Bandeira 218 (H); Santa Catarina: Riosinho, Bom Retiro, 1000 m, 24 Dec 1948, Reitz 2799 (NY); São Paulo: Iacupiranga, Jun 1881, Puiggari 570 (H), Yporanga in valley of Rio Ribeira, 130 m, Sep. Schiffner 2791 (BM, FH, H, NY), Serra do Cayazique, Santos, Jul 1901, Schiffner 390 (BM, H).

BOLIVIA. Santa Cruz, 1800 m, 25 Aug 1902, Williams 1980 (BM, H, NY).

JUAN FERNANDEZ. Masafuera, Mono Creek, 975 m, 20 Feb 1917, Skottsberg 267 (H).

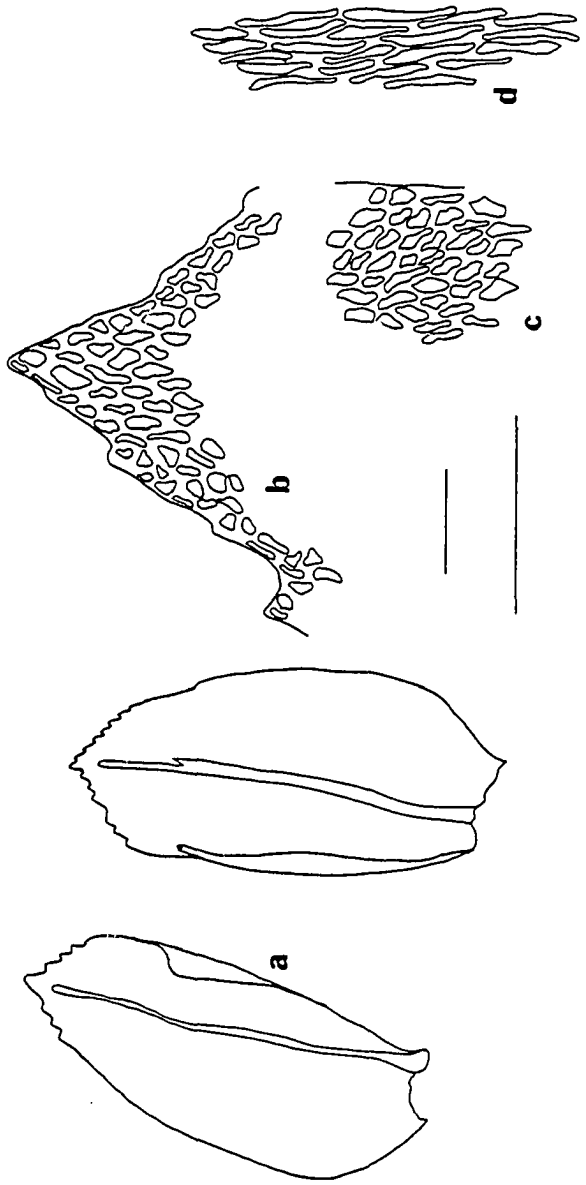
Discussion. Macroscopically, this species is easily recognized by the olive green color and coarse, rigid appearance. Some of the material studied showed linear marginal cells, oriented parallel to the margin. The costa is of even width from leaf base to apex, mostly ending two to five cells below the apex. Occasionally, some plants showed a narrower costa toward apex which mostly ended further from the leaf apex. Leaves may taper toward the apex or are of a uniform width from base. The apex of the stipe leaves is usually fragile and broken. The lamina of branch and stem leaves may become eroded, but the costae persists. Thamnobryum fasciculatum is distinguished from T. tumidicaule and T. alleghaniense by the robust stature, the slightly plicate leaves (when dry), usually broadly acute apex, ovate-oblong leaves and smooth costa. The strong costa and short apical cells support the placement of this species in Thamnobryum.

2. **Thamnobryum tumidicaule** (Wagner) Sastre, **comb. nov.**

Thamnium tumidicaule Wagner, Bryologist **55:** 145. 1952. Type. Costa Rica. Cartago: Flood plain in Río Reventazón below Santiago, 23 May 1930, Dodge 8251 (isotype, MO!). (Fig. 35 a-d).

Small to medium sized plants, 4-8 cm tall, dark green to yellow green, dull to slightly shiny, irregularly pinnate forming a sparse frond. Axillary hairs 4-5 cells long, stalk cell short rectangular; pseudoparaphyllia foliose, small. Primary stem covered with red-brown rhizoids; in cross-section with 3-4 layers of outer small thick-walled cells surrounding 7-8 layers of inner large hexagonal cells, central strand present; leaves erect-spreading, deltoid, 0.5 mm long, acute; margin entire; costa short-double; upper median cells irregularly rectangular, 34-39 um long, 8 um wide. Secondary stems perpendicular to substrate, in cross-section

Fig. 35. Thamnobryum tumidicaule (Standley 83301, NY). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaf upper median cells, x400; d, stem leaf basal cells, x400.



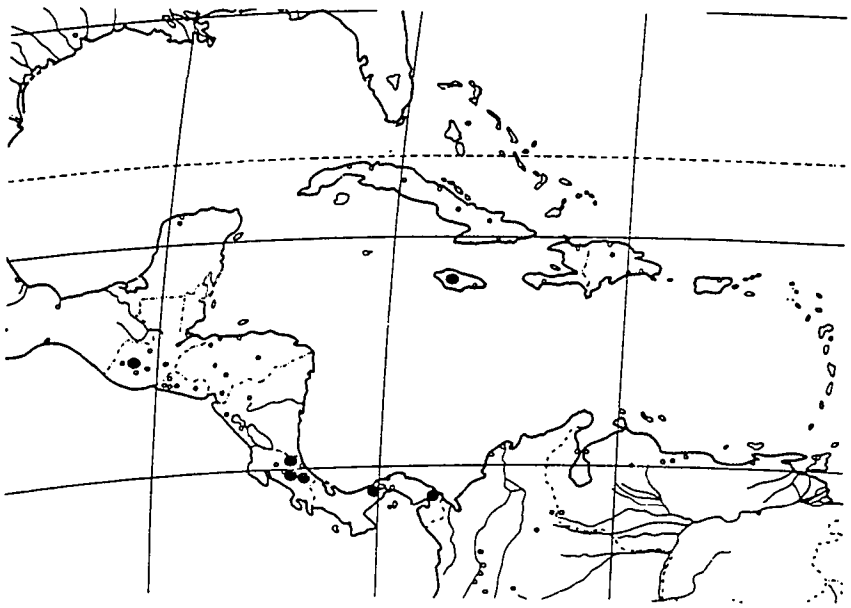
with 4-5 layers of outer small cells surrounding 10-12 inner layers of hexagonal cells, central strand present; stipe leaves erect-spreading to spreading, triangular, 0.8-1.0 mm long, acute; margin entire, recurved; costa single, 1/2 of leaf length; upper median cells linear, 34-39 um long, 8 um wide. Secondary stem leaves erect to erect-spreading, ovate to ovate lanceolate, 2.4-3.0 mm long, 1.0 mm wide, acute; margins serrate at apex, entire below; costa subpercurrent, strong, smooth at back; apical cells hexagonal to irregularly hexagonal, 13 um in diameter, upper median cells linear to rectangular, 34-44 um long; 13 um wide, basal cells linear to rectangular, 34-78 um long, 8 um wide; branch leaves smaller than stem leaves. Dioicous. Perigonia not observed. Perichaetial leaves lanceolate, 1.0 mm long, acute; margin entire; costa absent; upper median cells linear to rectangular, 39-78 um long, 10 um wide; paraphysis present. Sporophyte unknown.

Distribution and Ecology. (Fig. 36). Thamnobryum tumidicule is known from Costa Rica, Guatemala, Panama and Jamaica. This species is found from lowland to montane forests. As with many other species of this genus, it commonly grows in very wet, habitats like on rocks near streams and on dripping rock walls. It also grows as an epiphyte.

Specimens examined. GUATEMALA. Quezaltenango: Aguas Amargas, on the western slope of Volcán de Zunil, 2450 m, 14 Jan 1941, Standley 83301 (NY).

COSTA RICA. Cártago: Flood plain of Río Reventazón below Santiago, 740-750 m, 23 May 1930, Dodge 8251 (MO); Limón: Vicinity of U. S. Department of Agriculture Rubber Experiment Station, Los Diamantes on Río Santa Clara 1.6 km E of Guapiles, 200 m, 22 Jul 1949, Holm et al. 1272 (G).

Fig. 36. Distribution map of Thamnobryum tumidicaule.



PANAMA. Colón: Beyond bench mark, 2 hrs. walk in from end of Santa Rita Road, which terminates 17.1 km after leaving Boyd-Roosevelt Highway, 550 m, 29-30 May 1975, Crosby 10462 (MO); Darién: N of Punta Guayaba Grande, NW of Ensenada El Guayabo, 0-200 m, 25 Jan 1982, Knapp et al. 3136 (MO), Pirre Base Camp, Feb 1972, Gentry M-6 (MO); Panamá: Vicinity of falls of Río Caimito, near La Chorerra, 5 Apr 1969, Crosby 454913 (MO).

JAMAICA. Mabess river, below Vinegar Hill, 900 m, 9 Feb 1903, Underwood 1258 (MO, NY); St. Thomas: WNW Corn Puss Gap, along trail from the Gap to Bowden Pen, 500-660 m, 29 Jul 1966, Crosby 3261 (MO).

Discussion. Thamnobryum tumidicaule is characterized by the small stature, and slightly concave, erect-spreading leaves. Placement of this species in Thamnobryum is based only on vegetative characters since sporophytes have not been found. It has the short apical cells and strong costa characteristic of Thamnobryum.

5. **Porotrichum** (Bridel) Hampe, Linnaea **32:** 1983.

Climacium subg. Porotrichum Bridel, Bryol, Univ. **2:** 275. 1827.

Lectotype. Porotrichum longiroste (Hooker) Mitten, fide Dixon, Stud. Handb. Brit. Moss. 370. 1896.

Porothamnium Fleischer, Musci Fl. Buitenzorg **3:** 925. 1908. (no type designated).

Plants small to robust, light to dark green, dull to shiny, dendroid, complanate, regularly to irregularly pinnate; branches sometimes distally attenuate, flagelliform branches sometimes present. Axillary hairs with short-quadrate stalk cell and long rectangular cells above; paraphyllia absent; pseydoparaphyllia mostly

foliose. Primary stem creeping, nearly naked to covered with abundant rhizoids, in cross-section mostly elliptic, with outer small incrassate cells surrounding large hexagonal cells, central strand present; leaves clasping to erect-spreading, triangular to obovate-subulate, acute; margins entire to serrulate, plane to recurved; costa absent to present, short-double to single; upper median cells fusiform, linear to rectangular, smooth to papillose by projecting angles. Short to long stipitate, in cross-section elliptic, with outer small incrassate cells surrounding large thick-walled hexagonal cells, central strand present; stipe leaves clasping, erect-spreading, spreading to squarrose, broadly obovate, deltoid to triangular-subulate, acute; margins entire, plane to recurved; costa present or absent; single; upper median cells fusiform, linear to rectangular, smooth to papillose by projecting angles, pitted or unpitted alar cells undifferentiated to differentiated, forming small groups of short-quadrate to short-rectangular cells. Stem leaves erect to erect-spreading, smooth to slightly plicate when dry, triangular, ovate, ovate-lanceolate, ovate-oblong to oblong-ligulate, acute, broadly-acute to obtuse; margins mostly slightly serrate to serrate at apex, with serration sometimes reaching 3/4 of leaf length; costa single, 1/2 to 3/4 of leaf length; smooth or ending in a tooth at back; apical cells oval, rhomboidal to fusiform, upper median cells fusiform to linear, basal cells linear to rectangular, alar cells sometimes differentiated in small groups of short-quadrate cells, smooth to papillose by projecting angles, pitted throughout to pitted at base only or unpitted. Branch leaves mostly smaller than stem leaves, erect to erect-spreading, oval, ovate, oblong to oblong-ligulate, acute, broadly acute to obtuse; margins serrate at apex to 3/4 of leaf length, plane to recurved mostly at leaf base; cell pattern same as in stem leaves. Dioicous. Perigonial leaves ovate to lanceolate, abruptly apiculate to acute; margins entire; costa absent; upper median cells fusiform to linear. Perichaetial leaves ovate-subulate to oblong-subulate, margins entire; costa absent or present, single; upper median

cells fusiform to linear, pitted or unpitted. Setae short to long, mostly reddish-brown, smooth; capsule erect to horizontal, cylindric; exothecial cells short-quadrate to short-rectangular; stomata present; annulus present; operculum rostrate, short to long; peristome double, exostome teeth lanceolate to lanceolate from a broad base tapering at apex, striate at base to striate with overlying papillae becoming papillose only toward apex, sometimes hyaline at apex, at back with strongly projecting lamellae, mostly papillose; endostome with a high basal membrane, segments papillose to sparsely papillose, perforate, cilia present and evident or rudimentary. Calyptra cucullate. Spores spherical, papillose.

In the neotropics this genus is represented by 11 species. After revising all the species in the West Indies, Central and South America and also checking other treatments, such as De Sloover (1983), it was concluded that no gametophytic characters are present to support separating Porothamnium from Porotrichum. Some gametophytic characters that have been suggested to separate the two genera, such as size, stature and degree of glossiness, are variable in the group. Fleischer (1904-1923) segregated Porothamnium from Porotrichum on the basis of sporophytic characters. Porothamnium was characterized by a strongly cross-striate exostome base, the upper part cross-striate with overlying papillae. Cilia are well developed. This type of peristome is observed P. expansum and P. lancifrons. The exostome of Porotrichum was characterized as usually papillose with rudimentary cilia in the endostome. The differences in peristome morphology were not found congruent with any gametophytic characters. Since plants bearing sporophytes are rare and no gametophytic characters were found to separate the two genera Porothamnium is included in Porotrichum.

Outside of the neotropics, there are 22 species listed for Porotrichum and 10 for Porothamnium. Fritsch (1982) reported a chromosome count of 12 for Porothamnium bigelowii.

Keys of species of Porotrichum

1. Leaves at mid-stipe spreading to squarrose when dry; margins of stipe leaves recurved 2.

   2. Stipe leaves mostly squarrose; branch leaves mostly orbicular 1. P. thielianum.

   2. Stipe leaves mostly spreading; branch leaves ovate-lanceolate to oblong-ligulate 3.

      3. Lowland forest species; plants small, to 5 cm. tall; branch leaves ovate-lanceolate, apex acute; costa mostly ending in a tooth 2. P. subtriatum.

      3. Species of cloud forests or higher elevations; plants mostly more than 5 cm tall, to 10 cm tall; branch leaves ligulate to oblong, broadly acute to obtuse 4.

         4. Leaves mostly plicate when dry; stem and branch leaves with recurved margins 3. P. filiferum.

         4. Leaves mostly smooth when dry; stem and branch leaves with plane margins 4. P. expansum.

1. Leaves at mid-stipe erect-appressed or erect-spreading with spreading subulae from an erect base; margins of stipe leaves plane 5.

   5. Median cells of stem leaves oval (3-4:1); plants mostly in lowland forests 5. P. piniforme.

   5. Median cells of stem leaves fusiform to linear (5-10:1); plants mostly from lower montane, montane to subparamo 6.

6. Stem leaves mostly ovate-ligulate to ligulate

7.

7. Branch leaves mostly acute, serrate only at apex; upper median cells of stem leaves linear, slightly pitted

6. P. mutabile.

7. Branch leaves mostly broadly acute to obtuse, serrate in the upper 1/2; upper median cells of stem leaves fusiform to long hexagonal, unpitted

7. P. korthalsianum.

6. Stem leaves mostly ovate-lanceolate to broadly ovate

8.

8. Branch leaves ovate-lanceolate, acute; margins serrate in upper 1/2 8. P. longirostre.

8. Branch leaves obovate, broadly acute to obtuse; margins serrate to leaf base 9. P. lancifrons.

1. **Porotrichum thieleanum** (C. Müller) Mitten, J. Linn. Soc., Bot. **12:** 465. 1869.

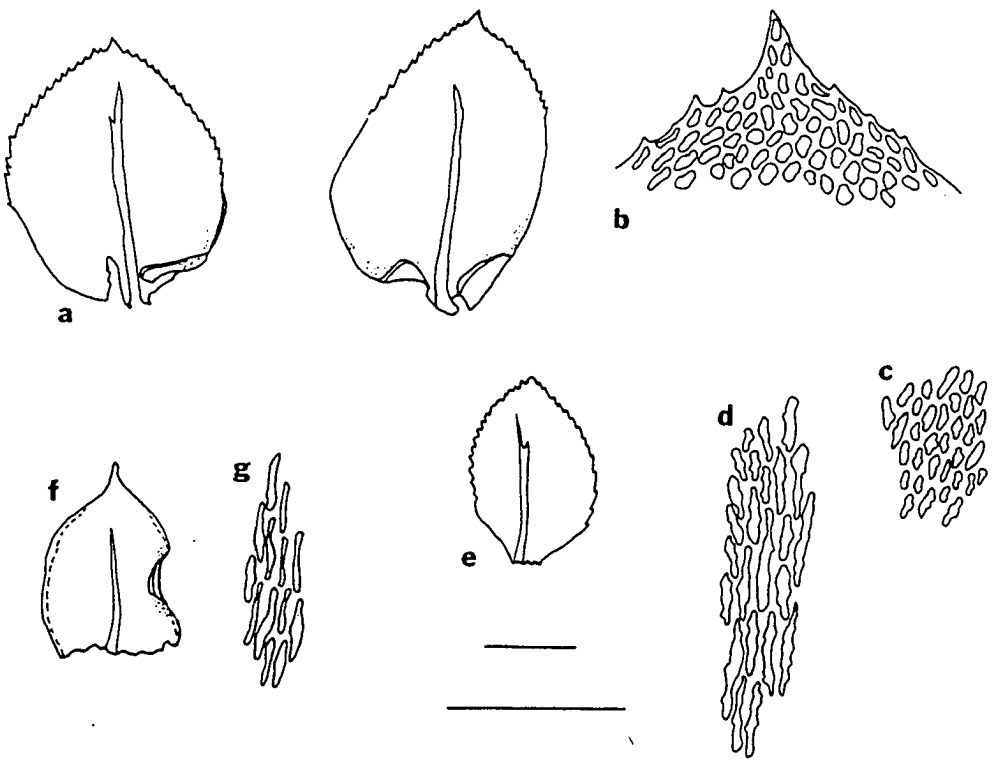
Hypnum thieleanum C. Müller, Syn, **2:** 227. 1851; Pinnatella thieleana (C. Müller) Brotherus ex Paris, Coll. 24. 1909. Type. Brazil. Sellow s.n. (lectotype, BM!).

Porotrichum denticulatum Mitten, J. Linn. Soc., Bot. **12:** 462. 1869; Thamnium denticulatum (Mitten) Kindberg, Hedwigia **41:** 239. 1902, **syn. nov.** Type. Brazil. In Sierra between Antonina and Corritiba, 450 m, humid tree trunks, Weir 69 (holotype, NY!); isotypes, BM!, NY!).

Pinnatella brasiliensis Bartram, J. Washington Acad. Sci. **42:** 181. 1952, **syn. nov.** Type. Brazil. Río Grande do Sul: Estacão São Salvador, tree trunks in forest, 600 m, Sehnem 2772 (holotype, FH!).

(Fig. 37 a-g).

Fig. 37. Porotrichum thielianum (Weir 69, NY). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaf upper median cells, x400; d, stem leaf basal cells, x400; e, branch leaf, x40; f, stipe leaf, x40; g, stipe leaf upper median cells, x400.



Plants small to medium, 3-6(10) cm. tall, pale green, dull, frondose, regularly pinnate to bipinnate flagelliform branches present, axillary or apical, leaves small, lanceolate. Axillary hairs 2-4 cells long, stalk cell short-rectangular; pseudoparaphyllia small, foliose. Primary stem is cross-section round to elliptic, with 3-4 layers of small incrassate cells surrounding 3-4 inner layers of hexagonal cells, central strand present; leaves erect-spreading to squarrose, obovate, abruptly acute; margins entire, recurved; costa absent; upper median cells irregularly fusiform to rectangular, 34-52 um long, 5-6 um wide, smooth. Secondary stem erect to perpendicular to substrate, elliptic in cross-section, with 2-3 outer layers of small cells surrounding 15-20 inner layers of large hexagonal cells, central strand present; stipe leaves squarrose when dry, spreading when wet, obovate-triangular, 1.0-1.5 mm long, acute; margins entire, recurved; upper median cells irregularly rectangular, (34)52-65 um long, 6-8 wide, pitted. Secondary stem leaves erect to erect-spreading, ovate, 2.0-2.5 mm long, 1.0-1.8 mm wide, acute to apiculate; margins serrate in upper 2/3, slightly recurved at base; costa strong, single, sometimes somewhat forked at distal end, 3/4 to 2/3 the length; apical cells rhombic, 13-26 um long, 8-10 um wide, upper median cells linear, 34-52 um long, 6 um wide, basal cells rectangular, 52-78 um long, 10-13 um wide; branch leaves erect to erect-spreading, ovate to orbicular, 1.4 mm long, 1.0 mm wide, apiculate; margins serrate from apex to leaf base, slightly recurved at base; costa 2/3 the leaf length; upper median cells rhomboidal, 21-26 um long, 6 um wide, Dioicous. Perichaetial leaves obovate-subulate, 1.0-1.5 mm long, 0.8-0.9 mm wide, margins serrulate at apex; costa single; marginal cells rectangular, upper medium cells irregularly rectangular, 65-78 um long, 6 um wide, pitted. Setae reddish-brown, 1.5-2.0 cm long, smooth; capsules erect, ovoid, 2.0 mm long; exothecial cells short-rectangular, thick-walled; exostome teeth lanceolate, striate below, papillose above; endostome segments from a high basal

membrane, papillose, perforate, cilia present. Calyptra cucullate. Spores spherical, 26 um in diametter, papillose.

Distribution and Ecology. (Fig. 38). Epiphyte in moist ravines about 400 and 600 m in southeastern Brazil.

Specimens examined. BRAZIL. Paraná: Between Antonina and Corritiba, 450 m, Weir 69 (BM, H, NY); Río Grande do Sul: Estacão São Salvador, 600 m, Sehnem 2772 (FH), s. l, Sellow s. n. (BM).

Discussion. Porotrichum thielianum is easily recognized by the squarrose stipe leaves with recurved margins. This species in unique among Porotrichum species because it has orbicular branch leaves and short-rhomboidal cells. It possibly is a southeastern Brazil endemic.

2. **Porotrichum substriatum** (Hampe) Mitten, J. Linn. Soc., Bot. **12:** 463. 1869.

Neckera substriata Hampe, Ann, Sci. Nat. Bot. ser. 5, **5:** 340. 1866. Porothamnium substriatum (Hampe) Fleishcer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925; Thamnium substriatum (Hampe) Kindberg, Hedwigia **41:** 227. 1902. Type. Colombia. Bogotá, San-Antonio, 1400 m, Lindig s. n. (holotype, BM!).

Porotrichum plicatulum Mitten, J. Linn. Soc., Bot. **12:** 461. 1869. Thamnium plicatulum (Mitten) Kindberg, Hedwigia **41:** 253. 1902, **syn. nov.** Type. Trinidad. In sylvis Arima, Purdie s. n. (syntype, NY!); Chaguanas, Black 92 (lectotype, NY!).

(Fig. 39 a-k).

Fig. 38. Distribution map of Porotrichum thielianum, neotropical material of P. substriatum and P. filiferum.

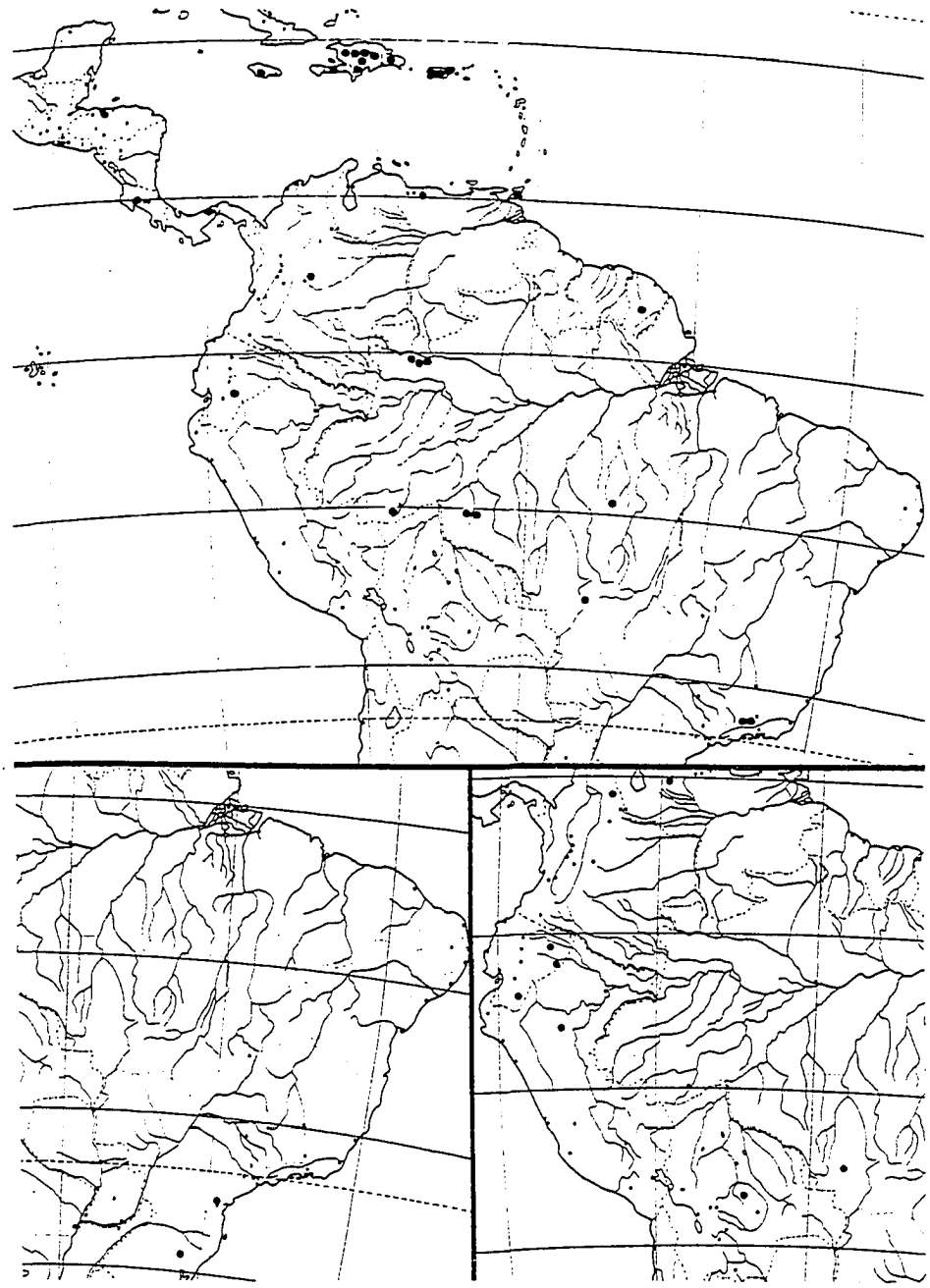
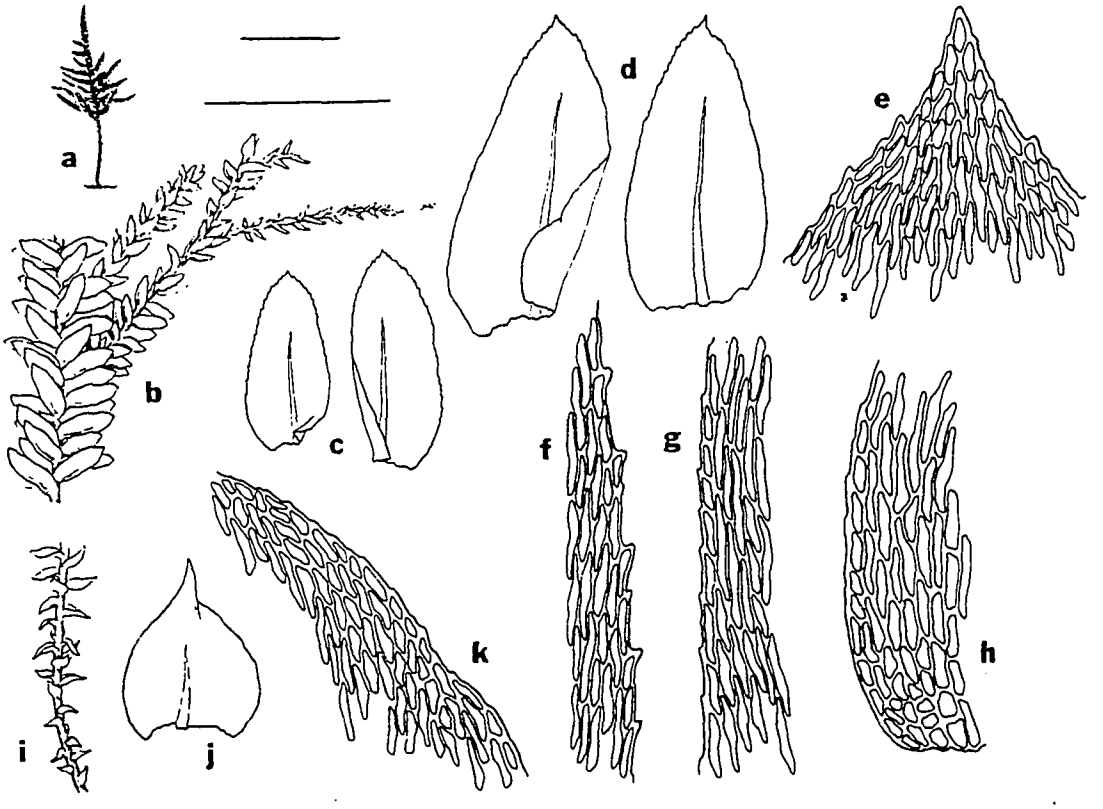


Fig. 39. Porotrichum substriatum (Buck 5033, NY). a, habit dry, x1; b, stem branch and flagelliform branches, x12; c, branch leaves, x40; d, stem leaves, x40; e, stem leaf appex, x400; f, branch leaf upper median cells, x400; g, stem upper marginal cells, x400; h, stem leaf basal and alar cells, x400; i, stipe with leaves, x12; j. stipe leafk x40; k, stipe leaf upper median and marginal cells, x400.



Plants mostly small, slender, 2.0-5.0 cm tall, slightly shiny, mostly forming a triangular frond, regularly pinnate to irregularly bipinnate, branches distally sometimes becoming flagelliform, leaves lanceolate. Axillary hairs 2-3 cells long, stalk cell shor quadrate; pseudoparaphyllia foliose. Primary stem in cross-section elliptic, with 2-3 outer layers of small, rounded, thick-walled cells surrounding 6-8 layers of large hexagonal inner cells, central strand present; leaves obovate-subulate, clasping at base; margins serrulate, recurved; costa single; upper median cells rectangular, 52 um long, 6 um wide. Secondary stem elliptic in cross-section with 4-5 layers of small cells surrounding 8-10 inner layers of large hexagonal, central strand present; stipe leaves squarrose to spreading, with a broad obovate base, sheating, 0.9-1.0 mm long, abruptly apiculate; margins entire, recurved at base; costa 2/3 the leaf length; upper median cells irregularly rectangular, 26-39(52) um long, 6 um wide; secondary stem leaves erect-spreading to spreading, slightly plicate when dry, ovate-lanceolate, 2.0-3.0 mm long, 0.9-1.0 mm wide, acute; margins serrate, recurved; costa reaching 3/4 the leaf length, ending in a tooth at back; apical cells rhomboidal, (18)21-28(39) um long, 6-8 um wide, upper median cells oval to linear, 39-52 um long, 6 um wide, basal cells rectangular, 42-52 um long, 6 um wide, papillose by projecting angles, alar cells somewhat distinct, irregularly quadrate; branch leaves ovate-lanceolate to ovate, acute; margins serrate 2/3 down; other characters same as stem leaves. Sporophyte unknown.

Distribution and Ecology. (Fig. 38). Porotrichum substriatum is known from the West Indies, Costa rica, Honduras, Panamá, Trinidad, Venezuela, French Guiana, Colombia, Ecuador, Brazil and Africa. It is a lowland and lower montane species occurring up to 1800 m. In South America its distribution follows mainly lowland forests east of the Andes. It grows on rocks or tree trunks of lowland forests.

Representative Specimens examined. COSTA RICA. Alajuela: Vicinity of Capulín, on the Río Grande de Tárcoles, 80 m, 2 Apr 1924, Standley 40142 (FH, NY).

HONDURAS. Atálantida: Lancetilla valley, near Tela, 20-600 m, 6 Dec 1927 - 20 Mar 1928, Standley 55617 (BM, FH, NY).

PANAMA. Colón: 0-25 minutes walk along path beginning at end of Santa Rita Ridge Road, 350-450 m, 21-23 May 1975, Crosby 10321 (MO), Vicinity of Cerro Jefe, 900 m, 4 Jan 1970, Lewis 7612 (G); Panamá: Along road above Godfy Lake, 650 m, 24 Mar 1969, Crosby 4335 (MO).

JAMAICA. Trelawny Parish: Cockpit Country, just N of Wilson's Run, 5-8 mi N of bridge at Troy, 500 m, 18 Apr 1981, Buck 55882 (NY).

HAITI. Grand'anse: Massif de la Hotte, along small stream entering Rivière Glace at junction of road from Beaumont to Camp Perrin, 710 m, 13 Nov 1982, Buck 9103 (NY), Mermelade, 900 m, 25 Aug 1903, Nash 841 (NY).

DOMINICAN REPUBLIC. Estrellata: Along Río Limpio at Colonia Río Limpio, 660 m, 23 Mar 1981, Reese 15412 (NY); Pedernales: Along road from Mencia to Aguas Negras, 4 km E of Mencia, 450 m, 14 Mar 1981, Buck 4499 (NY), Las Abejas, ca 40 km N along road from Cabo Rojo from junction of road from Ovideo to Pedernales, 1180 m, 13 Mar 1981, Buck 4384 (NY); Peravia: Central Cordillera, village of Quita Sueño, 700 m, 8 Apr 1982, Zanoni et at. 19918D (MO); Samaná: 3.5 km E of Lasa Terrenas, 47 m, 3 Nov 1981, Zanoni 176677 (NY); El Seibo: Cordillera Oriental, 16 km S of Miches, on road to El Seibo, 420 m, 28 Mar 1981, Buck 5033 (NY); La Vega: Loma Campana, Río los Plátanos, 1036 m, 2 Jan 1948, Allard 18433 (NY), vicinity of Piedra Blanca, along Maimon river, 200-500 m, 5 Nov 1947, Allard 16687 (NY), at base of Loma Caribe, NNE of Bonao, 160-180 m, 30 Jul 1981, Zanoni et al. 15766 (NY).

PUERTO RICO. Caribbean National Forest, along Hwy 988, 0.7 mi SE if intersection with Hwy 191, 150-200 m, 6 Mar 1981, Buck 4165 (NY), El Verde, vicinity of El Verde Biol. Station, trail to tower, 23 Feb 1981, Reese 14301 (NY), La Torecilla, NW of Barranquitas, 28 Oct 1939, Steere 4702 (NY), Mount Mandios, near Jayuya, Britton et al. 480 (NY).

COLOMBIA. Cundinamarca: Bogotá-San Antonio, 1400 m, Lindig s. n. (BM); No locality, 13 mar 1951, Schultes 11698a (FH).

VENEZUELA. Aragua: North slope of National Park La Cumbre, 900 m, 29 Dec 1938, Alston 5844a (BM).

TRINIDAD. Chaguanas, Black 92 (NY), Arima, Purdie s. n. (NY), no locality, Broadway s. n. (NY).

FRENCH GUIANA: Saül: La Fumée, 200-400 m, 21 Aug 1982, Boom et at. 1528 (NY), Maroni s. n. (BM).

ECUADOR. Morona Santiago: Cutucú, 1800 m, Ortega 456a (MO).

BRAZIL. Acre: 33 km SW of Río Branco along the road to Brasilía, 26 Feb 1978, Reese et al. 13265 (NY); Amazonas: Río Tucano, 275 m, 1 Dec 1965, Maguire et al. 60298 (NY), Slopes of Serra Curicuriari, from Igarapé Arabú, 450 m, 9-12 Jul 1979, Buck 2425, 2499 (NY); Matto Grosso: Veu de Noiva, Chapada dos Guimarães, 720 m, 25 Oct 1973, Prance et al. 19404 (NY); Pará: Serra do Cachimbo, km 777 on Cuiabá-Santarem hwy (Br 163), 400 m, 23 Apr 1983, Reese 16107 (NY); Rondonia: 128 km SW of Ariquemes at Mibrasa Mining Camp, 16 May 1982, McFarland et al. 184 (NY). Ariquemes, Alto Condeias, 3 km E of Mibrasa Mining Camp, 16 May 1982, Fife et al. 4135 (NY); São Paulo: Itapecirica, Barra Mansa, 1000 m, 18 Jul 1901, Schiffner 1574 (BM), Itanhaean, Río Mambu, 100 m, 30 Jul 1901, Schiffner 541 (BM).

Discussion. Macroscopically, P. substriatum is recognized by the small, slightly shiny, triangular fronds usually forming extensive mats over rocks or tree trunks in lowland forests. Another distinguishing feature is the squarrose stipe leaves and ovate-lanceolate stem leaves. When dry most plants are slightly plicate, but this character has been observed to be variable. Porotrichum plicatulum is considered conspecific since no differences were observed with the type of P. substriatum.

3. **Porotrichum filiferum** Mitten, J. Linn. Soc., Bot. **12:** 468. 1869.

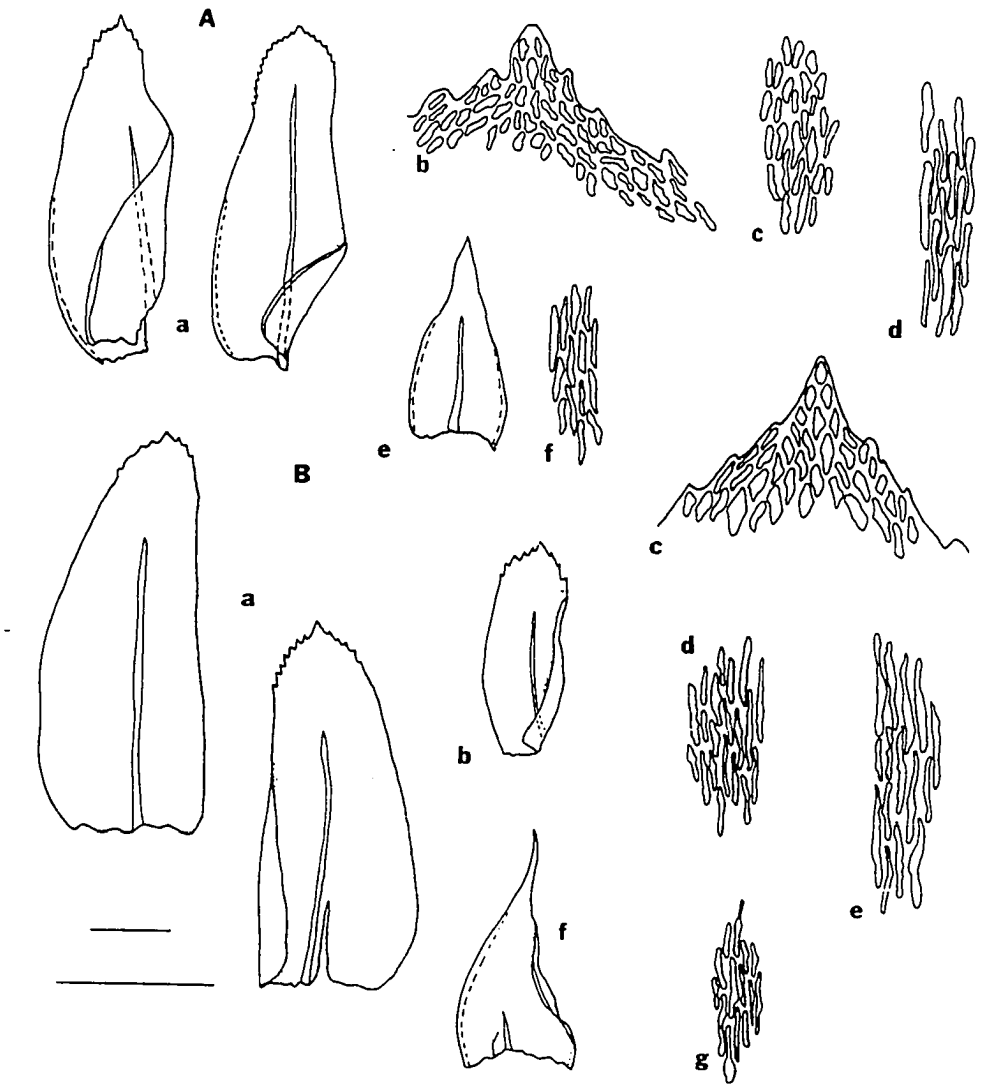
Thamnium filiferum (Mitten) Kindberg, Hedwigia **41:** 225. 1902; Porothamnium filiferum (Mitten) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925. Type. Ecuador. Andes Quitenses, River Bombonasa 450 m, Spruce 1365 (lectotype, NY!; syntypes BM!, G!; H-BR!); Perú: Andes Peruvianae, River Shilicaio, 600 m, Spruce 1366 (isotype, BM!, NY!); Tarapoto, 480 m, Spruce 1367 (syntype, NY!).

Thamnium mattogrossense Brotherus, Bih. Kongl. Svenska Vetensk. Akad. Handl. 26 Afd. **3(7):** 43. 1900; Porothamnium mattogrossense (Brotherus) Fleischer in Brotherus, Nat. Pfl, ed. 2, **11:** 198. 1925, **syn. nov.** Type. Brazil. Matto Grosso: Cupinis, Serra da Chapada, 20 Dec 1893, Lindman 399 (holotype, H-BR!).

Porotrichum strictum Herzog. Biblioth. Bot. **87:** 118. 1916, **syn. nov.** Type. Bolivia. San Mateo, 1800 m, Herzog 4483 (isotypes, H-BR!, NY!).

(Fig. 40A a-f).

Fig. 40. A, Porotrichum filiferum (Spruce 1365, NY). a, stem leaves, x40; b, stem leaf apex, x400; c, stem leaves upper median cells, x400; d, stem leaves basal cells, x400; e, stipe leaf, x40; f, stipe leaf upper median cells, x400. B. Porotrichum expansum (Jameson s. n., NY). a, stem leaves, x40; b, branch leaf, x40; c, stem leaf apex, x400; d, stem leaf upper median cells, x400; e, stem leaf basal cells, x40; f, stipe leaf x4; g, stipe leaf upper median cells, x400.



Slender, small to medium-sized plants, 6.0-8.0 cm tall, mostly yellow-green, dull to slightly shiny, frondose, irregularly pinnate to sometimes unbranched. Axillary hairs 2-3 cells long, stalk cells short rectangular; pseudoparaphyllia small foliose. Primary stem in cross-section elliptic, with 4-5 outer layers of small cells surrounding 8-10 inner layers of larger laxly hexagonal cells, central strand absent; leaves obovate to triangular, 0.8-0.9 mm long, acute; margins entire; costa single; upper median cells linear, 47-78 um long, 6 um wide. Stipe erect, reddish-orange to brown, long to short, in cross-section elliptic, with 3-5 outer layers of small cells surrounding 6 inner layers of hexagonal cells, central strand present; stipe leaves erect-spreading to spreading, broadly triangular-subulate to lanceolate in the upper part of the stipe, 1.0-1.2 mm long, decurrent, acute; margins entire, recurved; costa single; upper median cells linear, 52-65 um long, 6 um wide, pitted, basal cells rectangular, 34-44 um long, 6-8 um wide. Secondary stem leaves erect-spreading, slightly plicate when dry, oblong from a broad base to ligulate, 2.0-3.0 mm long, 1.0-1.5 mm wide; broadly acute to obtuse, apiculate; margins serrate at apex, to sometimes upper 1/2, mostly recurved at base to somewhat above; costa 2/3 the leaf length; apical cells short hexagonal, 21-26 um long, 8-10 um wide, upper median cells long hexagonal, 34-52 um long, 4 um wide, basal cells linear, 39-78 um long, 4-6 um wide, pitted; branch leaves oblong to ligulate, acute to obtuse; margins serrate at apex to upper 1/2; cell patterns same as in stem leaves. Dioicous. Perigonial leaves ovate, 0.9 mm long, abruptly apiculate; margins entire; upper median cells linear, 52-78 um long, 6 um wide, pitted. Perichaetial leaves ovate to oblong, abruptly subulate, 3.4-4.2 mm long, 1.0-1.5 mm wide, margins entire; costa absent; upper median cells linear to rectangular, 52-92 um long, 6 um wide, pitted. Setae orange to reddish, 2.0 cm long; capsule horizontal, cylindric, 2.0 mm long; exothecial cells short rectangular,

34-63 um long, thick-walled; stomate present; annulus present; operculum not observed; exostome teeth striate at base, becoming papillose distally, upper area of teeth not observed, endostome segments from a high basal membrane, papillose, perforate, cilia rudimentary. Calyptra not seen. Spores not observed.

Distribution and Ecology. (Fig. 38). Porotrichum filiferum occurs as an epiphyte at mid elevations in the Andes from Venezuela, Colombia to Bolivia and is also known from southwestern Brazil. Localities known for this species are on the eastern slopes of the Andes.

Specimens examined. COLOMBIA. Norte de Santander: Cordillera Oriental, Barrio Chucarima, Cinchona forest east of Río Valegrá, 1800-2100 m, 16 Nov 1942, Steere 7418 (NY).

VENEZUELA. Lara: Parque Nacional Yacambú, Sierra de Portuguesa. 1400-1900 m, 20-24 May 1978, Griffin et al. 331 (FLAS).

ECUADOR. Oriente: 2100 m, Allioni 469 (H); Pastaza: Bombonasa, Spruce 1365 (BM, G, H, NY); Zamora: Zamora, 1600 m, Ortega 593a (MO).

PERU. San Martín. Tarapoto, Spruce 1367 (NY), Shilicaio, 600 m, Spruce 1366 (BM, NY).

BRAZIL. Matto Grosso: Cupinis, Serra da Chapada, 20 Dec 1893, Lindman 399 (H-BR).

BOLIVIA. Cochabamba: San Mateo, 2000 m, Apr 1911, Herzog 4483 (H, BR, NY).

Discussion. This species is recognized by the spreading stipe leaves with recurved margins, slightly plicate leaves when dry, stem and branch leaves oblong and broadly acute with recurved basal margins. Leaves along the stem show variation from a broadly acute to obtuse apex.

4. **Porotrichum expansum** (Taylor) Mitten, J. Linn. Soc., Bot. **12:** 467, 1869.

Hypnum expansum Taylor, London J. Bot. **5:** 64. 1846; Thamnium expansum (Taylor) Kindberg, Hedwigia **41:** 236. 1902; Porothamnium expansum (Taylor) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. Type. Ecuador. On Pichincha, near Quito, 1827, Jameson s. n. (holotype, FH!; isotype, NY!).

Porotrichum lehmannii Bescherelle, Bull. Herb. Boissier **2:** 395. 1894; Thamnium lehmannii (Bescherelle) Brotherus, Nat. Pfl. **1(3):** 862. 1906; Porothamnium lehmannii (Bescherelle) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 200. 1925, **syn. nov.** Type. Ecuador. Río Pun, Ost. Cordillera of Tulcán, 2800-3500 m, 4 Feb 1881, Lehmann 685 (holotype, BM!; isotype, G!). (Fig. 40 a-g).

Plants medium to large, 4.0-11.0 cm tall, pale green to yellow green, shiny, complanate, frondose, irregularly pinnate, long stipitate. Axillary hairs 4-5 cells long, stalk cell short quadrate; paraphyllia absent; pseudoparaphyllia small, foliose. Primary stem creeping, in cross-section elliptic, with 2-3 outer layers of small cells surrounding 5-8 inner layers of hexagonal cells: leaves spreading, broadly-triangular, 1.0-1.2 mm long, acute; margin entire; costa single; upper median cells fusiform, 39-44 um long, 8 um wide, basal cells fusiform to long rectangular, 52-65 um long, 6 um wide, alar cells differentiated. Stipe erect, perpendicular to substrate, orange to red-orange, in cross-section elliptic, with

8-10 outer layers of small cells surrounding 15-20 inner layers of large, hexagonal cells, central strand present; leaves erect-spreading to mostly spreading, deltoid, acute, becoming subulate; margin entire to slightly serrate, recurved, sometimes only at base; costa single; upper median cells mostly fusiform to linear-rectangular, 52-65 (100) um long, 8 um wide, basal cells linear to rectangular, 63-100 um long, 6-8 um wide, alar cells differentiated. Stem leaves erect-spreading, ovate-ligulate to oblong-ligulate, 3.4-4.0 mm long, 1.5-1.7 mm wide, acute, sometimes broadly acute; margins plane, mostly serrate at apex, sometimes to 1/3 to 1/2 down; costa single, 3/4 of leaf length; apical cells mostly rhombic, 18-26 (31) um long, 10 (13) um wide, upper median cells long rhomboidal to fusiform, 52-78 um long, (6) 8 uw wide, basal cells fusiform to rectangular, 52-100 um long, 8-10 um wide, alar cells slightly differentiated in a small group, thick-walled, short-rectangular. Branch leaves mostly oblong; acute to broadly acute; serrate at apex to 2/3 down; costa and cell pattern same as in stem leaves. Dioicous. Perigonia not observed. Perichaetial leaves oblong-subulate, 5-6 cm long, margin entire; costa present; cells linear throughout, 92-130 um long, 6 um wide, pitted, papillose by projecting angles. Setae long, 1.5-2.0(4.0) cm, reddish-brown, smooth; capsule horizontal, cylindric, 2.0 mm long; exothecial cells short-rectangular; stomata present; annulus present; operculum rostrate; exostome teeth lanceolate, abruptly tapering at apex, brownish to orange at base becoming hyaline toward apex, striate at base to 3/4 of tooth length, becoming papillose at apex, dorsal surface smooth with projecting lamellae; endostome with a high basal membrane, segments papillose, perforate, cilia present. Calyptra not observed. Spores spherical, 13 um in diameter, papillose.

Distribution and Ecology. (Fig. 41). Porotrichum expansum is a species of montane and subpáramos. It occurs at high elevations in the Andes from Colombia and Ecuador.

Specimens examined. COLOMBIA. Norte de Santander: Loso and vicinity (N of Toledo), 2200-2400 m, 6-7 Mar 1927, Killip et al. 20450 (NY).

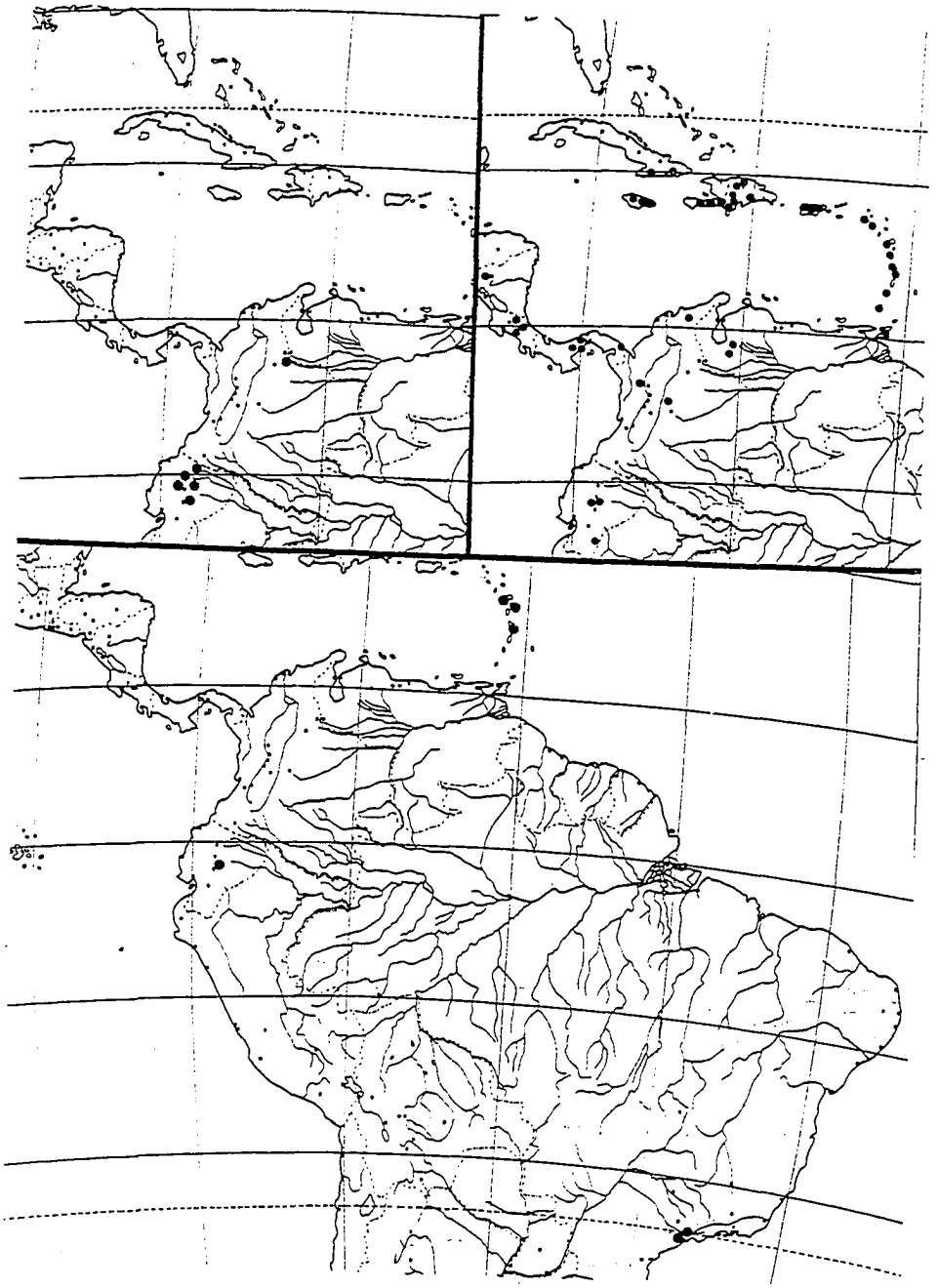
ECUADOR. Imbabura: 3 mi E of La Esperanza, beyond road over Río Taguando, 2850 m, 29 Nov 1978, Lewis 78-3127 (NY); Napo-Pastaza: Valley of Río Chingual E of El Pun, 2200-2700 m, 11 Aug 1943, Steere 8924 (NY); Pichincha: Vicinity of Río Alambi, along road leading W from Nono toward Tandayapa, N slopes of Mt. Pichincha, 2340 m, 7 Jun 1975, Crosby 10542 (NY), Cordillera Oriental, entrada al Oriente, 3000 m, 28 Oct 1945, Acosta Solis 11220 (NY).

Discussion. This species is characterized by the robust stature, stipe leaves with recurved margins and broadly ovate-ligulate to ligulate stem leaves. Stem leaves may be of variable shape along the stem, but they are mostly oblong-ligulate and serrate at apex to mid leaf. Stipe leaves may vary in shape also along the stipe, becoming subulate distally.

5. **Porotrichum piniforme** (Bridel) Mitten, J. Linn, Soc., Bot. **12:** 465, 1869.

Pilotrichum piniforme Bridel, Bryol. Univ. **2:** 260. 1827; Hypnum piniforme C. Müller, Syn, **2:** 228. 1851; Thamnium piniforme (Bridel) Kindberg, Hedwigia, **41:** 238. 1902; Pinnatella piniformis (Bridel) Fleischer, Hewigia **45:** 81. 1906. Type. Guadeloupe. Herb. Candolle (holotype, B!).

Fig. 41. Distribution map of Porotrichum exapansum, P. piniforme and P. mutabile.



Porotrichum humile Mitten, J. Linn. Soc., Bot. **12:** 466. 1869; Calyptothecium humile (Mitten) Brotherus in Thériot, Bull. Acad. Int. Geogr. Bot. **13:** 86. 4. 1904, **syn. nov.** Type. Ecuador. Tungurahua, 2000 m, Spruce 1360 (holotype, NY!); isotype, BM!).

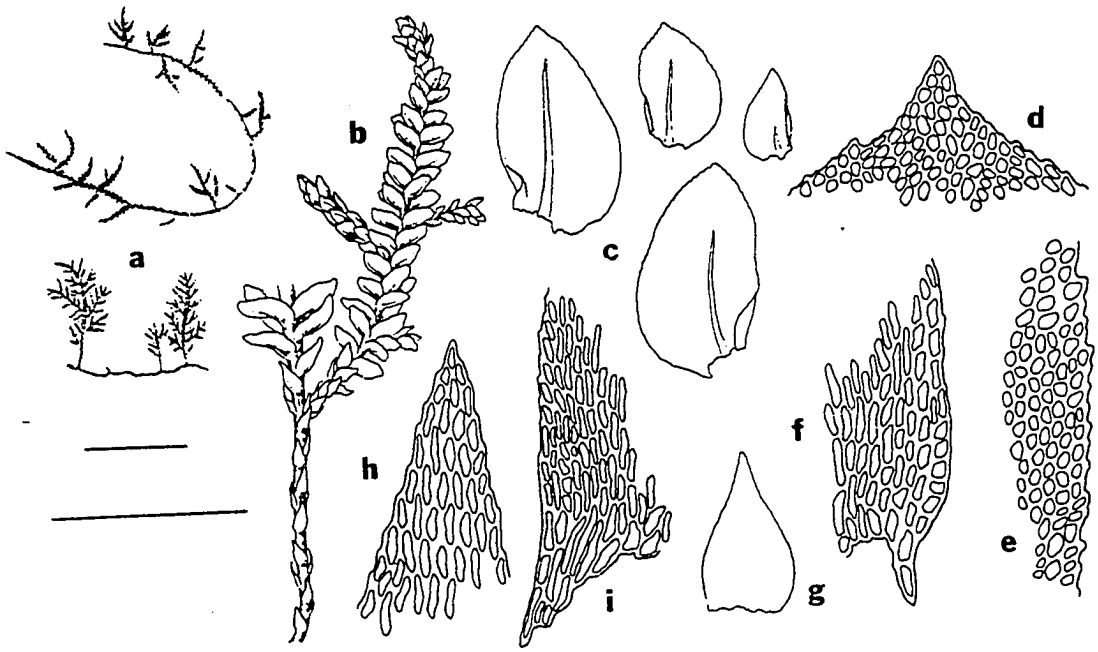
Homalia pendulina Schimper in C. Müller, Linnaea **39:** 458: 1875, nom. inval. in synon. Based on: Guadeloupe, L'Herminier (BM).

Pinnatella subpiniformis Brotherus, Denkschr. Akad. Wiss. Vien Math. Nat, Kl. **83:** 319. 1926. Type. Brazil. São Paulo: Serra do Cayazique, Santos, Schiffner 394 (lectotype H-BR!).

(Fig. 42).

Plants small, 3-5 cm tall, light green to yellow, slightly shiny, corticolous, frondose, complanate, branches tapering distally, becoming flagelliform branches. Axillary hairs 3-4 cells long, stalk cell short, quadrate; pseudoparaphyllia mostly filiform. Primary stem creeping, in cross-section elliptic, with 3-4 outer layers of rounded, small cells surrounding 9-12 inner layers of large hexagonal cells, central strand absent; leaves appressed, apices spreading, obovate-acute, 0.9-1.0 mm long; margins entire, sometimes incurved at apex; costa single; upper median cells irregularly fusiform, long rhomboidal to linear, 26-31 um long, 4-6 um wide. Secondary stem erect, in cross-section elliptic, with 3-5 layers of small rounded cells surrounding 10-12 inner layers of large hexagonal cells, central strand absent; stipe leaves erect-spreading from an erect to appressed base, ovate-acuminate, 1.0 mm long, 0.5 mm wide, acute, decurrent; margins serrulate; costa 2/3 the leaf length; upper median cells irregularly rectangular, 26 um long, 6 um wide, papillose by projecting angles, alar cells irregularly short-rectangular. Secondary stem leaves spreading, ovate-oblong, 1.5 mm long, 0.5-0.8 mm wide, slightly

Fig. 42. Porotrichum piniforme (Duss 1354, NY). a, small growth form (Duss 341, NY), x1; b, stipe and branch, x12; c, stem and branch leaves, x40; d, stem leaf apex, x400; e, stem leaf upper median and marginal cells, x400; f, stem leaf alar and basal cells, x400; g, stipe leaf, x40; h, stipe leaf apex, x400; i, stipe leaf basal and alar cells, x400.



asymmetric, acuminate; margins serrate to serrulate; costa 2/3 the leaf length, strong; apical cells oval to rhombic, 13 um long, 6 um wide, upper median cells oval, 18-21 um long, 6 um wide, basal cells rectangular, 26-31 um long, 4 um wide; branch leaves ovate. Sporophyte unknown.

Distribution and Ecology. (Fig. 41). This species if only known from the Lesser Antilles, Surinam, Ecuador and southern Brazil. It commonly grows as an epiphyte forming garlands or sparse mats on logs. Elevational range for Porotrichum piniforme is from sea level to 2000 m. In the Lesser Antilles it is frequently found near mountain summits and in very wet forests.

Specimens examined. GUADELOUPE. Vicinity of Grand Etang, 400 m, Crosby 4802 (NY), Etang, Duss 342 (NY), Pris de L'Eau near Vernoux, 23 Jun 1955, Farr 1713 (NY), Forests of Falion, 800 m, 7 Apr 1936, Allorge 17 (BM), No locality, Marie s. n. (BM, NY).

DOMINICA. From Bois Diable, at Four Hunt, 10 Jan 1914, Fishlock 24 (NY), near summits of Morne Couronne, 1200 m, 8 Jul 1892, Elliott 210 (BM), windward slopes of Morne Dialbotin, 17 Mar 1896, Elliot 2196 (BM).

ECUADOR. Tungurahua: At base of Tungurahua, 2000 m, Spruce 1360 (BM, NY), Baños, Spruce s. n. (NY).

BRAZIL. São Paulo: Serra do Cayazique at Santos, Jul 1901, Schiffner 394 (H-BR), Raiz da Serra, 20-50 m, 4 Jun 1901, Schiffner 713 (H-BR), Itú waterfall, Río Buturoba at Santos, 10 m, 12 Sep 1901, Schiffner 1532 (BM, H-BR), northern side of Cardoso island, Cananeia, 23 may 1974, Vital 3168 (NY).

Discussion. Porotrichum piniforme is easily recognized by the flat triangular fronds. It is distinguished from P. substriatum by the falt appearance, smooth leaves, and oval to rhombic cells. The type material of Porotrichum humile is a smaller and very branched form of P. piniforme. The former also has many small flagelliform branches which distort the typical growth form. Fleischer (1906) included P. piniforme in Pinnatella. The upper median cells rhombic to oval and serrate margin, place it within the concept of Porotrichum. Pinnatella is characterized by apical rounded to hexagonal cells and 1-2 papillae over the lumina. Since the sporophyte is unknown in this species the placement in the genus Porotrichum is based only one vegetative characters and in therefore provisional.

6. **Porotrichum mutabile** Hampe, Flora **45:** 456. 1862.

Neckera flabellata Hampe, Linnaea **31:** 525. 1862; Porotrichum variable Hampe, Ann. Sci. Nat. Bot. sér 5, **4:** 375. 1865. Type. Colombia. Tequendama, 2500 m, Lindig 2095 (lectotype, BM!).

Hypnum flagelliferum Hampe, Ann. Sci. Nat. Bot. sér. 5, **5:** 309. 1866; Porotrichum flagelliferum (Hampe) Mitten, J. Linn. Soc., Bot. **12:** 469. 1869; Thamnium flagelliferum (Hampe) Kindberg, Hedwigia **41:** 234. 1902; Porothamnium flagelliferum (Hampe) Fleishcer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925, **syn. nov.** Type. Colombia. Manzanos, 2700 m, Lindig s. n. (holotype, BM).

Porotrichum insularum Mitten, J. Linn. Soc., Bot. **12:** 462. 1869, **syn. nov.** Type. Dominica: M'Imray (lectotype, NY!; isotype, BM); Martinique, ex Herb, Schimper (syntype, NY!); Guadelupe, Perrottet (syntype, NY!).

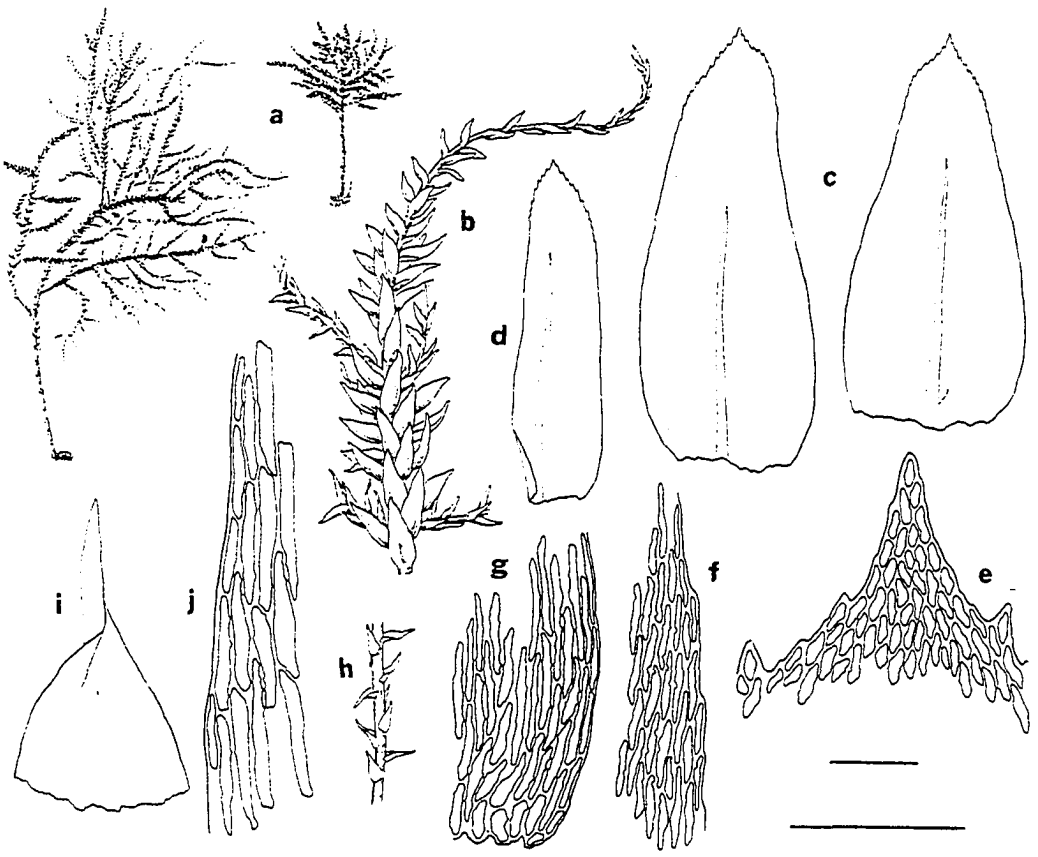
Porotrichum pittieri Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique. **32(1):** 188. 1894; Thamnium pittieri (Renauld et Cardot) Kindberg, Hedwigia **41:** 242. Type. Costa Rica: Irazu, Pittier 5648, Río Naranjo, Pittier 5704 (syntypes, G!, NY!).

Porotrichum hansenii C. Müller, Hedwigia **37:** 243. 1898; Thamnium hansenii (C. Müller) Brotherus, Nat. Pfl. **1:** 862. 1906, fide Crum, Scientific Survey of P. R. and Virgin Islands **7**(4): 528. 1958. Type. Jamaica. 1897. Hansen s. n. (n. v.)

(Fig. 43 a-j).

Plants medium to large, 3-10(13) cm tall, dark green, yellow green to yellow-brown, sometimes glossy, frondose, regularly pinnate to irregularly bipinnate, to sparsely branched, flagelliform branches distally at the apex or in leaf axils. Axillary hairs 2-3 cells long, stalk cell short-quadratge to short-rectangular; pseudoparaphyllia foliose. Primary stem creeping, in cross-section elliptic, with 3-4 layers of outer small cells surrounding 6-7 inner layers of large, thick-walled, hexagonal, central strand present; leaves erect-spreading, broadly obovate, short- to long-subulate, 0.8-1.0 mm long; margins entire, plane to somewhat incurved at subulae, costa single; upper median cells linear, 34-65 um long; 6-10 um wide, slightly pitted throughout. Secondary stem in cross-section elliptic, with 4-6(7) layers of outer small cells surrounding 8-10(12) layers of inner hexagonal, thick-wallwed cells, central strand present; stipe leaves erect-spreading from an erect or slightly appressed base, broadly triangular-subulate, 1.5-2.0 mm long, subulae becoming longer on more distal leaves on stipe; margins entire; costa single; cells linear throughtout, 52-100 um long, 8-10 um wide, pitted. Stem leaves erect to erect-spreading, sometimes faintly plicate when dry, ovate-ligulate to

Fig. 43. Porotrichum mutabile (Buck 9497, NY). a, small and large (Slageren 137, NY) habit form, x1; b, stem showing flagelliform branches, x1; c, stem leaves, x40; d, branch leaf, x40; e, stem leaf apex, x400; f, stem leaf upper median and marginal cells, x400; g, stem leaf basal cells, x400; h, stipe, x1; i, stipe leaf, x40; j, stipe leaf upper median and marginal cells, x400.



oblong-ligulate, 3.0-5.0 mm long, 1.0-1.5 mm wide, broadly acute to obtuse, short apiculate; margins distincly or scarcely serrate at apex; costa reaching 1/2-2/3 the leaf length, broad at base, sometimes tapering distally; cells at apex rhomboidal, 26-31 um long, 8 um wide, slightly pitted, median cells linear, 31-65 um long, 6 um wide, basal cells linear, 52-78 um long, 4-6 um wide, pitted, mostly thick-walled, papillose by projecting angles; branch leaves erect-spreading to spreading, oblong-ligulate, acute; margins serrate only at apex; costa 1/2 to 2/3 the leaft length; upper median cells linear to irregularly rectangular, 39-65 um long, 6 um wide, pitted. Dioicous. Perichaetial leaves oblong-subulate, 2.0-3.0 mm long; margins entire; costa absent; marginal cells rectangular, 25-20 um long, 8 um wide, upper median cells linear, 31-65 um long, 8 um wide, pitted. Seta 4.0-5.0 mm long, reddish, smooth; capsules 2.0 mm long; exothecial cells short-rectangular, thick-walled; exostome teeth lanceolate, striate at base, striate with overlying papillae, becomign papillose toward apex; endostome segments lanceolate, papillose, perforate, cilia rudimentary. Calyptra not observed. Spores not observed.

Distribution and ecology. (Fig. 41). This species is widespread in the West Indies, Central America and northern South America as far south as Ecuador. Porotrichum mutabile occurs as an epiphyte or saxicole in lowland forests to cloud forests (from sea level to about 2100 m), but it is more frequently found between 500-1500 m.

Representative specimens examined. NICARAGUA. Esteli: Cerro Quiabú, 1600 m, 25 Dec 1982, Moreno 19249A (MO, NY).

COSTA RICA. Alajuela: San Pedro de San Ramón, 23 Jul 1932, Brenes 24 (NY), vicinity of La Palma, 1450-1550 m, 6-8 May 1906, Maxon 384a (NY); Heredia: Las Vueltas area, valley of Río Patria, where regional road 113 crosses river, 2100 m, 29 Mar 1973, Crosby et al. 6417 (MO); San José: N of La Palma area, slopes S of Río Zurqui, 1600 m, 23 mar 1973, Crosby et al. 6244 (MO).

PANAMA. Cocle: N of El Valle de Anton, base of Cerro Pilón, 1000 m, 27 Mar 1969, Crosby 4398B (MO); Colón: 1-2 hr. walk along path beginning at end of Santa Rita ridge Road, 350-450 m, 22-23 May 1975, Crosby 10356 (MO); Darien: Serranía de Pirre, narrow ridge from Altos de Nique to Cerro Pirre, 1430-1480 m, 27 Jul 1976, Croat 37833 (MO); Panamá: Cerro Campana, 750-900 m, 15 May 1975, Crosby 10075 (MO); Veraguas: 1.7 km along road leading E just above Escuela Agrícola, Alto de Piedra, N-lower slope of Cerro Tute, 750 m, 18 May 1975, Crosby 10268 (MO).

CUBA. Santiago de Cuba: La Gran Piedra, 1000-1200 m, 4 Aug 1982, Buck 7638 (H, NY), 4-5 Mar 1911, Shafer 9112 (H), Slopes of Turquiño Peak, 10-26 Jun 1936, Acuña 369 (NY), Cobre range, Dec 1928, Clemente 2330 (NY).

JAMAICA. New Haven Gap, 1600 m, 4 Dec 1896, Harris 20 (H), upper slopes of John Crow Peak, 1650-1750 m, 12 Mar 1920, Maxon 1727 (BM, NY), Maxon 1068 (BM), 2 Feb 1903, Underwood 798 (NY); St. Andrew Parish: Just S of Hardwar Gap, along Fairy Glen Trail, 1200-1500 m, 12 Apr 1981, Crosby 13789 (NY), St. Catharine Peak, 29 Aug 1906, Nichols 91 (NY); St. Thomas Parish: Along trail from Portland Gap to Blue Mountain Peak, 1780 m, 10 Aug 1966, Crosby 3488 (NY); Trelawny Parish: Cockpit Country, near Troy, 13-18 Sep 1906, Britton 274 (NY).

HAITI. Sud'est: Massif de la Selle, 5 km E of Seguin on road to Mare, 1780 m, 22 Nov 1982, Buck 9497 (NY), 19 km S of Kencoff on road from Port-au-Prince to Seguin, 1600 m, 10 Nov 1982, Buck 9000 (NY); Grand'anse: Massif de la Hotte, on the southern slope of Ma Blanche, 1400 m, 7 Aug 1917, Ekman 512b.

DOMINICAN REPUBLIC. Barahona: Montiada Nueva, SE of Polo, 1060 m, 21 Aug 1946, Howard s. n. (NY); Elias Piña: Sierra de Neiba, along the Haitian border, 1400 m, Jul 1967, Norris et al. 6881a (NY); Estrelleta: Sierra Neiba, along Internacional Hwy, 1800 m, 27 Nov 1979, Smith 10254 (NY); Independencia: 4 km S of El Aguacate on road to Pedernales, 1300 m, 21 Mar 1981, Buck 4693 (NY); Pedernales: Las Abejas, 55 km N of Port of Cabo Rojo, on Alcoa road, 1090 m, 5 May 1982, Steere 22829 (NY), Las Abejas, ca 40 km N along road from Cabo Rojo from junction of road to Ovideo, 1170 m, 13 Mar 1981, Buck 4350 (NY); Santiago: Pico Diego de Ocampo, 1170 m, 17 May 1976, Judd 1540 (NY); La Vega: Pyramids site, 40 km S of Constanza, 2300 m, 3 Apr 1981, Buck 5350 (NY).

PUERTO RICO. Fajardo: Caribbean National Forest, Luquillo Division, along trail from road 186 to top fo El Toro, 1074 m, 25 Feb 1981, Buck 3573 (NY), along trail to Mt. Britton, 941 m, 24 Feb 1981, Reese 14352 (NY), Sierra de Naguabo, El Duque, NW side and summit, 750-1080 m, 13 Aug 1914, Shafer 3717 (BM, H), NW slope of Sierra de Luquillo above el Verde, 26 Jan 1940, Steere 6305 (MO), Middle slopes of Mount El Toro, 12 Oct 1939, Steere 4342 (MO), Summit of Mount Britton, 6 Oct 1939, Steere 4248 (MO), Sierra de Cayey, Guavate Purchase Unit, 3 Nov 1939, Steere 4734 (MO, NY); Ponce: Cordillera Central S of Jayuya, 20 Mar 1940, Steere 6899 (NY), Cerro Punta, Cordillera Central S of Jayuya, 20 Jan 1940, Steere 6225 (MO), Reserva Forestal de Maricao, along Hwy 120, near picnic area, 875 m, 28 Feb 1981, Reese 14572 (NY).

SABA. Mount Scenery, 800 m, 6 Aug 1981, Wiersma 234M (NY).

ST. KITTS. Belmont Estate, 8 Sep - 5 Oct 1901, Britton et al. 406 (NY); Trinity Palmetto Point Parish: Mount Misery, Camp Crater Mountain, 600-700 m, 9 Aug 1967, Wadsworth 675a (NY).

GUADELOUPE. Basse Terre: Road la Travesée, 600 m, 20 Jul 1976, De Sloover 23.616 (MO), along trail between Plateau de Papaye and Ravine Chaude, 26 Nov 1959, Proctor 20163 (MO), Matouba, 1902, Duss 1050 (H), Basse Terre, 15 Apr 1981, Sloover 33857 (H, MO), River Saint-Louis, 22 Feb 1936, Allorge 16 (BM), 1877, Marie s. n. (BM).

DOMINICA. Herb. Mus. Hamb. (H) Laudat, 30 Jun 1902, Lloyd 87 (NY), Bois Diable, Four Hunt, 330 m, 10 Jan 1914, Fishlock 7 (NY): St. George Parish: Girondel, 25 Mar 1978, Hegewald 9568 (NY); Boiling Lake, Noel 23 (BM), Morne Micotrin, 1060 m, 13 Jan 1896, Elliott 1122 (BM), Windward slope of Diablotin 1000 m, 17 Mar 1896, Elliott 2190b (BM).

MARTINIQUE. Palée, 1899, Duss 37 (H), Sulfurense des Deux-Choux, 680 m, 5 Jan 1941, Stèhle 3870 (NY), between Deux-Choux and Calvaire, Gros Morne, 700 m, 24 Dec 1940, Stehle 3819 (NY).

ST. VICENT. Charlotte Parish: Perseverance, slope of Mt. Brisbane, 420 m, 12 Apr 1962, Cooley 8621a (NY), Mt. St. Andrews, 750 m, 21 Dec 1891, Elliott 70 (BM). Richmond Peak, 100 m, 1 Feb 1892, Elliott 170b (BM).

GRENADA. Mt. S. Catherine, 800 m, Dec 1889, Eggers 6179 (H), Azimas Mountains, 17 Nov 1905, Broadway 1837 (NY).

TRINIDAD. St. George: Northern range, trail up southern slopes of Cerro del Aripo, 480 m, 5 Jul 1965, Crosby 2203 (MO).

COLOMBIA. Antioquia: Urrao, ca 58 km S of Urrao toward Betulia, before the slopes toward Valle Pabón, 2770 m, 28 Jun 1985, Churchill, Sastre et al. 13251 (NY); Cundinamarca: On road Mosquera-La Mesa, below La Merced, place above las Quebradas, 2340 m, 19 Dec 1967, Hammen et al. 2633 (MO).

VENEZUELA. Trujillo. Between La Peña and Agua de Obispo, 22 km from Carache, 2400-2500 m, 1 Mar 1971, Steyermark 105001 (MO), Boconó, above the village of Santa Rita, along trail leading to the Páramo de Santa Rita, Aug 1975, Griffin et al. 1233 (FLAS, NY).

ECUADOR. Morona Santiago: Cutucú, 1800 m, Ortega 458a (MO); Pichincha: Vicinity of Río Alambí, along road leading W from Nono toward Tandayapa, N slopes of Mt. Pichincha, 2320 m, 7 Jun 1975, Crosby 10560 (MO).

Discussion. This species is characterized by the ovate-ligulate to oblong-ligulate stem and branch leaves, serrate only at the apex. Distally, the branch leaves are wide spreading and tend to become ligulate with a narrower leaf apex. The stipe leaves are usually spreading from an erect base and those that are more distal along the stipe have longer subula. Flagelliform branches were observed more commonly in collections from very wet forests. Plants of this species in general are dark green to yellow-green with a wiry texture. The name "mutabile" alludes to the different growth forms of this species. Plant size as well as leaf orientation are very variable. This species has been confused commonly with Thamnobryum fasciculatum from which it can be distinguished by its less crowded stipe leaves, branch leaves becoming narrower distally, slender costa, and fusiform to linear apical cells. Apices of stem leaves and the ligulate branch leaves clearly separate P. mutabile from P. korthalsianum.

Four different localities (Bogotá, Tequendama, Canoas and Choachi) with one collection number (2095) are cited in the protologue, the one labeled as Tequendama was selected as lectotype.

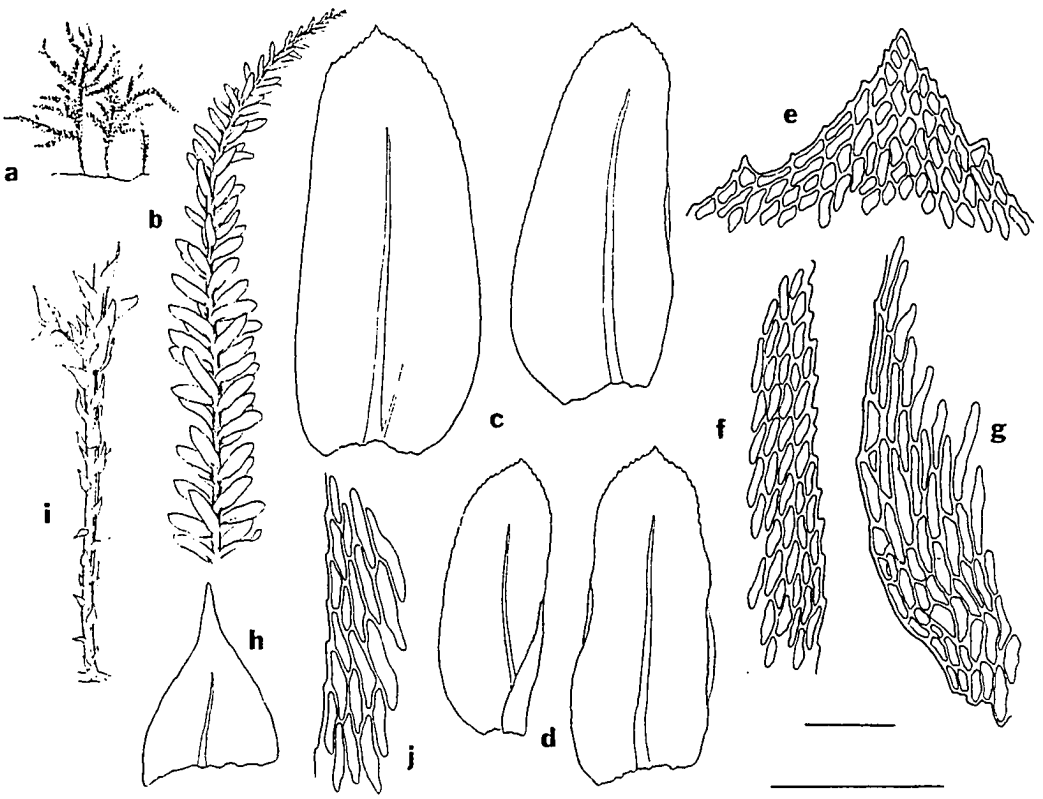
7. **Porotrichum korthalsianum** (Dozy & Molkenboar) Mitten, J. Linn. Soc., Bot. **12:** 463. 1869.

Neckera korthalsiana Doxy & Molkenboer, Prodr. Fl. Bryol. Surinam. **42:** 1854. Type. Surinam, ex herb. Dozy et Molkenboer (isotypes, BM!), NY!).

Porotrichum cobanenses C. Müller, Bull. Herb. Boissier **5:** 202. 1877; Thamnium cobanesnse (C. Müller) Williams, Contr. U. S. Natl. Herb. **16:** 24. 1912, **syn. nov.** Type. Guatemala. Alta Verapaz: in sylva prope Cobán, ad arbores, 4800 ped. altum, 14 Feb 1886, Türckheim s. n. (isotypes, BM!, NY!). (Fig. 44 a-j).

Plants medium size to large, 7.0 cm tall, yellow-green to green, glossy, irregularly branched, sparsely frondose. Axillary hairs 3-4 cells long, stalk cell short rectangular; pseudoparaphyllia foliose. Primary stem creeping, in cross-section elliptic, with 3-4 outer layers of rounded cells syrrounding 4-5 layers of inner hexagonal, thick-walled cells; leaves obovate-subulate, 0.5 mm long; margins entire to slightly serrate at apex; costa present; upper median cells irregularly rectangular, 39-57 um long, 6 um wide. Secondary stem erect. Stipe mostly short to sometimes long; in cross-section with 4-5 outer layers of rounded cells surrounding 7-10 layers of inner thick-walled cells, central strand present; stipe leaves erect-spreading to spreading, broadly triangular-subulate, 1.0-1.5 mm long, margin entire, plane or slightly recurved at base; costa single; cells mostly linear throughout, 39-60(78) um long, 6 um wide, slightly pitted. Secondary stem leaves ovate-ligulate to mostly ligulate, 2.0-3.0 mm long, 0.8-1.0 mm wide, broadly acute to obtuse, short apiculate; margins serrate at apex, sometimes upper half serrulate, sometimes somewhat recurved at base; costa 2/3-3/4 of the leaf length; apical

Fig. 44. Porotirchum korthalsianum (Steere 5869, NY). a, habit, x1; b, branch showing flagelliform branch, x1; c, stem leaves, x40; d, branch leaves, x40; stem leaf apex, x400; f, stem leaf upper median and marginal cells, x400; g, stem leaf basal cells, x400; h, stipe leaf, x40; i, stipe, x1; j, stipe leaf upper median and marginal cells, x400.



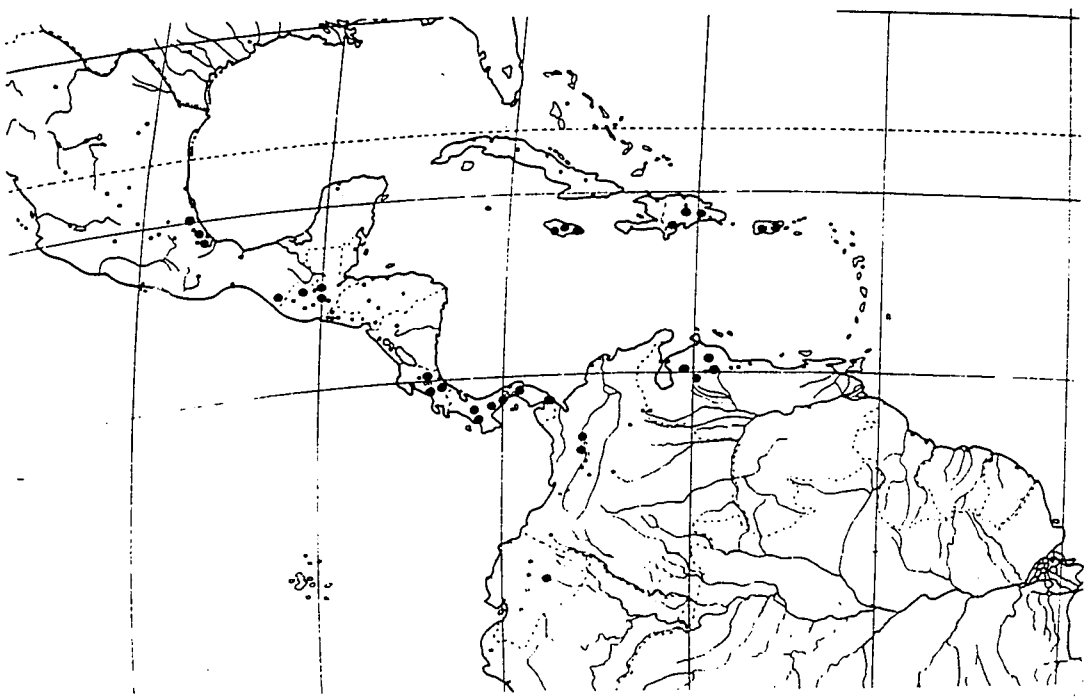
cells rhomboidal, 21-26 um long, 10 um wide, upper median cells long rhomobidal to fusiform, 39-60 um long, 6-8 um long, basal cells fusiform to rectangular, 52-78 um long, 8-10 um wide; branch leaves oblong, ligulate, broadly acute to obtuse; margins serrate at apex becoming serrulate below; flagelliform branches rare. Dioicous. Perigonial leaves ovate-subulate, 1.0-1.4 mm long, margins entire; costa absent; upper median cells fusiform, 52-78 um long, 8 um wide, pitted. Perichaetial leaves oblong-subulate, 2.0-4.0 mm long, margins entire; costa mostly absent, single; upper median cells fusiform, 60-78 um long, 6-8 um wide, pitted. Seta 1.0 cm long, smooth; capsule erect, ovoid, 1.0-2.0 mm long; stomata present; exothecial cells quadrate; exostome teeth lanceolate, papillose; endostome with a high basal membrane, segments papillose, perforate. Calyptra and spores not observed.

Distribution and Ecology. (Fig. 45). This species is a typical epiphyte of lower montame and cloud forest in the West Indies, Central America and northern South America.

Representative specimens examined. MEXICO. Chiapas: Motozintla and Huixtla, 1300 m, 14 Mar 1979 Eggers s. n. (NY); Veracruz; Jalapa, 1500 m, 12-20 Dec 1909, Murrill 23a (NY), near the summit of Cerro de Cuhuatepetl, 939-1150 m, 31 Aug 1944, Vera 3348 (NY), Zacuapan, Apr 1908, Purpus 4303 (NY), Jalapa, 1150 m, 12-20 Dec 1909, Murrill et al. 1 (NY).

GUATEMALA. Alta Verapaz: Río Cobán, between Cobán and San Pedro, 1200 m, Johnson 602 (NY), Cobán, 1350 m, Jul 1908, Türckheim 7142 (NY); Baja Verapaz: On road near Jicaro, 1300 m, 21 Feb 1945, Sharp 2701 (MO); Quiché: Along Juarco River below Nebaj, 1800 m, 5 Feb 1945, Sharp 2386 (MO).

Fig. 45. Distribution map of Porotirchum korthalsianum



COSTA RICA. Alajuela: Colinas de San Ramón de San Pedro, 18 Jan 1934, Brenes 18995 (NY); Heredia: S slope Volcán Barba, 1 km WNW of Río Ciruelas, 1900 m, 3 May 1975, Crosby 9888 (MO); San José: Cerro de Piedra Blanca, above Escasú, 31 Jan 1924, Standley 32529 (H).

PANAMA. Chiriquí: SW of Campamento de Fortuna, Cerro de la Fortuna, 1000-1200 m, Sep 1976, Salazar et al. 663 (NY); Coclé: N of Valle de Anton, base of Cerro Pilón, 1000 m, 28 Mar 1969, Crosby 4413 (MO); Darién: Cerro Mali, 1200 m, 16 Jan 1975, Mori et al. 4311 (MO); Panamá: below Su-Lin Motel, Cerro Campana, 1000 m, 31 Mar 1969, Crosby 4496 (MO); Veraguas: NE slope below Cerro Tute, 3.5 km leading E just above Escuela Agrícola, Alto Piedra, 800-1000 m, 19 May 1975, Crosby 10276 (MO).

JAMAICA. Lower Buzza, 16 Jan 1897, Harris 11065 (NY); New Haven Gap, 1700 m, 4 Dec 1896, Harris 11073 (NY), Olyde river valley, below Cinchona forest, 1200 m, 31 Jan 1903, Underwood 381 (NY).

DOMINICAN REPUBLIC. La Vega: Vicinity of pyramids, 13.8 km S of Valle Nuevo, 44.7 km S of Constanza, 2200 m, 30 Apr 1982, Buck 8061 (NY), 4.7 km S of Constanza, 1800 m, 27 Apr 1982, Shaw 5459 (NY).

PUERTO RICO. Fajardo: Sierra de Luquillo, old Catalina Yunque Trail, 4 Jan 1940, Steere 5869 (MO); Ponce: Adjuntas, Reserva forestal de Guilarte, along trail up Monte Guilarte, 1205 m, 2 Mar 1981, Buck 3935 (NY).

COLOMBIA. Antioquia: Jardín-Riosucio, 1920 m, 12 May 1986, Escobar et al. 858 (NY).

VENEZUELA. Lara: N of Urachiche, border between Yaritagua and Lara, 1450 m, 28 Mar 1975, Steyermark et al. 111725 (MO); Portuguesa: 15-18 kms NNW of Ospina, 700-800 m, 1 Nov 1982, Steyermark et al. 126995 (MO).

ECUADOR. León: Valle of Río Macuchi, 1500 m, 8 Sep 1943, Steere 8951 (NY); Napo: Valley of Río Chingual E of El Pun, 2200-3000 m, Steere 8918 (NY).

Discussion. Macroscopically, this species can be recognized by the shiny green color, spreading stipe leaves and obtuse branches. It can be separated from P. mutabile by the slender and soft appearance of the plants, obtuse branch leaves and distal branch leaves which are erect and not spreading as in P. mutabile. Stipes may be short or well developed. The type specimen of P. korthalsianum includes plants of small stature which represent an extreme of growth form in this species. Basal leaf margins may be plane or recurved. Recurved margins are mostly observed in the smaller plants.

8. **Porotrichum longirostre** (Hooker) Mitten, J. Linn, Soc., Bot. **12:** 461. 1869.

Neckera longirostris Hooker, Musci, Exot. **1:** 1. 1818; Thamnium longirostre (Hooker) Kindberg, Hedwigia **41:** 233. 1902. Type. Temperate region in "jugis Andium," Humboldt & Bonpland s. n. (holotype, BM!; isotype, NY!).

Leskea gymnopoda Taylor London J. Bot. **5:** 62, 1846; Porotrichum gymnopodon (Taylor) Mitten, J. Linn. Soc., Bot. **12:** 465. 1869; Thamnium gymnopodum (Taylor) Kindberg, Hedwigia **41:** 243: 1902; Porothamnium gymnopodum (Taylor) Fleischer, Musci Fl. Buitenzorg **3:** 926. 1908, **syn. nov.** Type. Ecuador. Western slopes of Pichincha, Jameson s. n. (holotype, FH!).

Hypnum floridum Taylor, London J. Bot. **6:** 339. 1847; Porothamnium floridum (Taylor) Williams, Bryologist **31:** 113. 1928. Type. Ecuador. Near Quito, 22 Dec 1846, Jameson s. n. (holotype, FH!).

Porotrichum scoposum Hampe, Ann. Sci. Nat. Bot. sér. 5: **4:** 374. 1865; Thamnium scoposum (Hampe) Kindberg, Hedwigia **41:** 243. 1902, **syn. nov.** Type. Colombia. Bogotá, Guadalupe, 2900 m, inter frutices, Aug 1863, Lindig s. n. (holotype, BM!; isotype, NY!).

Porotrichum minus Hampe, Ann. Sci. Nat. Bot. sér. 5, **4:** 376. 1865; Thamnium minus (Hampe) Kindberg, Hedwigia **41:** 245. 1902. **syn. nov.** Type. Colombia. Bogotá. Tequendama, Canoas, 2500 m, Lindig 2095 (holotype, BM).

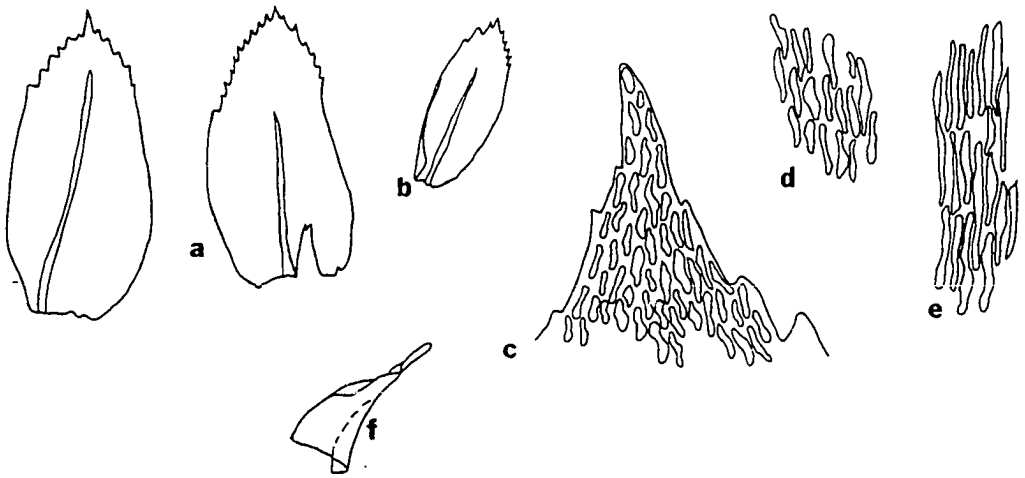
Porotrichum mexicanum Schimper ex Bescherelle, Mém. Soc. Sci. Nat Cherbourg **16:** 246. 1872; Thamnium mexicanum (Schimper ex Bescherelle) Kindberg, Hedwigia **41:** 234. 1902. Type. Mexico. Orizaba, (no collector) (holotype, BM!; isotypes, G!, NY!).

Porotrichum plagiorhynchum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique. **32.** 186. 1894; Thamnium plagiorhynchum (Renauld & Cardot) Kindberg, Hedwigia **41:** 233. 1902. Type. Costa Rica. Barba, 2500-2800 m, Pittier 5644 5724 (syntypes, NY!).

(Fig. 46 a-f).

Plants mostly medium-sized, 4.0-7.0 cm tall, pale green to yellow-green, typically frondose, irregularly pinnate to bipinnate; branches becoming attenuate distally. Axillary hairs 3-4 cells long, stalk cell short-quadrate; pseydoparaphyllia foliose. Primary stem mostly covered by rhizoids, in cross-section elliptic, with 3-4 outer layers of small cells, surrounding 6-7 layers of inner hexagonal, thick-walled cells, central strand present; leaves somewhat clasping at base, broadly triangualr, acute; margin entire; costa absent or present, single; upper median cells linear to irregularly rectangular, 52 um long, 6 um wide. Stipe erect, short-

Fig. 46. Porotrichum longirostre (Humboldt & Bonpland s. n., BM). a, stem leaves, x40; b, branch leaf, x40; c, stem leaf apex, x400; d, stem leaf upper median cells, x400; e, stem leaf basal cells, x400; f, stipe leaf, x40.



to long-stipitate, reddish-brown; in cross-section elliptic, with 3-4 outer layers of small cells surrounding 6-10 layers of inner hexagonal, thick-walled cells, central strand present; stipe leaves erect to erect-spreading, base somewhat appressed, becoming eroded, obovate-triangular, 1.0-1.5 mm long, larger distally, acute; margin entire, plane; costa single, short; upper median cells mostly linear, 34-65 um long, 6 um wide. Secondary stem leaves erect to erect-spreading, sometimes faintly striate when dry, ovate-lanceolate, 2.28-3.0 mm long, 1.0-1.5 mm wide, broadly acute to acute, short to long apiculate margin serrate at apex, becoming serrulate below the apex; costa 2/3 to 3/4 the leaf length; apical cells rhombic to rhomboidal, 13-26 um long, 8-10 um wide, median cells linear to long fusiform, 39-65 um long, 6 um wide, basal cells linear to rectangular, 39-78 um long, 6 um wide, sometimes with slightly thickened ends; branch leaves oval to oval-ligulate, size variable, acute; apex sharply serrate, serrulate below apex to base; costa 2/3 the leaft length; upper median cells long-hexagonal, 26-39 um long, 6 um wide; branch leaves ovate, acute; margins serrate in upper half. Dioicous. Perigonia not observed. Perichaetia on main stem or branches, leaves ovate-subulate, 2.0-2.5 mm long; margins entire; costa absent; upper median cells fusiform to linear, 52-78 um long, 6-8 um wide, prorulate. Setae 2.0-3.0 cm long, reddish brown; capsule erect to slightly horizontal, ovoid-cylindric, 2.0 mm long; exothecial cells quadrate to short-rectangular; stomata present; annulus present; operculum conic, long rostrate; exostome teeth striate with overlying papillae at base, papillose above, at back papillose; endostome segments from a high basal membrane, papillose, perforate, papillose on both surfaces, cilia mostly short. Calyptra not observed. Spores spherical, 18 um in diameter.

Distribution and Ecology. (Fig. 47). This species is widespread in the West Indies, Central and South America, where it is a very common epiphyte in lower montane, montane and subpáramo vegetation. It is mostly found from 1500 to 3000 m.

Representative specimens examined. MEXICO. Veracruz: Acajete, 1750 m, 3 May 1980, Ventura 17106 (MO).

GUATEMALA. San Marcos: Slope of Tajumulco above El Porvenir, 3000 m, 25 Feb 1946, Sharp 5468 (MO); Sololá: Volcán Tolimán (side facing Volcán Atitlán), 2700-3100 m, 13 Jun 1942, Steyermark 47568 (MO).

EL SALVADOR. Ridge trail in direction of Honduritas from Hacienda Monte Cristo Area, 29 Oct 1977, Watson ES-0090 (MO).

COSTA RICA. Alajuela: Slope of Volcán Poás, at the bridge just S of the hacienda El Tirol, 780 m, 2 Jul 1967, McAlpin 332 (MO). Biological Reserve of Monte El Verde, 0.5 km along trail leading SE to Brillante section of reserve, 1500 m, 6 May 1975, Crosby 10010 (MO); Cártago: I. C. E. Tapantí Project area, 15 km ESE of city of Cártago, 1400 m, 13 Mar 1973, Crosby et al. 6077 (MO), Santa Clara de Cartago, 1950 m, 20 Jul 1923, Maxon et al. 8177, 8216 (H); Heredia: Volcán Barba, Pacific slope, above Sacramento, 2600 m, 6 Feb 1979, Griffin et al. D232 (MO), Porrosati area, valley of Río Ciruelar at end of regional road 114, N of village of Barba, 2250 m, 30 Mar 1973, Crosby et al. 6459 (MO); San José: SE slopes of Cerros de Zurqui, N of village of San Luis Norte, 1840 m, 28 Mar 1973, Crosby at el. 6378 (MO), N of La Palma area, slopes S of Río Zurqui, on regional road 220 beyond San Jerónimo, 1600 m, 23 Mar 1973, Crosby et al. 6245 (MO).

Fig. 47. Distribution map of Porotrichum longirostre.

ECUADOR. Azuay: Gualaquiza, 20 Aug 1909, Allioni 8353 (H), Gualaquiza, at Rosario, 1000 m, 10 Jun, Allioni 437 (H).

PERU. Huanuco: Above Mito, about 20 km N of Huanuco, 2700 m, Apr 1923, Bryan 216 (MO).

BRAZIL. Minas Gerias: In Serra de Caldas, Mosén 426, 427 (H), Serra de Itatiaia, Mont Serrat, 900 m, Dusén 1574 (H).

Discussion: As reported by Bartram (1949) in Mosses of Guatemala, this taxon shows great variation is stem leaf shape, ranging from ovate-lanceolate, ovate, to ovate-ligulate. There is also variation in the stipe leaf angle of orientation which can range from being completely appressed against the stipe to slightly erect-spreading. The oval-ligulate upper branch leaves with coarsely serrate apices are the best characters by which to recognize this variable species. Much variation is also observed in the branching pattern or growth habit, for example, P. scoposum was described on the basis of a compact and brush-like habit but the branch leaves are consistent with the characters mentioned above. Hampe (1865) commented in this diagnosis that the distinguishing character between the two species is the profusive branching. Plants may range from a triangular, regularly pinnate frond to a broad, sparsely branched frond.

9. **Porotrichum lancifrons** (Hampe)

Hypnum lancifrons Hampe, Linnaea **32:** 158. 1863; Porotrichum lancifrons (Hampe) Mitten, J. Linn, Soc., Bot. **12:** 462. 1869; Thamnium lancifrons (Hampe) Kindberg, Hedwigia **41:** 235, 1902; Porothamnium lancifrons (Hampe) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925, **syn. nov.** Type. Colombia. Manzanos, 2700 m, Jul, Lindig 2117 (holotype, BM!).

Hypnum neckeraeforme Hampe, Ann. Sci. Nat. Bot. sér. 5, **5:** 309. 1866; Thamnium neckeraeforme (Hampe) Kindberg, Hedwigia **41:** 226. 1902; Porothamnium neckeraeforme (Hampe) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925. **syn. nov.** Type. Colombia. Bogotá, Choachi, 2600 m, Sep 1860, Lindig s. n. (holotype, BM!).

Porotrichum striatum Mitten, J. Linn. Soc., Bot. **12:** 462. 1869; Porothamnium striatum (Mitten) Fleischer in Brotherus, Nat. Pf. ed. 2. **11:** 198. 1925, **syn. nov.** Type. Brazil. Sierra between Antonina et Corritiba, Weir 76 (lectotype, NY; syntype BM!).

Porotrichum explanatum Mitten, J. Linn. Soc., Bot. **12:** 468. 1869; Thamnium explanatum (Mitten) Kindberg, Hedwigia **41:** 227. 1902; Porothamnium explanatum (Mitten) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925, **syn. nov.** Type. Ecuador. Andes Quitenses, Quito, Jameson s. n.; Perú. Andes Peruvianae, Tarapoto, Spruce s. n. (lectotypye, NY!; syntype, NY!).

Porotrichum ramosissimum Hampe, Vid. Medd. Naturh. For. Kjoebenh. ser. **9, 7:** 155. 1874; Thamnium ramosissimum (Hampe) Kindberg, Hedwigia **41:** 241. 1902; Porothamnium ramosissimum (Hampe) Fleischer in Brotherus, Nat. Pfl. 2. **11:** 198. 1925, **syn. nov.** Type. Brazil. Rio de Janeiro. Glaziou 6388a (holotype, BM!).

Porotrichum porrectulum C. Müller, Linnaea **42:** 408. 1879; Porothamnium porrectulum (C. Müller) Fleischer in Brotherus, Nat. Pfl. 2, **11:** 199. 1925, **syn. nov.** Type. Argentina. Río Seco, at San Andrés, 17 Sep 1873, Lorentz s. n. (isostypes, H-BR!, NY!).

Porotrichum minutistolo C. Müller, Bull. Herb. Boissier **6:** 113. 1898; Thamnium minutistolo (C. Müller) Brotherus, Nat. Pfl. **1(3):** 869. 1906; Porothamnium minutistolo (C. Müller) Fleischer in Brotherus, Nat, Pfl. ed. 2, **11:** 198. 1925, **syn. nov.** Type. Brazil. Serra Itatiaia, 1900 m, Mar 1894, Ule 1886 (isotype, H-NR!).

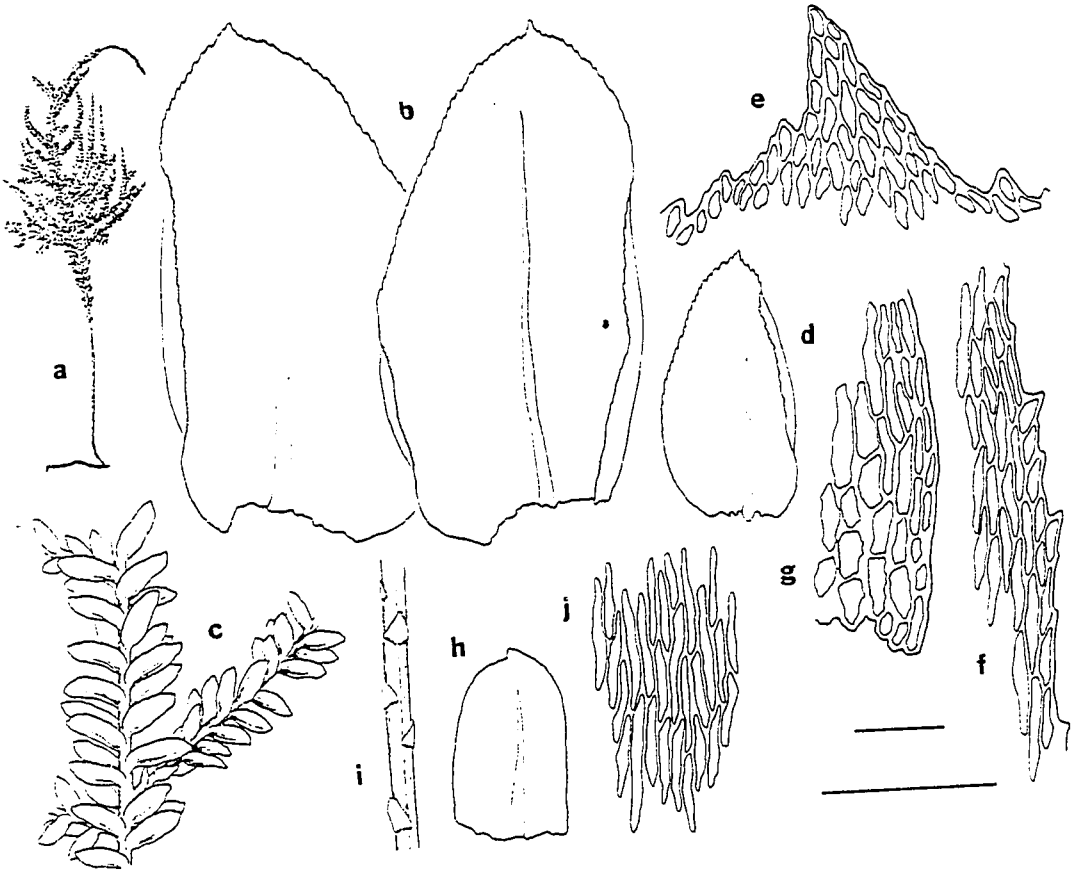
Thamnium campylocladum C. Müller, Bull. Herb. Boissier **6:** 118. 1898; Porothamnium campylocladum (C. Müller) Fleischer in Brotherus, Nat. Pfl. ed. 2, **11:** 199. 1925, **syn. nov.** Type. Brazil. Sa. Catarina: Serra Geral, Apr 1891, Ule 1193 (isotype, H-BR!).

Porotrichum riograndense C. Müller, Hedwigia **39:** 288. 1900; Thamnium riograndense (C. Müller) Brotherus, Nat. Pfl. **1(3):** 862. 1906; Porothamnium riograndense (C. Müller) Fleischer in Brotherus. Nat. Pfl. ed. 2, **11:** 199. 1925, **syn. nov.** Type. Brazil. Rio Grande do Sul: Forromeco, Morrodiablo, Kunert 1888; Sa. Catharina: Serra do Oratorio, Apr 1889, Ule 526 (syntype, H, BR!).

(Fig. 48 a-j).

Plants mostly robust, 9-11(13) cm tall, green to yellow green, mostly shiny, stipitate, "frondose". Axillary hairs 4-5 cells long, 1-2 short, quadrate stalk cells; pseudoparaphyllia foliose. Primary stem creeping, in cross-section elliptic, with 2-3 outer layers of thick-walled, rounded, small cells, surrounding 10-12 inner layers of large, thick-walled, hexagonal cells, central strand present; leaves erect to slightly erect-spreading, broadly ovate, 1.0 mm long, 0.9 mm wide, acute; margin entire; upper median cells linear, 95-120 um long, 6 um wide, papillose by projecting angles. Stipe long perpendicular from substrate, orange to dark brown, in cross-section round to elliptic, with 4-5 outer layers of small cells surrounding

Fig. 48. Porotrichum lancifrons (Harros 11046, NY). a, habit, x1; b, stem leaves, x40; c, stem and branch, x40; d, branch leaf, x40; e, stem leaf apex, x400; f, stem leaf upper median and marginal cells, x400; g, stem leaf alar cells, x400; h, stipe leaf, x40; i, stipe, x1; j, stipe leaf upper median cells, x400.



16-20 inner layers of thick-walled, hexagonal cells, central strand present; leaves erect-appressed, broadly obovate-apiculate, 1.5-2.0 mm long, 1.0 mm wide; margins entire, plane; costa short, single; upper median cells linear, 31-39 um long, 8 um wide; secondary stem leaves erect-spreading, mostly broadly ovate to broadly obovate, broadly acute, apiculate; margins serrate mostly of leaf apex, sometimes 1/3 down; costa extending 2/3 to 3/4 the leaf length; apical cells rhombic to short fusiform, 31-39 um long, 10 um wide, upper median cells fusiform, 50-65 um long, 6-8 um wide, basal cells linear to rectangular, 70-92(100) um long, 8 um wide, alar cells slightly differentiated; branch leaves smaller than stem leaves, obovate ligulate, apiculate; margins serrate from apex to base, slightly recurved at base; costa and cell pattern the same as in stem leaves. Dioicous. Perigonial leaves ovate, abruptly apiculate; margins entire; costa absent; upper median cells linear, 65-100 um long, 8 um wide. Perichaetial leaves oblong-subulate, 2.0-2.5 mm long, 1.0 mm wide; margins entire; costa absent; upper median cells linear, 80-100 um long, 8 um wide, pitted throughout. Seta 0.5-3.0 cm long, reddish-brown; capsule erect to horizontal, ovate-cylindric, 2.0-3.0 mm long; exotherical cells short rectangular; operculum rostrate; annulus present; exostome teeth striate below, papillose above, hyaline toward apex, endostome segments from a high basal membrane, papillose, perforate, cilia present. Calyptra not observed. Spores 13 um in diameter.

Distribution and ecology. (Fig. 49). This is a species typical of high elevations in the West Indies, Central and South America. It occurs from 500-3000 m, but it is more abundant 1500 to 2000 m.

Fig. 49. Distribution map of Porotrichum lancifrons.

Representative specimens examined. MEXICO. Chiapas: Tenejapa, in the Colina Achlum, 2700 m, 23 Aug. 1966, Breedlove 15227 (MO); Oaxaca: Ixtlán, 58 km N of Ixtlán, 11 km of high point at Cerro Pelón, 2000 m, 27 Oct 1969, Mickel et al. B4246 (NY); Veracruz: 13 km NE of Huayacocotla, on road to Zilacatipán, 1750 m, 10 May 1979, Juárez 1036 (MO).

COSTA RICA. Cartago: I. C. E. Tapanti Project area, 15 km SE of E of city center of Cartago, 1400 m, 13 Mar 1972, Crosby et al. 5711 (MO), just SE of summit of Cerro de la Muerte ridge, 45.7 km SE of El Emplame, along Interamerican Highway, 3050 m, 27 Apr 1975, Crosby 9784 (MO); Heredia: Immediate vicinity of Laguna Barba, 2600 m, 1 May 1975, Crosby 10926 (MO), Las Vueltas area, valley of Río Patria, vicinity where regional road 113 crosses the river, 2100 m, 29 Mar 1973, Crosby 6448 (MO); Limón: Cordillera Talamanca, Atlantic slope, Cerros Tararia, 2400-2600 m, 10 Sep 1984, Davidse et al. 28867 (MO); San José: Cerros de Zurqui, forest N of village of San Luis Norte, 1750 m, 23 Apr 1975, Crosby 9692 (MO).

CUBA. Santiago de Cuba: Sierra Maestra, La Bayamonesa, 1725 m, 4 May 1916, Ekman 7200 (BM).

JAMAICA. Blue Mountain Peak, 2200 m, 31 Dec 1896, Harris 11046 (MO, NY), Summit of Blue Mountain Peak, 2100-2200 m, 7-9 Jul 1926, Maxon 9933 (BM).

DOMINICAN REPUBLIC. Peravia: La Nevera, 2100 m, 7 Mar 1976, Liogier 24956 (MO, NY); La Vega: 4.7 km S of Constanza, then 8 km toward Pinar Parejo, 1800 m, 27 Apr 1982, Buck 7816 (NY).

VENEZUELA. Lara: Yacambú National Park, Sierra de Portuguesa, La Fría, 1400 m, 21 May 1978, Griffin et al. 64 (MO); Táchira: Junin, páramo de Tamá, above village Páex, Au 1975, Griffin et al. 353 (FLAS, NY); Trujillo: El

Romeral, area of páramo La Cristalina, 2900 m, 5 Aug 1973, Ruiz-Teran 9075 (FLAS, NY).

COLOMBIA. Antioquia: Medellín, ca 25 NW of Medellín, road to Boquerón, 2400-2600 m, 28 Jun 1986, Churchill & Sastre et al. 13925 (NY), Urrao, below Páramo Frontino, 3150-3500 m, 1 Jul 1985, Churchill & Sastre et al. 13422 (NY); Boyacá: Sierra Nevada de Cocuy, San José Valley, 3250 m, 11 Sept 1957, Crubb et al. B461 (BM); Magdalena: Parque Nacional de Santa Marta, 2900 m, Rangel et. al. 347 (FLAS, NY).

BRAZIL. Minas Gerais: Serra do Itatiaia, Retiro, 6 Jun 1902, Dusén s. n. (NY), Mountains of Itatiaya, 2750 m, 18 Nov. 1901, Schiffner 467 (BM); São Paulo: Apiahy, um 1880, Puiggari 570 (H).

BOLIVIA. Santa Cruz, 1800 m, 25 Aug 1902, Williams 1978 (BM, NY).

Discussion. Porotrichum lancifrons may be recognized by the erect stipe leaves, broadly ovate stem leaves, and distinctly papillose cells by projectin angles. Branch leaves are ovate to obovate with margins serrate to the leaf base. The great number of synonyms included here reflects the tremendous variation observed in this species. Plants may vary in size, reaching 15 cm tall. Seta length also was observed to range from 5 mm to 3 cm long. Vegetatively the type of Porotrichum explanatum matches that of P. lancifrons. The only difference observed was that in P. explanatum the seta is longer than that of P. lancifrons. This is also the situation as illustrated by Brotherus (1925) for P. ramosissimum, with setae of 5.0 mm, but which is vegetatively similar to P. lancifrons. Some collections studied from Costa Rica contained both forms and intermediates growing together. Seta length is another variable character in this species. Stem leaves usually are flat and wide spreading.

Appendix

Voucher specimens used in anatomical study.

1. Neckeropsis disticha (Hedw.) Kindb.

   Puerto Rico. Ciales, hwy 149, 2 km from town center on road to Manatí, limestone hills, Dec 1985, Sastre s. n. (NY).

2. Neckeropsis undulata (Hedw.) Reich.

   Puerto Rico. Ciales, hwy 149, 2 km from town center on road to Manatí, limestone hills, Dec 1985, Sastre s. n. (NY).

3. Neckera andina Mitten

   Peru. Cuzco: Anta, Indahuaco, 2 Jul 1977, Hegewald et al. 8877 (NY).

4. Neckera chilensis Schimp. ex Mont.

   Colombia. Antioquia: Sonsón, 12 km E of Sonsón on road to Nariño, 2580 m, 23 Jun 1985, Churchill & Sastre 13004 (NY).

5. Neckera scabridens C. Müller

   Colombia. Antioquia: La Ceja, 5.5 km SE of La Ceja and La Unión, 2420 m, 21 Jun 1985, Churchill & Sastre 12843-c (NY).

6. Porotrichum filiferum Mitten

   Ecuador, Bombonasa, Spruce s. n., (NY).

Literature Cited

Allen, B. H. & M. R. Crosby. 1986. Revision of the genus Squamidium (Musci: Meteoreaceae) J. Hattori Bot. Lab. 61: 423-476.

Bartram, E. B. 1928. Mosses of Jamaica. Jamaica Nat. 1: 15-20.

_____. 1949. Mosses of Guatemala. Fieldiana, Bot. 25: 1-442.

Berthier, I. 1971. Recherches sur la structure et le développment de l'apex du gamétiphyte feuillé des mousses. Rev. Bryol. Lichénol. 38: 421-551.

Bopp, M. 1984. Cell pattern and differentiation in bryophytes. In: Barlow, P. W. & D. J. Carr (eds.), Positional controls in plant development. 157-191. Cambridge Univ. Press, London.

Bridel, S. E. 1827. Bryologia Universa seu Systematica and amnuim Muscorum Frondosorum Hucusque Cognitorum cum Synonymia Ex Auctoribus Probatissimis. Lipsiae.

Brotherus, V. F. 1906. Neckeraceae. In: Engler, A. & K, Prantl, Die natürlichen Pflanzenfamilien 1(3): 835-863.

_____. 1925. Neckeraceae. In: Engler, A. & K. Prantl (eds.), Die natürlichen Pflanzenfamilien ed. 2, 11: 178-202.

Buck, W. R. 1980. Animadversions on Pterighnandrum with special commentary on Forsstroemia and Leptopterigynandrum. Bryologist 83: 451-465.

_____ & D. H. Vitt. 1986. Suggestions for a new familial classification of pleurocarpous mosses. Taxon 35: 21-60.

Bruch, P., W. P. Schimper & T. Gümbel. 1836-1855. Bryologia Europaea seu genera muscorum europaerum monographice illustrata, 65 fasc. Stuttgart.

Crum, H. 1951. The Appalachian-Ozarkian Element in the Mosses of Mexico with a Checklist of all known Mexican Mosses. Ph D. Thesis. Univ. Michigan.

De Sloover, J. L. 1983. Note de bryologie africaine XII. - Porotrichum et Porothamnium. Bull. Jard. Bot. Natl. Belgique. 53: 97-152.

Fleischer, M. 1904-1923. Die Musci der Flora von Buitenzorg zugleich Laubmoosflora von Javamit Berücksichtigung aller Familien und Gattungen der gesamten Laubmooswelt Vol 1-3. E. J. Brill, Leiden.

_____. 1906. Neue Familien, Gattungen und Arten der Laubmoose. Hedwigia 45: 53-87.

Frey, W. 1970. Blattentwicklung bei Laubmoosen. Nova Hedwigia 20: 463-556.

Fritsch, R. 1982. Index to plant chromosome numbers-bryophyte. Regnum Vegetabile 108: 1-256.

Hallet, J. N. 1972. Morphogénèse du gamétophyte feuillé du Polytrichum formosum Hedw. I. Etude histochimique, histoauloadiographique et cytopholometrique du point végètatif. Ann. Sc. Nat. Bot. 13: 19-118.

Hedwig, J. 1801. Species Muscorum Frondosorum descriptio et tabulis aensis 77 coloratis illustrata. Leipzig.

Jaeger, A. & F. Sauerbeck. 1870-1880. Adrumbratio florae muscorum totius orbis terrarum.

Mitten, W. 1869. Musci Austro-Americani. Jour. Linn. Soc., Bot. 12: 1-659.

Müller, C. 1851. Synopsis Muscorum Frondosorum omnuim Hucusque Cognitorum. Vol. 2. Berlin.

Ninh, T. 1984. A revision of Indochinese Homaliodendron. Jour. Hattori Bot. Lab. 57: 1-39.

Richards, P. W. 1984. The ecology of tropical forest bryophytes. In: R. M. Schuster (ed.), New Manual of Bryology 2: 1233-1279.

Robinson H. 1975. The Mosses of Juan Fernandez Islands. Smithsonian Cont. Bot. 27: 1-88.

Schimper, W. P. 1855. Corollarium Bryologiae Europaeae, conpectum diagnosticum familiarium, generum et specierum, adnotationes novas atque emendationes complectens. Stuttgart.

Thériot, I. 1928. Mexican Mosses Collected by Brother Arsène Brouard II. Smithsonian Misc. Coll. 81: 1-26.

Touw, A. 1962. Revision of the moss genus Neckeropsis (Neckeraceae) I. Asiatic and Pacific species. Blumea 10: 373-425.

_____. 1971. A taxonomic revision of the Hypnodendraceae (Musci). Blumea 19: 211-354.

Wagner, K. A. 1951. The Neckeraceae of North America. Ph D. Thesis. Univ. Michigan.

Wijk, R. van der. 1957. Distichous and pseudodistichous mosses. Acta Bot. Neer. 6: 386-392.

_____, W. D. Margadant & P. A. Florschütz. 1959-1969. Index Muscorum. Utrecht, Netherlands.