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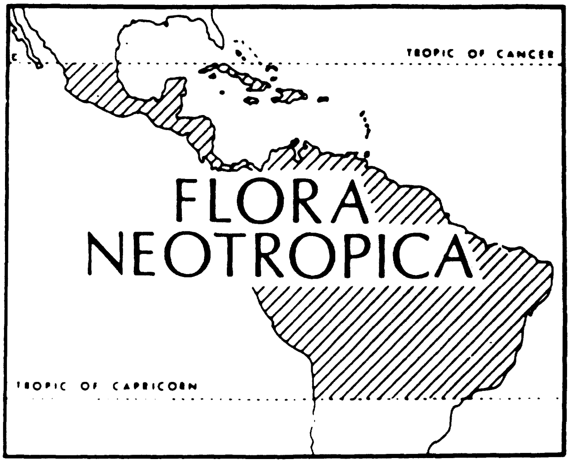
FLORA NEOTROPICA

MONOGRAPH 62

LEJEUNEACEAE: PTYCHANTHEAE, BRACHIOLEJEUNEAE

by

S. Rob Gradstein



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LEJEUNEACEAE: PTYCHANTHEAE, BRACHIOLEJEUNEAE[1]

S. R. GRADSTEIN

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[1] Studies on Lejeuneaceae subfamily Ptychanthoideae 24.

ABSTRACT

Gradstein, S. Rob (Herbarium, University of Utrecht, Heidelberglaan 2, 3584CS Utrecht, The Netherlands). Lejeuneaceae: Ptychantheae, Brachiolejeuneae. Flora Neotropica **62**: 1–216. 1994. The Lejeuneaceae (Hepaticae) are represented in the New World by an estimated 50 genera and several hundreds of species. This monograph treats the 22 New World genera of the tribes Ptychantheae and Brachiolejeuneae. Of about three hundred previously described species, 65 species have been retained. They are mostly epiphytes of humid tropical forests at low or mid elevations. Most of the species are restricted to the neotropics and the greatest species diversity is found in northwestern South America and the Guianas. Dry regions have only few species. Over 25% of the species are limited to undisturbed rain forest and about 10% are threatened with extinction due to deforestation.

The species of tribes Ptychantheae and Brachiolejeuneae are characterized by undivided underleaves and have traditionally been classified in the subfamily "Ptychanthoideae" or "Holostipae." In this treatment the Ptychantheae are retained in the Ptychanthoideae, but the Brachiolejeuneae are moved to the subfamily Lejeuneoideae, with which they share many unique sprophytic features: thin-walled capsules, elaters with rudimentary spirals, decussate tetrads, rectangular spores, etc. In the Ptychantoideae the capsule walls are thickened, the elaters have a distinct spiral, and the spores are isodiametric and arranged in tetrahedral tetrads. The sporophytic differences are correlated with a remarkably different spore-discharge process in the two groups. In the Ptychantheae capsule dehiscence is violent and spore discharge explosive. In Brachiolejeuneae it is much more gentle. The sporophytic features of the Ptychantheae are shared with *Frullania* and are interpreted as a xeromorphic adaptation. The better drought resistance of spores and sporelings and the frequently convoluted leaves of the taxa of Ptychantheae are further xeromorphic features of this group.

Generic relationships within the Ptychantheae and the Brachiolejeuneae have been assessed by means of a cladistic analysis of the genera recognized world-wide. The cladograms show the existence of three clades in the Ptychantheae and two in the Brachiolejeuneae, which are ranked as subtribes. The use of the "genus complex" as a unit of generic classification in the Lejeuneaceae has been abandoned.

The following new names and combinations are proposed: *Acanthocoleus aberrans var.laevis, Archilejeunea bischleriana, A. ludoviciana subsp. ludoviciana, A. ludoviciana subsp. porelloides, A. porelloides subsp. chocoensis, Brachiolejeunea sect. Phyllorhizae, Brachiolejeunea conduplicata, Lejeuneaceae tribe Nipponolejeuneae, Lejeuneaceae subtribe Acrolejeuninae, Lejeuneaceae subtribe Brachiolejeuninae* and *Lejeuneaceae subtribe Stictolejeuninae.*

RESUMEN

Gradstein, S. Rob (Herbarium, University of Utrecht, Heidelberglaan 2, 3584CS Utrecht, The Netherlands). Lejeuneaceae: Ptychantheae, Brachiolejeuneae. Flora Neotropica **62**: 1–216. 1994. Las Lejeuneaceae (Hepaticae) están representadas en el Nuevo Mundo por aproximadamente 50 géneros y algunos cientos de especies. La presente monografía trata los 22 géneros de la tribu Ptychantheae y Brachiolejeuneae del Nuevo Mundo. De aproximadamente 300 especies descritas anteriormente, 65 han sido retenidas en este trabajo. Ellas son en su mayor parte epífitas de la selva húmeda tropical. La mayor parte de las especies son restringidas a los neotrópicos y la mayor diversidad de especies se encuentra en el noroeste de Suramérica y en Guianas. Regiones secas poseen pocas especies. Por encima del 25% de las especies están limitadas a selva no intervenida y cerca del 10% están amenazadas de extinción debido a la deforestación.

Las especies de las tribus Ptychantheae y Brachiolejeuneae se caracterizan por tener anfigastros no divididos y pertenecen tradicionalmente a la subfamilia "Ptychanthoideae" o "Holostipae." En este trabajo las Ptychantheae están clasificados en las Ptychanthoideae pero las Brachiolejeuneae están trasladadas a la subfamilia Lejeuneoideae con la cual comparten muchos caracteres únicos del esporofito: cápsulas de pared delgada, elateras con espiral rudimentario, tetrados decusados, esporas rectangulares, etc. En Ptychanthoideae las cápsulas tienen paredes gruesas, elateras con espiral, tetrados tetrahédricos, esporas isodiamétricas, etc. Las diferencias esporofíticas están relacionadas con una notable diferencia en el proceso de descarga de esporas. En las Ptychantheae la dehiscencia de la cápsula es violenta y se presenta una explosiva descarga de esporas. En Brachiolejeuneae esta es mucho mas suave. Los caracteres esporofíticos de las Ptychantheae se encuentran también en *Frullania* y son interpretados como una adaptación xeromórfica. La mejor resistencia a la sequía de las esporas y la frecuencia de hojas convolutas de las Ptychantheae son además rasgos xeromórficos de este grupo.

Relaciones genéricas dentro de las Ptychantheae y las Brachiolejeuneae han sido evaluadas por medio de análisis cladístico. Los cladogramas muestran la existencia de tres clades en las Ptychantheae y dos en las Brachiolejeuneae, las cuales son clasificadas como subtribus. El uso del "genus complex" como una unidad de clasificación genérica en las Lejeuneaceae ha sido abandonada. Se propusieron los siguientes nuevos nombres y combinaciones: *Acanthocoleus aberrans var.laevis, Archilejeunea bischlerianan, A. ludoviciana subsp. ludoviciana, A. ludoviciana subsp. porelloides, A. porelloides subsp. chocoensis, Brachiolejeunea sect. Phyllorhizae, Brachiolejeunea conduplicata, Lejeuneaceae tribe Nipponolejeuneae, Lejeuneaceae subtribe Acrolejeuninae, Lejeuneaceae subtribe Brachiolejeuninae* y *Lejeuneaceae subtribe Stictolejeuninae.*

INTRODUCTION

The Lejeuneaceae are the largest family of the Hepaticae and are represented in the New World by several hundreds of species in about 50 genera. They are mostly epiphytes of humid tropical forests at low or mid elevations and are an important floristic component of these forests. More than three-fourths of the hepatic species of lowland rain forest are Lejeuneaceae and in montane rain forests Lejeuneaceae account for about 15–30% of hepatic diversity.

This monograph treats the 22 New World genera of the Lejeuneaceae tribes Ptychantheae and Brachiolejeuneae. Because of their undivided underleaves the members of these tribes are traditionally called "holostipous" Lejeuneaceae. Bifid underleaves characterize the "schizostipous" Lejeuneaceae or tribe Lejeuneae, which are not treated here.

Spruce (1884) described the "Holostipae" and "Schizostipae" in his classical treatment of the Hepaticae of the Amazon and the Andes. His work was based on extensive fieldwork in South America and lead to a natural system of genera still largely valid today. The majority of the genera treated in this volume were first described by Spruce. The second major contribution to neotropical Lejeuneaceae was made by Evans (e.g., 1904, 1907, 1908) who described the Caribbean taxa and discovered several new characters.

The important taxonomic contributions by Spruce and Evans were obscured by the work of Stephani (1898–1912) who published descriptions of all the genera and species hitherto recognized and added numerous new ones. Unfortunately, many of the species are synonyms of previously described taxa. Liverwort species are often widespread and usually exhibit great morphological variation of characters. Misinterpretation of this variation can easily result in the description of ill-founded new taxa.

The work by Stephani and others necessitated a major revision of the described species. Asiatic Holostipae were revised by Verdoorn (1934) and Mizutani (e.g., 1961, 1986), those from Africa by

VandenBerghen (e.g., 1984, 1984a) and Jones (e.g., 1970) and from Australia by Thiers and Gradstein (1989). Some New World taxa were revised by Fulford (1941, 1942a), Schuster (1954, 1980) and Stotler and Crandall-Stotler (1974).

My work on the holostipous Lejeuneaceae began with a world-wide revision of the genus *Acrolejeunea* (Gradstein, 1975). Subsequently, I have undertaken other generic monographs, in collaboration with my students (e.g., Gradstein, 1985; van Slageren, 1985; Kruijt, 1988; Teeuwen, 1989). Extensive fieldwork in almost all phytogeographic regions of Tropical America has allowed me to become familiar with the habitats of the species and to study characters of the living plants such as growth form and oil bodies. The many unique terpenoids elaborated by these species and stored in the oil bodies were studied by Dr. Yoshinori Asakawa (Tokushima Bunri University, Japan) and his staff, and flavonoid metabolites were checked by Dr. R. Mues (University of Saarbrücken) and by my student R. Kruijt. Of almost three hundred species of Ptychantheae and Brachiolejeuneae described from the New World, I have retained 65 in this monograph. In addition, a few varieties and subspecies are recognized. More than three-fourths of the taxa I have been able to collect myself.

The species concept applied in this monograph is similar to the one used in my previous revisions (e.g., Gradstein, 1975; for a discussion see also Sipman, 1983). The concept is based on the assumption that the more differences can be found among groups of populations, the more likely it is that a biological species is at hand. No attempt has been made to apply a "true" biological species concept, as it was technically impossible to perform the necessary analyses and experiments to demonstrate the existence of genetical isolation. Accordingly, species are defined here by the presence of two or more independent, diagnostic characters whereas taxa which differ from their nearest relative by only one character are treated as varieties; allopatric varieties are treated as subspecies. The definitions have not been applied very rigidly, however, and in a few instances I have given species rank to taxa defined by only one good character or by dependent diagnostic features, for example *Brachiolejeunea conduplicata*, *Neurolejeunea sastreana* and *Symbiezidium dentatum*. In all of these cases the distinguishing feature(s) were so prominent and the taxon so distinct that species level seemed more appropriate than varietal level.

All species recognized in this monograph can be identified by means of vegetative characters. Reproductive features (gametoecia, sporophytes, asexual devices), ultrastructure, chemistry and ecology have been extensively used in the systematic evaluation but have not been taken as sole evidence to define species. Since reproductive organs are frequently lacking in the collections, I have made a special effort to construct keys that work for sterile material.

All species are fully described but specimens are cited only selectively. Private collections are not cited except for rare taxa and for specimens not duplicated in institutional herbaria. As customary in the Flora Neotropica, illustrations are provided for selected taxa only, especially for type species. For non-illustrated species references are provided to figures published elsewhere.

I have tried to provide an exhaustive listing of synonymy for valid New World names; invalid names and Old World names have been cited selectively only. The nomenclature of the genera of Lejeuneacae is complicated and confusing (see Gradstein et al., 1982; Zijlstra, 1982) and I may therefore well have missed some names which ought to have been mentioned. "Excluded species," listed at the end of each generic treatment, are cited only for taxa which are not treated in this monograph. Usually these are species of the tribe Lejeuneae.

I am much indebted to my students who have dedicated themselves with much enthusiasm to the task of helping revising some of the genera treated in this monograph. Without the important publications of Michiel van Slageren, Rob Kruijt and Mariette Teeuwen, this monograph would have taken much longer to complete. The treatment of the genus *Marchesinia* has been prepared together with Dr. Patricia Geissler, Geneva, who has monographed the genus on a world-wide basis.

I hope that this Lejeuneaceae treatment will stimulate others to pay more or attention to this fascinating family of liverworts. Also, I would hope that this volume will eventually be supplemented by a revision of the neotropical members of the tribe Lejeuneae.

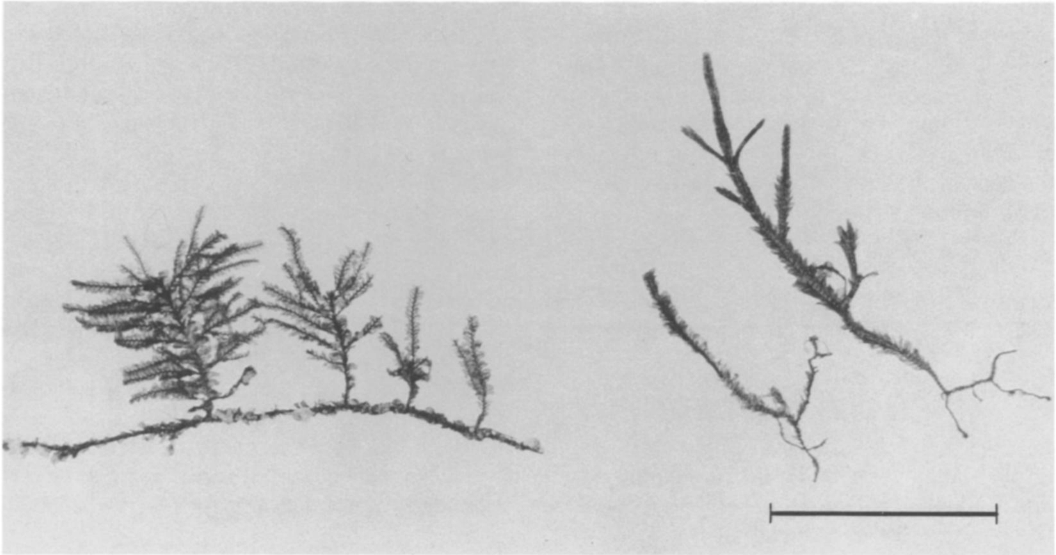

FIG. 1. Growth habit of Ptychantheae. Left: dendroid growth of *Fulfordianthus pterobryoides*. Right: projecting growth of *Thysananthus amazonicus*; note flagellae at stem base.

MORPHOLOGY AND ADAPTATION

The Lejeuneaceae show many unique morphological features. For some of these, a special terminology is being employed. To facilitate the use of this monograph, brief explanations of the main morphological characters are provided in this section. A discussion of the variation of the main characters is also given along with an assessment of the character's taxonomic utility and adaptive significance. The discussion does not pretend to be comprehensive and reference may be made to the monographs of the genera *Acrolejeunea*, *Frullanoides* and *Brachiolejeunea* (Gradstein, 1975; van Slageren, 1985) and other papers for further detail. A discussion of the distribution of character states is provided in the CLASSIFICATION section.

Growth Habit

The species of Ptychantheae and Brachiolejeuneae usually grow in dense mats over bark or rock, rarely on leaves or soil. Some grow tightly appressed to the substrate, especially the more tiny ones. Such a prostrate, creeping growth is characteristic of the species of *Acrolejeunea*, *Acanthocoleus* and *Stictolejeunea* subgenus *Leptostictolejeunea*. Others, including the more robust taxa, grow more loosely and frequently turn away from the substrate. This may be called "projecting" growth (Thiers, 1988). Most species with projecting growth turn upwards and become ascending to erect (Fig. 1). A few may project downwards and become more or less pendent, especially when growing on small branches or twigs (e.g., *Thysananthus amazonicus*, *Dicranolejeunea axillaris*). The degree by which the species turn away from the substrate varies and is not a very useful taxonomic character. It is often an indication of the fertility of the plants as they are usually the fertile shoots of the plants which are projecting. Branches with gemmae or caducous leaves are also frequently turned away from the substrate. Thus, it would seem that dispersal of spores and propagules is promoted by the projecting growth habit of the plants.

A specialized form of projecting growth is seen in the genera *Bryopteris*, *Dendrolejeunea* and *Fulfordianthus*. These are dendroid or fan-shaped taxa with long creeping, stoloniform stems which give rise, at more or less regular intervals, to freely branched, erect leafy stems (Fig. 1). The leafy stems stand away perpendicular from the substrate and in very long plants they may become pendent. Often the leafy stems are densely pinnate. The dendroid habit is very conspicuous in the field and is an excellent generic character. Nevertheless, it has hardly been used in the taxonomy of the Ptychantheae. Probably this is due to the fact that the dendroid habit is usually not evident in herbarium specimens, which normally consist of broken stems. The dendroid taxa usually grow in permanently moist habitats, in the understory of rain forests or in cloud forests. The continually high relative humidity that characterizes these environments is apparently an important factor that allows the plants to grow far away from the substrate and assume erect or pendent growth.

Branching

The branch systems of the Ptychantheae and Brachiolejeuneae have been studied in detail by Thiers (1984, 1985) and may be discussed only briefly. The branching characters within the family is highly diversified and also quite variable. The most constant and taxonomically important features are the presence or absence of *Frullania*-type and *Lejeunea*-type branches (e.g., Figs. 25B, 37A, 54), flagellae and innovations, and the innovation leaf sequence. Most genera of Ptychantheae and Brachiolejeuneae may produce both *Frullania*-type and *Lejeunea*-type branches (Fig. 37A). The degree by which they are produced differs, however. In the genus *Dicranolejeunea*, *Frullania*-type branches are the dominant branch type but in the closely related genus *Acanthocoleus Lejeunea*-type branches predominate. The species of *Frullanoides* may be divided into a group in which *Frullania*-type branching is common and one that rarely produces them. In some genera vigorous, vegetative shoots are of the *Frullania*-type and weaker or sexual shoots are of the *Lejeunea*-type. The frequency of *Frullania*-type branching is clearly variable and is to be used with care in taxonomy. In *Ptychanthus striatus*, a species characterized by *Frullania*-type branching, Kitagawa (1984) found that after four years of cultivation *Frullania*-type branches had entirely disappeared. The plants showed reversals to juvenile conditions and had pendular leaf segmentation at the bases of the stems.

Some authors have suggested that the shape and size of the first leaf appendages of the branches might provide good taxonomic character but Thiers (1985) has shown that these are variable features without much taxonomic significance. An interesting character which has been little investigated is the position of the half leaf relative to the *Frullania*-type branch (Crandall, 1969). In *Bryopteris diffusa* I have observed that the half-leaf is inserted across the dorsal base of the branch and entirely covers the lower dorsal surface of the branch, which therefore is visible only after removal of the half-leaf. In *B. filicina*, however, the half-leaf is inserted on lateral, adaxial surface of the branch and is positioned in front rather than on top of the branch, which as a consequence can be observed in dorsal view without removal of the half-leaf. A half-leaf similar to the one found in *B. diffusa* is also present in *Ptychanthus*, a genus closely related to *Bryopteris*. Thus, this character would seem to be taxonomically important and further investigation seems worthwhile.

A branching feature that has received little attention is the presence of flagelliform branches ("flagellae") along the older portions of the stems (Fig. 1). These branches carry leaves which are much smaller than ordinary branch leaves. Moreover, the flagelliform branches are always curved backwards, towards the stem base. Flagellae are very frequent in some of the more robust genera of Ptychantheae (*Thysananthus*, *Mastigolejeunea*, *Spruceanthus*). They have also been observed, occasionally, in *Lopholejeunea subfusca*, *Neurolejeunea breutelii* and robust species of *Schiffneriolejeunea*. I believe that the flagellae are some kind of specialized means of attachment, additional to rhizoids. Interestingly, they are completely lacking in the dendroid taxa (*Bryopteris*, *Ptychanthus*, etc.) which adhere to the substrate by their stoloniform stems.

Presence or absence of innovations (branches originating directly below the perianths and associated with the inner bracts) is an excellent generic character in the Ptychantheae and Brachiolejeuneae. Variation is only seen in the genera *Stictolejeunea* and *Symbiezidium*, which have gynoecia with a short, single innovation or gynoecia that lack them. Both produce their gynoecia on very short specialized gynoecial branches (Figs. 37A, 42A). The predominance of single or paired innovations is not a very good generic character but may often be diagnostic at the species level (Thiers, 1985). Some genera which normally lack innovations, e.g., *Acrolejeunea* and *Lopholejeunea*, may occasionally pro-

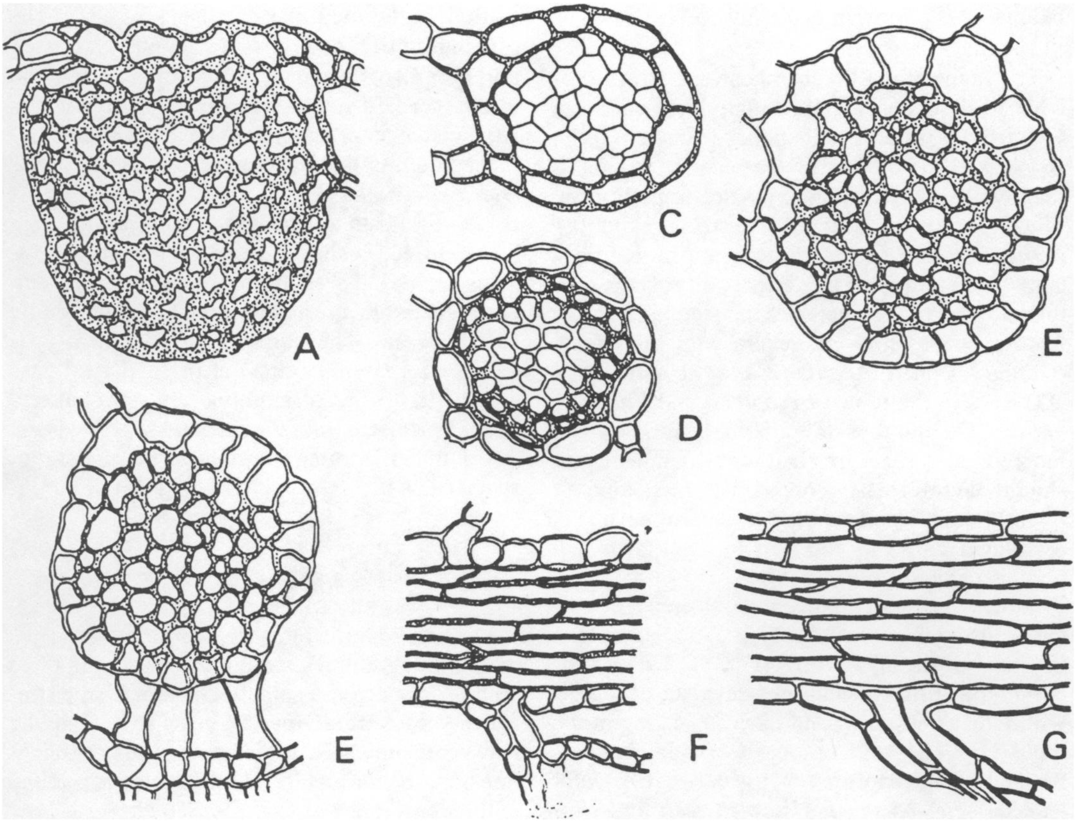

FIG. 2. Stem anatomy and underleaf attachment of Ptychantheae and Brachiolejeuneae. **A.** Stem cross section of *Mastigolejeunea auriculata*, showing enlarged dorsal epidermis. **B.** Ibid. *Frullanoides liebmanniana*, showing hyalodermis and thick-walled medulla cells. **C.** Ibid. *Acanthocoleus aberrans*, showing hyalodermis and thin-walled medulla cells. **D.** Ibid. *Dicranolejeunea axillaris*, showing bulging epidermis cells and subepidermis. **E.** Ibid. *Acrolejeunea fertilis*, showing underleaf attachment by means of four "superior central cells." **F.** Stem longitudinal section of *Acrolejeunea fertilis*, showing bistratose underleaf attachment. **G.** Ibid. *Lindigianthus cipaconeus*, showing tristratose underleaf attachment. After van Slageren (1985).

duce "pseudo-innovations." These are branches which originate between "subinvolucral" female bracts, below the inner series. True innovations may also occur in these genera and are usually deformed branches associated with unfertilized gynoecia (Gradstein, 1975, 1991).

The sequence of leaf production on the innovation begins with a lateral leaf (Figs. 21A, 28) or an underleaf (Fig. 52) and is thus either "lejeuneoid" or "pycnolejeuneoid" (Grolle, 1980). Mizutani (1970) introduced the terms "*Radula-Lejeunea*-type" and "*Radula-Jubula*-type" for the two types of innovation leaf sequence but in this treatment I have accepted Grolle's terminology. The innovation leaf sequence is an excellent generic feature within Ptychantheae and Brachiolejeuneae. In *Archilejeunea* it is constant at the subgeneric level and in *Acanthocoleus* it varies at species level. Infraspecific variation of the innovation leaf sequence is very rare in the Ptychantheae and Brachiolejeuneae and has been reported only in *Tuzibeanthus chinensis* and *Fulfordianthus evansii* (Thiers, 1985). The observation in the latter species may have been erroneous, however (B. M. Thiers, pers. comm.). Sometimes the first leaf and underleaf of the innovation are produced at nearly equal levels and the innovation leaf sequence may be difficult to determine. In this case the position of the underleaf relative to the leaf should be determined from subsequent leaf cycles towards the apex of the innovation.

Stem Anatomy

The stems of the Ptychantheae and Brachiolejeuneae show considerable anatomical variation and provide important generic characters (e.g., Bischler, 1965). Most of the characters can be readily observed in stem cross sections (Fig. 2). The diameter of the stems varies from about 0.1 mm in the tiny species to 0.5 mm in dendroid taxa. The number of epidermal cell rows is correlated with the diameter of the stem and varies from about 10 rows in genera with thin stems (*Odontolejeunea*, *Acanthocoleus*) to more than 100 rows in the robust *Bryopteris* and *Fulfordianthus*. The number of epidermal cell rows is a more precise measure than stem diameter and should therefore be more useful in taxonomy (even though it is less easy to determine!). It is correlated with the width of the ventral merophyte (see below).

In many genera the epidermis cells (called "cortex" cells by many hepaticologists) are larger than the inner or medullary cells (Fig. 2). Such an enlarged epidermis is usually characteristic of species with rather thin stems and may be lacking in the robust taxa. However, in some taxa with thin stems the epidermis cells are not enlarged, e.g., in *Archilejeunea*, *Leucolejeunea*, *Neurolejeunea* and *Nipponolejeunea*. In most species of *Mastigolejeunea* and some other taxa only the dorsal epidermis cells are enlarged (Fig. 2A). The presence or absence of an enlarged epidermis is an important generic character.

Variation is also observed in the thickening of the epidermal walls. In *Brachiolejeunea* and related genera the epidermis cells have very thin walls, in many other genera they are thickened. Following Schuster (1963), an enlarged epidermis consisting of thin-walled cells may be called a "hyalodermis."

Cell wall thickening and pigmentation of epidermis and medulla are also important generic features. A zone of thick-walled cells in 2–6 layers between epidermis and medulla characterizes the stems of all dendroid taxa and of *Stictolejeunea squamata* and *Dicranolejeunea axillaris*. This zone is called a subepidermis ("assise intermédiaire," Bischler, 1965). The origin of the subepidermis has not been investigated and may be different in the various genera in which it occurs. In *Dicranolejeunea axillaris* the subepidermis seems to be made up of thick-walled outer medullary cells (Fig. 2D). The subepidermis is obviously an adaptation to support upright (or pendent) growth of the plants and is observed in many erect-growing liverworts. An unusual stem feature are the outwardly bulging epidermis cells characteristic of the genus *Dicranolejeunea* (Fig. 2D).

Leaves and underleaves are attached to the stem by modified, U-shaped cells or attachment cells (Figs. 2E–G). These are probably modified epidermis cells and are a unique feature of the family Lejeuneaceae. The number of attachment cells (="superior central cells") at the underleaf base may be 2, 4 or 8 (or more in very robust stems) and is correlated with the robustness of the stem. The number is often constant at the generic or species level.

Merophytes

Merophytes are the three stem sectors (two lateral, one ventral), which arise from the three cutting faces of the apical cell. In most Lejeuneaceae the lateral merophytes, to which the leaves are attached, do not meet along a straight line but are interlocking along the dorsal midline of the stem (Evans, 1935). Consequently, the row of epidermis cells along the dorsal midline is alternatively associated with the dorsal base of the leaves of opposite lateral merophytes (Fig. 45F). The dorsal cell row is usually straight but in species of *Acrolejeunea* and *Frullanoides* with densely imbricated leaves the row may be zig-zag (Gradstein, 1975).

In the genus *Brachiolejeunea* the dorsal midline of the stem is marked by peculiar lamellate outgrowths or paraphyllia (van Slageren & Gradstein, 1981). The paraphyllia are 1–4 cells high and are present throughout the leafy axis except at the base of *Frullania*-type branches. A single paraphyllium extends along the entire length of the lateral merophyte, from one dorsal leaf base to the next (Figs. 45F–G). The paraphyllia form a conspicuous ridge on the stem. Their height is a useful character for species recognition. The function of the paraphyllia is unknown.

The width of the ventral merophytes, to which the underleaves attached, is a measure for the robustness of the stem and is a useful taxonomic character (Schuster, 1954). It is usually expressed as the number of epidermal cell rows seen across the ventral surface of the stem, between and beyond the opposite bases of the underleaves. Within the direct neighbourhood of the underleaf bases the number of cells is more variable (Kruijt, 1988). In most Ptychantheae and Brachiolejeuneae the ventral merophyte is 4 or more cells wide. Very broad ventral merophytes, up to 20 or more cells wide, are found in the genus *Fulfordianthus*. The strongest reduction is seen in the genera *Acanthocoleus*, *Dicranolejeunea* and *Odontolejeunea* (Brachiolejeuneae) which have 2(–3) cells wide ventral merophytes (Fig. 48D). By their thin stems and narrow merophytes these genera approach the members of the subfamily Lejeuneoideae which usually have 2 cells wide ventral merophytes.

Variation in the width of the ventral merophyte is observed in most taxa, in particular in those with robust stems, and may be environmentally controlled. In *Stictolejeunea squamata* the ventral merophytes is usually 8-18 cells wide but tiny lowland forms have thinner stems with 4 cells wide ventral merophytes. In the genus *Acanthocoleus* the ventral merophyte is normally only 2 cells wide but 4–6 cells wide ventral merophytes have been observed in robust mountain forms of *A. javanica* and in *A. trigonus* from northern Argentina and Bolivia. In *Lindigianthus*, however, the ventral merophyte is very stable and always 4 cells wide.

Ventral merophyte width is also correlated with the number of cells by which the underleaves are attached to the stem, the attachment cells or "superior central cells" (see above). Stems with broad ventral merophytes have more attachment cells than those with narrow merophytes.

Leaves

The leaves of all Ptychantheae and Brachiolejeuneae are divided into a dorsal lobe and a smaller ventral lobule and are attached to the stems along a J-shaped insertion line (Figs. 14C, 29B, etc.). Crandall-Stotler and Guercke (1980) reported short transverse insertions, similar to those found in *Nipponolejeunea*, *Cololejeunea* and *Jubulaceae*, in the genus *Bryopteris* (Ptychantheae). However, I have found that the insertion in *Bryopteris* is J-shaped like in other Ptychantheae (Fig. 26B). Some variation in insertion length may be observed but I have not found this variation to be taxonomically very significant.

Branch and stem leaves have basically similar morphologies, although they usually differ in size. Moreover, branch leaves may have fewer lobule teeth than stem leaves. In *Fulfordianthus pterobryoides* dentation of the leaf margins is more pronounced on branch leaves than on stem leaves. Leaf dimorphy is rare in Lejeuneaceae and occurs mainly in dendroid species. The leaves of the creeping, stoloniform stems in these taxa, for example in *Bryopteris*, may be quite different from those of the erect, leafy stems. In some species asexual reproduction is associated with heterophylly, e.g., in *Caudalejeunea cristiloba* and *C. reniloba*, which produce gemmiparous shoots with unusually large underleaves. Moreover, the leaves of these gemmiparous branches are much more strongly dentate than the ordinary vegetative leaves.

The most important leaf characters are those of the lobules or watersacs and of the cells. The lobules, which are usually interpreted as an adaptation of the plants to epiphytic growth, provide many species characters, e.g., lobule shape, and the number, length, form and position of the teeth. In many species the free margin of the lobule (= the margin opposite and more or less parallel to the keel) has several teeth (Figs. 35B–C, 46B–C). The hyaline papilla, which characterizes the apex of the lobule of Lejeuneaceae, is always inserted on the inner surface of the lobule, proximal to the base of the first tooth (Figs. 45C, 47C). The first tooth is the one nearest to the distal end of the free margin, except in *Acrolejeunea pycnoclada* and *Frullanoides corticalis* which have an "extra" tooth. Only in the genus *Neurolejeunea* the papilla is "distal" in position. However, the tooth in *Neurolejeunea* which has the papilla at its distal base is the second tooth, much like in other genera with distal hyaline papillae (*Cheilolejeunea*, *Omphalanthus*, etc.). The first lobule tooth in *Neurolejeunea* has become reduced or, in *N. sastreana*, has become modified into a huge, papilla-like projection (Figs. 39F–G). A tendency for reduction of the first lobule tooth is seen in the genus *Blepharolejeunea* which has a short, blunt first tooth and elongated, sharp second tooth (Fig. 47C). In *B. incongrua* the first tooth is frequently incurved and inconspicuous.

The junction of the free margin with the ventral margin of the leaf lobe may be gradual or abrupt and the form of the junction is often characteristic for the species. An interesting morphological feature that has been overlooked by most previous workers is the fact that the distal end of the free margin is sometimes connate with the surface of the leaf lobe across 2–3 cells before merging into the ventral leaf margin. It is a species character in *Lopholejeunea* and serves to distinguish sterile material of *L. subfusca*. It is also found in *Archilejeunea porelloides*.

There is much evidence that the size of the watersac may be influenced by the humidity of the environment. Very small lobules are characteristic of *Bryopteris*, *Fulfordianthus*, *Thysananthus amazonicus*, *Stictolejeunea* and *Symbiezidium*, all of which grow in humid rain forest. Large lobules are common in *Acrolejeunea*, *Frullanoides* and *Schiffneriolejeunea* which are genera of more open, dryer habitats. Cornelissen and ter Steege (1989) compared populations of *Symbiezidium barbiflorum* from the outer canopy of Guyanan rain forest with those of the more shaded, moister understory and found that the canopy plants had much bigger lobules. *Stictolejeunea squamata* produces smaller lobules in humid montane cloud forests than in lowland forests (Gradstein, 1985b). Reduction of lobule size (Fig. 16C) may eventually result in entire loss of lobules, e.g., in *Archilejeunea parviflora* and in the species of *Acanthocoleus* (Kruijt, 1988). The degree of lobule reduction varies among the taxa and may sometimes be a useful taxonomic character, even though it is environmentally controlled. The genera *Acrolejeunea*, *Frullanoides* and *Schiffneriolejeunea* are characterized by the total absence of lobule reduction. *Archilejeunea parviflora* differs from *A. auberiana* and *A. bischleriana* by its much more frequently reduced lobules. Plants with fully reduced lobules occur only in very wet habitats, e.g., on periodically submerged rocks in streams. *Archilejeunea parviflora* is not the only species of this genus which may produce elobulate forms; they have also been found in Africa (VandenBerghen, 1951), apparently in similar habitats.

A dark brown to blackish plant color may be observed in many genera but in only few groups the darkish pigmentation is concentrated in the cell walls. *Lopholejeunea*, *Marchesinia* and *Frullanoides* are the main genera with darkish pigmented cell walls. In addition, it is found in *Neurolejeunea* sect. *Aneurolejeunea* and in some species of *Mastigolejeunea*.

The leaf cells of the members of the Ptychantheae and Brachiolejeuneae are very uniform in size and about 25–40 µm long in midleaf. Smaller leaf cells are characteristic of *Fulfordianthus*, *Neurolejeunea*, *Stictolejeunea* and *Thysananthus* subgenus *Sandeanthus*. These are also the only groups with more or less evenly thickened cell walls and no distinct trigones or intermediate thickenings (Fig. 25D). Trigone shape furnishes important generic characters and may be simple-triangular to radiate (Figs. 16F, 43F), or cordate (Fig. 35F). When large, trigones may become bulging (Fig. 17F) and confluent (Fig. 23F). The cordate trigone type is usually found in elongated cells and the other types are normally associated with isodiametric cells. An exception is *Spruceanthus theobromae* which has triangular-radiate trigones, yet strongly elongated cells. In the genera of the Ptychantheae the trigone types are usually distinct but in plants of *Acanthocoleus*, *Blepharolejeunea* and *Odontolejeunea* (Brachiolejeuneae) with very tiny trigones it may be very difficult or even impossible to distinguish between cordate and simple-triangular trigones.

In genera with elongated leaf cells and cordate trigones there is usually a marked tendency for the leaves to become suberect and strongly wrapped around the stem when dry. In those with isodiametric leaf cells (and lacking cordate trigones!), however, leaves are usually widely spreading when dry and either plane or weakly convoluted only. The tribal classification of the Ptychanthoideae by Gradstein (1975) was based on this combination of characters. However, the correlation between leaf position in the dry state and leaf areolation is not very evident in all genera and breaks down in the genera *Caudalejeunea*, *Fulfordianthus*, *Verdoornianthus* and in the genera of Brachiolejeuneae with obscure trigones. This tribal classification is now superseded by a subdivision based on sporophyte characters (see below). An interesting correlation between leaf position and areolation was observed in the genus *Odontolejeunea* by Teeuwen (1989). Dry leaves of *Odontolejeunea lunulata* are usually irregularly convoluted or crisped, with the lobe margins curved down as usual, whereas those of *O. rhomalea* tend to have the outer margins of the leaf lobes curved upwards. In the

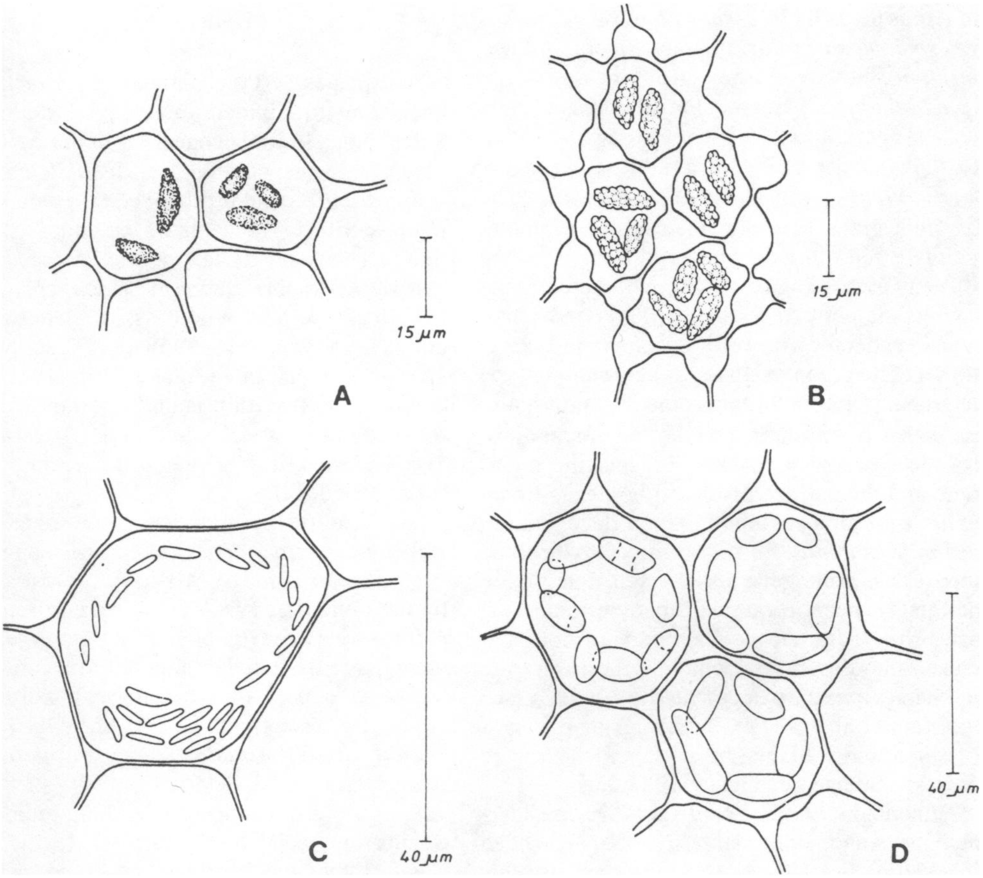

FIG. 3. Oil bodies of the Lejeuneaceae. **A.** Finely segmented, *Jungermannia*-type oil bodies of *Anoplolejeunea conferta*. **B.** Coarsely segmented, *Calypogeia*-type oil bodies of *Aureolejeunea paramicola*. **C.** Homogeneous, *Massula*-type oil bodies of *Lindigianthus cipaconeus*. **D.** Homogeneous, *Bazzania*-type oil bodies of *Symbiezidium barbiflorum*.

latter species the leaf cells are arranged in latitudinal rows, extending from the dorsal to the ventral leaf margin, and are more or less broader than long. In *O. lunulata*, however, the leaf cells are isodiametrical and arranged in longitudinal rows as usual in all Ptychantheae and Brachiolejeuneae. The leaf inrolling of *O. rhomalea* is unique among the species of Ptychantheae and Brachiolejeuneae and is most probably due to the unusual arrangement and shape of the leaf cells.

Oil bodies are produced in all genera except *Fulfordianthus* and *Stictolejeunea*. The latter genus has specialized oil cells or ocelli instead. I have seen oil bodies of all neotropical genera of Ptychantheae and Brachiolejeuneae. As in other liverwort families, morphological features of the oil bodies are a very useful generic character. They separate *Schiffneriolejeunea* from *Acrolejeunea*, *Blepharolejeunea* from *Brachiolejeunea*, *Lindigianthus* from *Dicranolejeunea*, *Spruceanthus* from *Archilejeunea* and *Thysananthus*, and *Fulfordianthus* from *Thysananthus*. The oil body type is also an important diagnostic feature of the subtribes recognized in this monograph (see CLASSIFICATION).

There are two basic oil body types in the Ptychantheae and the Brachiolejeuneae: homogeneous, smooth oil bodies and segmented, granular oil bodies. Different types of homogeneous and segmented oil bodies may be recognized (e.g., Schuster, 1992); in my work I have found a subdivision into four types, as proposed by Gradstein et al. (1977), most convenient (see Fig. 3). Homogeneous oil bodies are usually small and numerous per cell ("*Massula*-type" oil bodies) as in *Acrolejeunea* and many other genera; in *Symbiezidium*, however, they are few and large ("*Bazzania*-type"). Segmented oil bodies may be coarsely granulose ("*Calypogeia*-type") as in *Mastigolejeunea* or finely granulose ("*Jungermannia*-type") as in *Dicranolejeunea*, etc. The size of the granules is more than 1 µm in diameter in *Calypogeia*-type oil bodies, the granules are distinctly protruding beyond the outer membrane and the oil body resembles a "grape-cluster." Upon degeneration the oil body simply falls apart into separate granules. In the *Jungermannia* type the granules are rather inconspicous and usually less than 1 µm in diameter; the individual globules are scarcely protruding beyond the membrane and the surface of the oil bodies is finely papillose or almost smooth. Upon degeneration the *Jungermannia*-type oil body usually become more or less homogeneous before disintegration and this has been a source of many errors in the past. It has led to erroneous reports of homogeneous oil bodies in taxa which in the fresh state are characterized by segmented oil bodies (see Gradstein et al., 1977). The erroneous observations were mostly taken from plants which were not fresh and had degenerate oil bodies.

Segmented oil bodies may also vary considerably in size and additional terminology has been proposed by Schuster (1992) to account for this variation.

Most genera have only one oil body type but in some two different oil body types occur. The genus *Marchesinia* can be subdivided into two subgenera based on its oil bodies (Geissler, 1990; Schuster, 1992). In *Odontolejeunea* two species have homogeneous oil bodies and in a third one, *O. decemdentata*, they are segmented (A. Schäfer-Verwimp, pers. comm.). The neotropical species of *Acanthocoleus* have segmented oil bodies but homogeneous oil bodies have been reported in some of the palaeotropical species (Kruijt, 1988). The latter reports are in need of verification, however, because the small, *Jungermannia*-type oil bodies of this genus may soon turn homogeneous upon drying of the material. It is not known whether the observations of oil bodies in the palaeotropical species were taken from fresh material or from herbarium specimens. If taken from dried material, the oil body data would certainly not be trustworthy.

Underleaves

All species of Ptychantheae and Brachiolejeuneae have undivided underleaves and are thus holostipous. In some genera the underleaf apex is emarginate, especially in *Caudalejeunea* and *Fulfordianthus*, but bifid underleaves are lacking in these tribes. The depth of the underleaf insertion is a very useful taxonomic character. Most genera of Brachiolejeuneae have deeply arched underleaf insertions whereas in the dendroid genera of the Ptychantheae underleaf insertions are always straight. In the genus *Frullanoides* the depth of the insertion is an important character for recognition species and in *Marchesinia* and *Symbiezidium* it is a diagnostic feature at the subgeneric level.

The base of the underleaf at the place of attachement to the stem, as seen in longitudinal stem section (Fig. 2F–G), is bistratose or tristratose (Winkler, 1970). All genera of Brachiolejeuneae, except *Stictolejeunea* and *Neurolejeunea*, have tristratose underleaf attachments. In the other genera they are normally bistratose, although unusually thick underleaf bases have been reported in *Caudalejeunea* and *Verdoornianthus* (Gradstein, 1974, 1978). The latter observations were not supported by longitudinal sectioning and need to be verified. In the genus *Blepharolejeunea* both bistratose and tristratose attachments occur (van Slageren & Kruijt, 1985).

The underleaf attachments of the Brachiolejeuneae have been studied in detail by van Slageren (1985), Kruijt (1988), and Teeuwen (1989). The latter two authors showed that the number of cells in the attachment layers, seen in longitudinal section, differs sometimes among species and may be a useful taxonomic character. The stalk-like underleaf attachment of *Brachiolejeunea*, for example, is made up of more cells than the short attachment of *Acanthocoleus*. The attachment of *Odontolejeunea rhomalea* consists of 5 cells, that of *O. lunulata* of only 4 cells. The data indicate that longitudinal sectioning of stems may reveal new taxonomic features additional to those obtained from cross sections. They may also be useful for differentiating between cortical and medullary cells in complex stems, e.g., in *Myriocoleopsis* (Gradstein & Vital, 1975).

Unicellular rhizoids are produced on the underleaf bases, as usual in the Lejeuneaceae. They arise in bundles from a group of rather small, bulging cells at the base of the underleaves. Often the apex of the rhizoids proliferates into a hand-shaped pattern, which enhances attachment of the rhizoids to the substrate.

Specialized circular rhizoid discs are elaborated in epiphyllous plants (Fig. 54A). Lejeuneaceae is probably the most successful plant family to have invaded the phyllosphere. Hundreds of epiphyllous species of Lejeuneaceae have been described. With their characteristic rhizoid discs, they are capable of attaching firmly to the smooth, slippery surface of the leaf. The rhizoid discs are a unique feature of the Lejeuneaceae and are obviously an adaptation to epiphyllous growth. Within the family the discs are without taxonomic value. They may be produced in all genera occurring on leaves, even in those which are only occasionally epiphyllous such as *Symbiezidium* and *Stictolejeunea*.

Sex Distribution

The majority of the species of Ptychantheae and Brachiolejeuneae are monoicous, at least potentially. In the Ptychantheae monoicous taxa are mostly autoicous (androecia and gynoecia on different shoots), rarely paroicous. In the Brachiolejeuneae, however, paroicous species are much more common (e.g., Fig. 52). Presence of paroicy or autoicy is usually stable within species except in *Thysananthus amazonicus* which may be autoicous or paroicous.

Strictly dioicous species account for about 30% of the neotropical species (Gradstein, 1987). They are much rarer than previously believed. Longton and Schuster (1983), for instance, estimated that about 85% of the species of Ptychantheae and Brachiolejeuneae are dioicous. Their high figure is probably based on the fact that populations of only one sex are very common in the monoicous taxa. In the past these unisexual populations have frequently been described as different, dioicous taxa, for instance in the genus *Odontolejeunea* (Teeuwen, 1989). Recently, Stotler and Crandall-Stotler (1974) recognized two subspecies in *Bryopteris fruticulosa* (= *B. filicina* in this treatment), one monoicous and one dioicous. Except for their different sex distribution, the two taxa were fully identical. In this treatment, populations differing only in sex distribution are not described as taxa but are considered polyoicous species. Many of them are common, widespread taxa, e.g., *Marchesinia brachiata*, *Mastigolejeunea auriculata*, *Bryopteris filicina*, *Odontolejeunea lunulata*, *Acrolejeunea emergens*, *Acrolejeunea torulosa*, *Neurolejeunea breutelii*, and *Frullanoides corticalis*. In some of them, monoicous populations are more common than dioicous ones, others are more frequently dioicous. Extreme examples are *Neurolejeunea breutelii* and *Frullanoides corticalis*. All specimens examined of these species were dioicous which the exception of one which was autoicous.

Sex distribution varies randomly throughout the ranges of the polyoicous taxa, at least within the neotropics. A correlation with geography was not observed. Geographical differentiation was only found in the dioicous *Bryopteris diffusa*. This species produces gynoecia throughout its vast neotropical range but androecia are more unevenly distributed and are mostly found in South American populations. In material from the West Indies and Central America they were virtually lacking. The occurrence of sexual reproduction in this species is obviously limited by the uneven distribution of the males. Indeed, perianths (and sporophytes) were only observed in South American material.

Androecia

Androecia may be produced on elongated branches, or on very short, specialized male branches. The latter are characterized by the lack of vegetative leaves. Specialized male branches are rare in Ptychantheae and are characteristic of *Bryopteris* (Fig. 26) and *Mastigolejeunea innovata*. In the Brachiolejeuneae they are much more common. The specialized male branches are usually elongated in shape and never capitate as in many Lejeuneoideae and *Frullania*. Bracteoles are normally present all along the length of the male spikes except in *Stictolejeunea*, *Neurolejeunea* and *Symbiezidium* which have reduced bracteoles as in most Lejeuneoideae. Male bracts are usually smaller than vegetative leaves and provided with larger, more strongly inflated lobules (Fig. 14B). The lobule teeth are usually reduced. In some genera the bracts may be unmodified, however, and difficult to distinguish from vegetative leaves.

Male bract lobules may be epistatic or hypostatic (Gradstein, 1975). Epistatic lobules are characterized by the free margin (in ventral view) curving behind the lobule of the younger bract (Fig. 54A), whereas in hypostatic lobules the free margin distinctly overlaps the younger bract (Figs. 14B, 30A). Unmodified male bracts always have epistatic lobules whereas in modified bracts lobules are usually hypostatic, more rarely epistatic. The lobule difference remains distinct in distant bracts (e.g., Fig. 52). Hypostatic lobules are much more common in Lejeuneaceae than epistatic lobules, which seem to be restricted to a few genera of Ptychantheae and Brachiolejeuneae. The lobule type is usually constant at the generic level except in *Thysananthus* in which it is a species character.

Antheridia always occur in pairs in the axils of the modified bracts but unmodified bracts usually have only one single antheridium.

Gynoecia

The position and arrangement of the gynoecia present some rewarding characteristics. In *Bryopteris*, *Stictolejeunea* and *Symbiezidium* the gynoecia are produce on specialized, abbreviated shoots without vegetative leaves (Figs. 27B, 37A). Innovations, are lacking in these genera or are short sterile and produced singly. In the other genera of Ptychantheae and Brachiolejeuneae the gynoecia are produced on stems or branches which carry vegetative leaves in addition to the bracts. Innovations, when present, are produced singly or in pairs and are frequently fertile. A brief discussion of innovation morphology is provided above in the BRANCHING section.

Thiers (1985) recognized four patterns of spatial arrangement of the gynoecia in the genera of Ptychantheae and Brachiolejeuneae: (1) simple (innovations lacking or short sterile), (2) monochasial (innovations single and frequently fertile), (3) dichasial (innovations in pairs and repeatedly fertile), and (4) diffuse (innovations variable). In some genera one pattern predominates, especially in those with simple arrangements, but in many genera several patterns may be found. A dichasial arrangement is particularly characteristic of *Fulfordianthus* (Fig. 25A), *Frullanoides* and *Blepharolejeunea*, whereas monochasia predominate in *Ptychanthus*, *Odontolejeunea* (Fig. 54) and many species of *Mastigolejeunea* and *Thysananthus*.

The female involucre usually consists of 1–2 series of female bracts and bracteoles and a perianth. When innovations are lacking, bracts and bracteoles may be more numerous and in 2–5 series. In taxa with innovations the bracts are frequently inserted on the innovations. Attachment of the female bracteole to the innovation is much more rare and is characteristic of *Acanthocoleus gilvus* (Kruijt, 1988).

Morphological characters of the inner bracts and bracteoles are often useful for species recognition but are less important at the generic level. The species of *Thysananthus* may be distinguished from *Mastigolejeunea* by their toothed female bracts and *Dicranolejeunea* is distinguished from *Acanthocoleus* by its sharply toothed female bracteoles. Reduced lobules are characteristic of the female bracts of *Dicranolejeunea*, *Acanthocoleus* and *Odontolejeunea*. Other genera produce large lobules or lobules which are variable in size. *Frullanoides* and *Brachiolejeunea* are characterized by the presence of a large wing along the keel of the inner female bracts. Wings occur also in *Blepharolejeunea*, *Lindigianthus*, *Neurolejeunea* and *Mastigolejeunea* but in these genera they are small and sometimes lacking.

Perianths of the genera of Ptychantheae and Brachiolejeuneae are basically 3-keeled (2 lateral, 1 ventral keel) but frequently additional keels or plicae are produced. The number of keels is a useful taxonomic character and may be characterize taxa of different rank. The presence or absence of two ventral keels or plicae, for instance is a subgeneric character in *Lopholejeunea* and *Schiffneriolejeunea* whereas in *Acanthocoleus aberrans*, *Archilejeunea fuscescens* and *Symbiezidium transversale* it serves to characterize varieties. *Frullanoides*, *Trocholejeunea*, *Acrolejeunea*, *Ptychanthus* and *Tuzibeanthus* always have pluriplicate (5–10–keeled) perianths and in *Fulfordianthus*, *Dendrolejeunea*, *Thysananthus* and *Bryopteris* they are always sharply trigonous. In *Mastigolejeunea*, however, species are more variable in this respect and may produce either trigonous or pluriplicate perianths.

The elaboration of long cilia or lacinia on the perianth keels is a feature of many genera of the

Brachiolejeuneae. In the Ptychantheae this character is more rare and is only observed in the genus *Lopholejeunea* (but toothed keels are found in *Thysananthus* and *Archilejeunea*). Auriculate perianths, finally, are characteristic for *Neurolejeunea* and *Stictolejeunea*.

Sporophyte

All genera of Ptychantheae and Brachiolejeuneae have a typical Jubulean sporophyte, characterized by (1) a reduced foot which does not enter the gametophyte but remains within the (stalked) calyptra, (2) a very short seta, and (3) a globose, bistratose capsule with long, vertically arranged elaters, which are attached to the valves with their upper and lower ends, and a reduced number of spores, which germinate within the capsule and produce small endosporous protonemata. After capsule dehiscence the elaters remain attached with their upper ends to the valves.

Sporophytes characters are of little importance at the species or genus level (van Slageren & Berendsen, 1985). Instead, they are of great significance at higher taxonomic levels. Van Slageren and Berendsen showed that the tribes Ptychantheae and Brachiolejeuneae are distinguished by their very different capsules. In the Ptychantheae, the inner capsule wall is covered by an orange brown thickening layer and is perforated by numerous pores or "fenestrae" (Figs. 4, 5). Crandall-Stotler and Geissler (1983) described the development of this peculiar fenestrate wall. There are normally 72 elaters per capsule (sometimes less), and the upper ends of the elaters are attached to the surface and the margins of the valves in a very regular pattern. All elaters have a distinct, brown spiral band. The spores are isodiametrical and are arranged in tetrahedral tetrads in the unopened capsule (Fig. 5C–D). The spore surface is covered by numerous sharp spines or verrucae and a distinct rosette marking is present on each of the eight spore facets (Fig. 7A–B).

In the Brachiolejeuneae, the inner capsule wall is pale and has nodulose wall thickenings similar to those found in the outer wall. A fenestrate sheeth of thickening is completely lacking (Fig. 6) or rudimentary in *Stictolejeunea*. There are 34 elaters, 8 or 9 per valve, and the upper ends of the elaters are attached to the valve margins only. The spiral band is rudimentarily developed and pale-colored. The spores are distinctly elongated-rectangular and are arranged in decussate tetrads in the unopened capsule (Figs. 6C, 7C). The spore wall is covered by numerous bluntish processes. Rosettes may be present in some species but usually they are rudimentarily or lacking (Fig. 7D).

A marked difference between the two tribes is seen in the spore-discharge process of the capsules. In the Ptychantheae, capsule dehiscence is violent and the spores are hurled away from the capsule. The explosive discharge is according to the spiral-spring mechanism described by Goebel and others (see Schuster, 1966: 176) for *Frullania*. The valves of the capsule are spreading after dehiscence (Figs. 4A, 5A). In the Brachiolejeuneae, however, capsule dehiscence proceeds slowly and the valves remain erect after dehiscence (Fig. 6A). Presumably, the rapid outward bending of the valves of the Ptychantheae is due to the very asymmetric thickening of the capsule wall and the spiralled elaters in this group, causing tension. Upon opening of the capsule, this tension is released and a more relaxed, recurved position is assumed by the valves.

The capsules of the Brachiolejeuneae are similar to those found in the Lejeunoideae and support the placement of the Brachiolejeuneae in this subfamily (see CLASSIFICATION). The Ptychantheae capsules correspond closely with those of Nipponolejeunea and the Jubulaceae. It is not certain whether the development of the ptychanthoid capule wall thickenings are homologous with those found in the Jubulaceae (Crandall-Stotler & Geissler, 1983). The wall thickenings in the latter family are usually described as "reticulate" (*Frullania*) or "annular" (*Jubula*). This matter would require further study. At any rate, the present data on capsule morphology clearly indicate that Ptychantheae capsules are much more similar to those of the Jubulaceae than of the Lejeuneoideae.

The sporophyte characters mentioned above have first been described for the Japanese Lejeuneaceae by Mizutani (1961), except for the tetrad and spore ornamentation patterns which are new. The different tetrad configurations can clearly be observed in longitudinal sections through the undehisced capsule (Figs. 4C, 6C). Tetrahedral tetrads are common in the Hepaticae but I am not aware of the occurrence of decussate

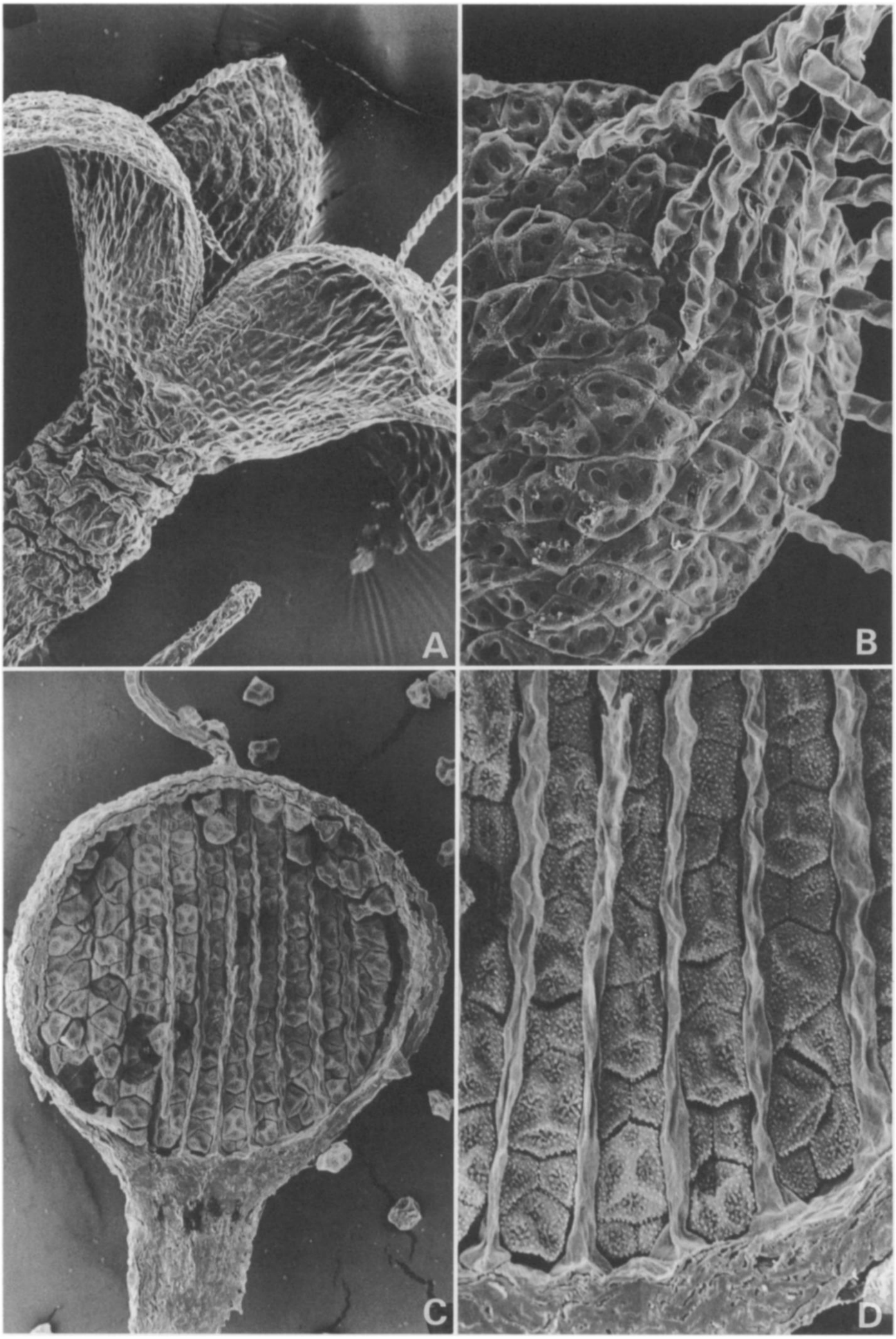

FIG. 4. Capsule morphology of selected Ptychantheae (ptychanthoid-type). **A.** Dehisced capsule of *Caudalejeunea hanningtonii*. **B.** Ibid., detail of valve apex (inner surface) showing elater attachment and *fenestrate*-type wall perforations. **C.** Longitudinal section of mature capsule of *Mastigolejeunea auriculata*, showing elater arrangement and isodiametric spores arranged in tetrahedral tetrads. **D.** Ibid., detail.

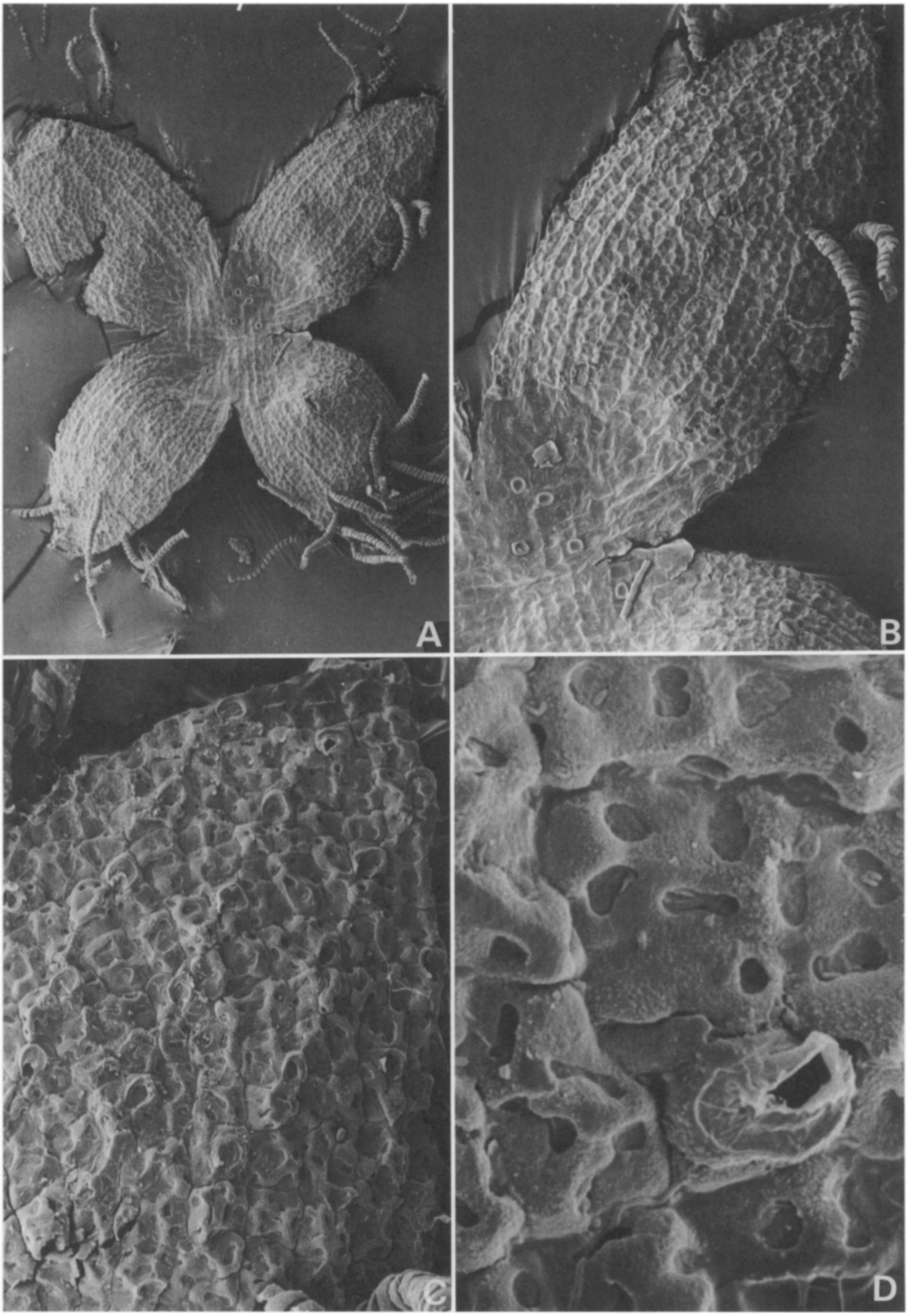

FIG. 5. Capsule valves and elaters of *Fulfordianthus pterobryoides* (ptychanthoid-type). **A.** View of the four valves (inner surface) of the dehisced capsule; note well-developed spiral bands of elaters **B.** Detail; rings on smooth valve base mark the attachment points of elaters before dehiscence. **C.** *Fenestrate*-type wall perforations of cells near valve apex (inner surface). **D.** Detail, showing elater attachment point.

tetrads in other liverworts (see Maheswari, 1950 for discussion). Decussate tetrads may therefore be a unique feature of the Brachiolejeuneae and the Lejeuneoideae.

Other sporophytic features significant to the subdivision Ptychantheae-Brachiolejeuneae are seen in the seta. In both groups the seta is normally made up of 16 outer rows of cells and 4 inner rows. However, in the Ptychantheae additional cell divisions may result in thicker setae, e.g. in *Bryopteris*, *Trocholejeunea*, *Marchesinia* and *Acrolejeunea*. In Brachiolejeuneae thicker setae are unknown. Instead, a slight decrease in the number of cell rows may occasionally occur in that tribe. In *Acanthocoleus trigonus* I observed that the upper part of the seta had 16 outer rows whereas in the lower portion the number of cells was only 12–14.

Prior to elongation the seta cells are usually arranged on the same vertical level. During seta elongation, the cells may remain evenly tiered or may elongate to different vertical levels and become unevenly tiered. Elongated setae with evenly tiered cells are called "articulate" (Fig. 52), those which are not evenly tiered are "non-articulate." Within Lejeuneaceae, articulate setae are characteristic for the Lejeuneoideae and, significantly, are also found in all genera of Brachiolejeuneae (except, may be, *Stictolejeunea*?) In the Ptychanthoideae, however, they occur only in *Frullanoides*, *Lopholejeunea* and *Schiffneriolejeunea*. All other genera of Ptychanthoideae have non-articulate setae.

The articulation and the occasional reduction of the number of cell rows in the seta of the Brachiolejeuneae are further evidence for the close relationship between Brachiolejeuneae and the members of the subfamily Lejeuneoideae. This subject will be further discussed in the CLASSIFICATION section.

The different sporophyte types found in Ptychanthoideae and Lejeunoideae seem to have adaptative significance. Many Lejeuneoideae grow exclusively in shaded, humid environments and are very common in the permanently moist understory of the rain forest. In the Ptychanthoideae, however, fewer taxa are restricted to these moist habitats and more are common in open, dryer environments or in the outer forest canopy. These are also the preferred habitats of the species of *Frullania* (Jubulaceae), which have a similar type of capsule. The thicker setae and thickened capsule walls of the *Frullania's* and the Ptychanthoideae may thus be interpreted as xeromorphic traits, to protect the sporophytes against desiccation. On average, spores of Ptychanthoideae and Jubulaceae also seem to be more resistant to desiccation than those of the Lejeunoideae. Van Zanten and Gradstein (1988) found that spores of Ptychanthoideae and Jubulaceae (10 species) survived 18–19 days of desiccation on average, those of Lejeuneoideae (19 species) only 7–8 days. Data on sporeling viablity yielded similar results. The explosive spore-discharge of the Ptychanthoideae and Jubulaceae, moreover, should enhance dispersal in the open habitats where chances for wind dispersal are better than in the sheltered habitats. Finally, the strongly convoluted leaves of many Ptychanthoideae in the dry state may also be considered adaptations of these plants to drought.

Asexual Reproduction

Most species are probably capable of regeneration from leaf cells and in some, e.g., *Mastigolejeunea auriculata*, production of small regenerant shoots on dorsal leaf surfaces is very common (Fulford, 1942, 1942a). *Marchesinia brachiata* may reproduce via unspecialized caducous or fragmenting leaves. Specialized propagules for asexual reproduction are rare in the Ptychantheae and Brachiolejeuneae. They are only found in *Acrolejeunea* subgenus *Acrolejeunea* (caducous leaves), *Caudalejeunea* (gemmae) and *Odontolejeunea* (cladia). The occurrence of vegetative propagation in *Odontolejeunea* and *Caudalejeunea* is probably an adaptation of these plants to their growth on leaves and fine twigs. The asexual devices are found in many epiphyllous or ramicolous species and may enhance quick establishment and dispersal of the plants in these ephemeral habitats (Longton & Schuster, 1983; Thiers, 1988).

An unusual device of vegetative reproduction is found in species of *Acrolejeunea* subgenus *Acrolejeunea*, which propagate by means of small, modified caducous leaves arising from upright flagelliform shoots (Fig. 33C, H). In liverworts this mode of asexual reproduction is otherwise only found in the genus *Rectolejeunea* and in *Frullania bolanderi*. The morphology and germination of the caducous leaves of *Acrolejeunea*

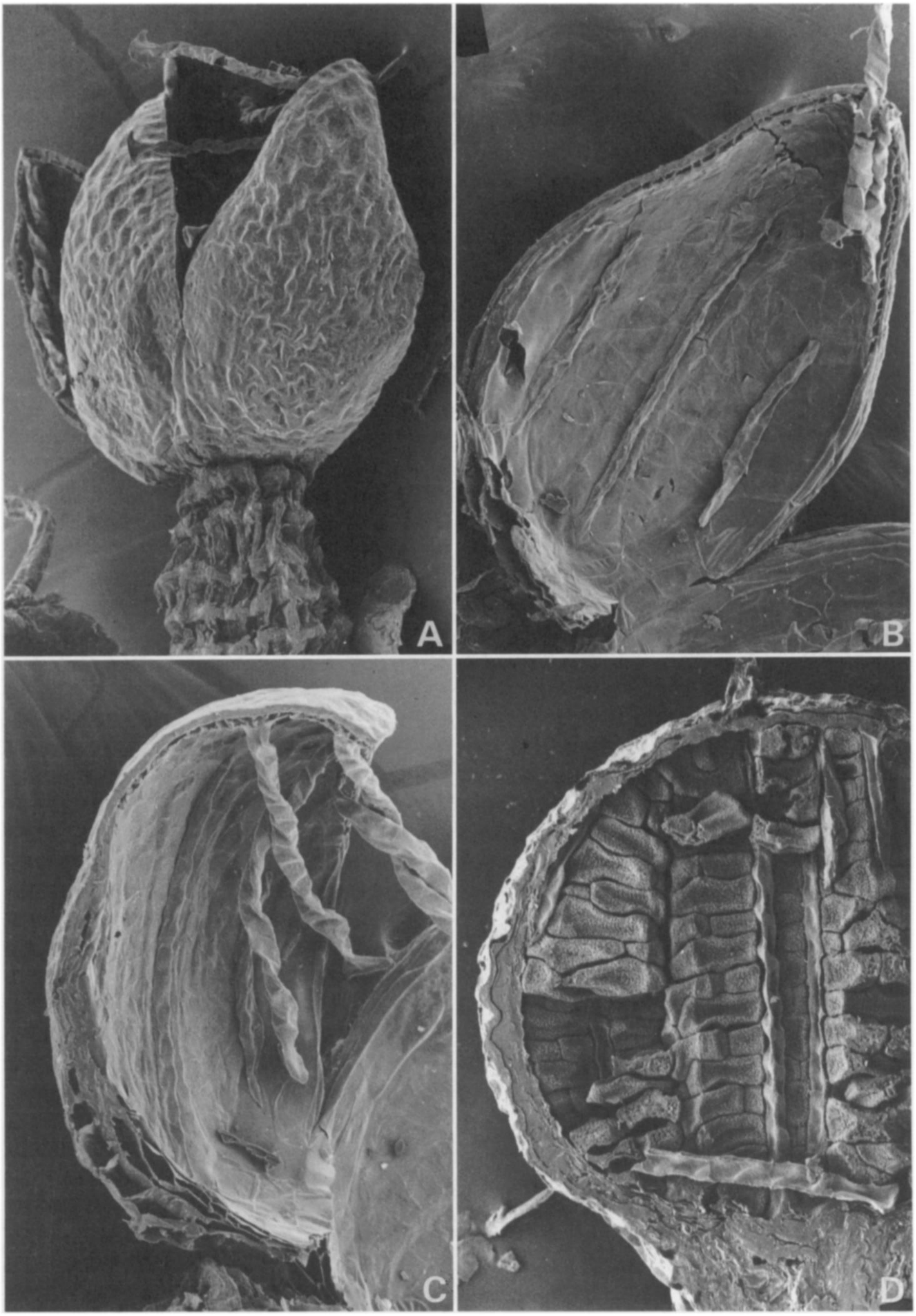

FIG. 6. Capsule morphology of *Brachiolejeunea laxifolia* (lejeunoid-type). **A.** Dehisced capsule. **B.** View of inner valve surface with three rudimentary elaters. **C.** Longitudinal section of mature capsule, showing elater arrangement and rectangular spores arranged in decussate tetrads. **D.** Ibid., showing marginal elater attachment.

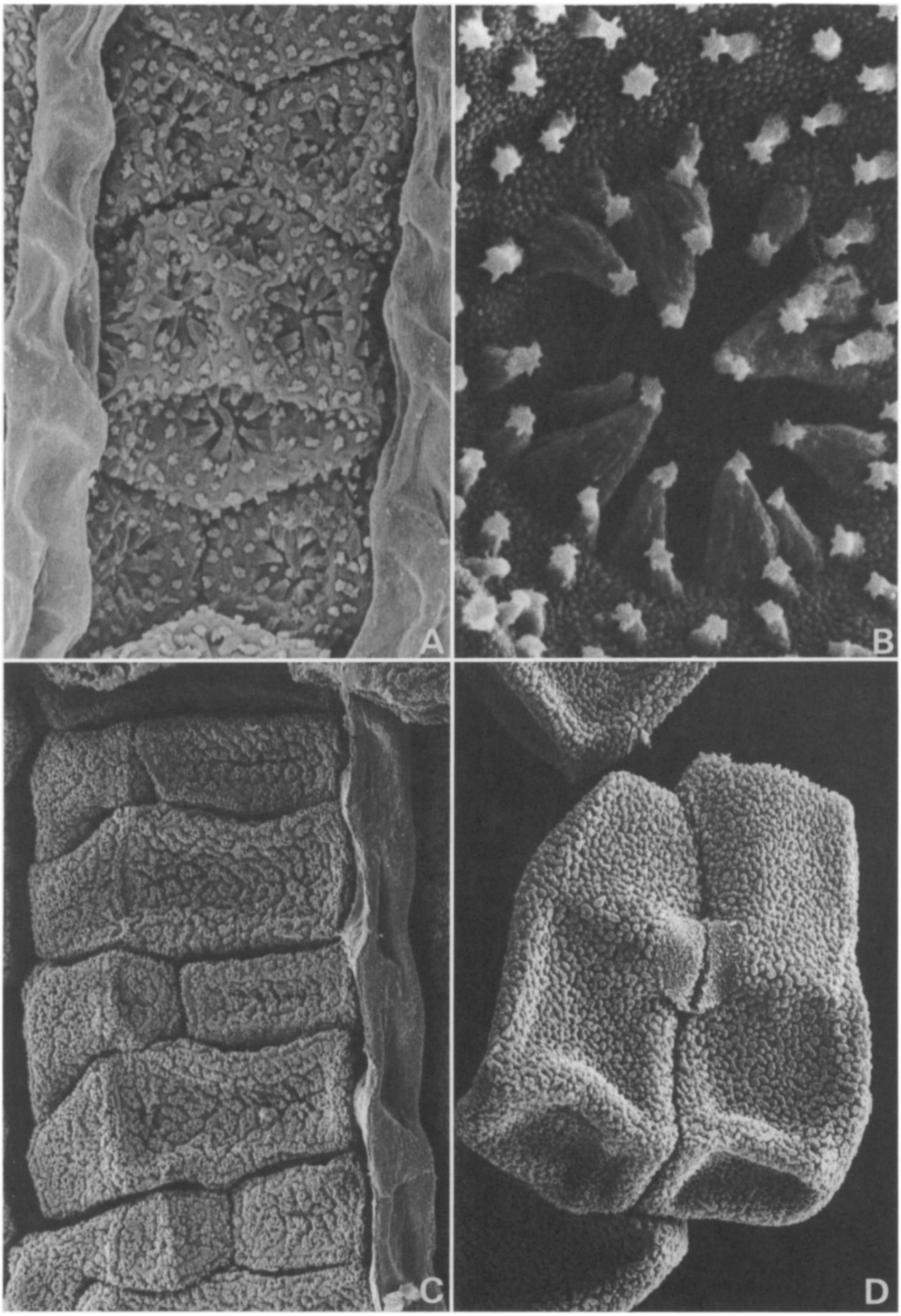

FIG. 7. Spores and tetrads of the Ptychantheae (A–B) and the Brachiolejeuneae (C–D). **A.** Tetrahedral tetrads of *Mastigolejeunea auriculata*; rosettes on spore surface mark location of foramina. **B.** Spines and foramen of *Acrolejeunea pycnoclada* spore surface. **C.** Decussate tetrads of *Brachiolejeunea laxifolia*. **D.** Two mature spores of *Brachiolejeunea leiboldiana*, showing verrucose surface without foramina.

has been described by Gradstein (1975). The shape of the caducous leaves in this genus has proven a useful criterion for species recognition. In the genus *Odontolejeunea*, Teeuwen (1989) found that the species can be recognized by leaf characteristics of the cladia.

KARYOLOGY

Chromosome numbers and morphology have been studied in 11 genera (30 species) of Lejeuneaceae (Fritsch, 1991). About half of them are members of the tribe Ptychantheae, the others belong to the Lejeuneae. Chromosomes of the Brachiolejeuneae remain unknown. The two karyological features appear to be very uniform and provide no insights in the relationships of the genera. More than 90% of the species have nine chromosomes. A few have 8 chromosomes and an additional micro-chromosome, and one species of *Lejeunea* has 9 or 10 chromosomes. *Trocholejeunea sandvicensis* is the only species with a base number n=8. A diploid race with 16 chromosomes has also been found in the latter species. This is the only occurrence of polyploidy in the family.

It thus appears that a haploid number of n=9 is characteristic of the Lejeuneaceae. As shown by Fritsch (1991), the same base number is found in many other liverwort families.

CHEMISTRY

Liverworts produce many unique terpenoids which are stored in the oil bodies. These substances often show strong biological activity and may play an important role in the defense of the plants against environmental hazards. In recent years several chemical studies have been conducted on the terpenoids of the Lejeuneaceae, especially of members of the Ptychantheae and Brachiolejeuneae (e.g., Asakawa, 1982; Asakawa & Inoue, 1987; Gradstein et al., 1981, 1985, 1988). Flavonoids have also been investigated (Kruijt et al., 1986; Gradstein et al., 1988; R. Mues, pers. comm.). The main purpose of these studies was to determine the secondary metabolite content of the different genera, to assess the chemotaxonomic relevance of the identified compounds and to assess the biological activity of the detected compounds. Selected secondary metabolites detected in the Ptychantheae and Brachiolejeuneae are shown in Fig. 8.

The available data are usually insufficient to assess chemical variation at the species level, due to the limited number of samples investigated per species. At higher taxonomic levels (genus, tribe) the chemical evidence is more significant and presents some rewarding as well as some enigmatic characteristics. About 60 species in 26 genera have been checked for the occurrence of terpenoids. It appears that most of the taxa elaborate large quantities of sesquiterpenes and/or diterpenes; few biosynthesize monoterpenes. Triterpenes are very rare in the Lejeuneaceae (and also in other liverworts) and have thus far been detected only in a species of *Diplasiolejeunea*.

Probably the most interesting group of substances from a chemotaxonomical point of view are the pinguisanes. These are unique liverwort sesquiterpenes which have thus far been detected in a limited number of liverwort families only (Asakawa, 1982). Within the Lejeuneaceae they occur almost exclusively in the Ptychantheae, often in large quantities. About 25 different compounds have been detected, about half of which have thus far been isolated and identified. Based on their presumed biogenesis, the known pinguisanes fall into two groups: the *pinguisanines* and the *pinguisones*. Pinguisanines (Fig. 8A) occur exclusively in *Acrolejeunea*, *Trocholejeunea* and *Frullanoides* and are excellent markers of these genera. Eight different pinguisanine-type substances were detected, five of which have never been found in any other plant group. They occurred in all investigated species of the three genera and usually 3–4(–7) different pinguisanines were found in each sample. The chemical results are clearly supportive of current taxonomic concepts since the three genera are also closely related morphologically and are usually considered to constitute a separate genus complex (Gradstein, 1975).

The distribution of the pinguisones (Fig. 8B) is more puzzling. They have been detected in six genera, including three closely related members of the Ptychantheae: *Thysananthus*, *Ptychanthus* and *Bryopteris* (see CLASSIFICATION). Each of the three genera produced a different substance. Two further substances were found in the genera *Acrolejeunea* and *Blepharolejeunea*. The distribution of the pinguisones seems less significant than that of

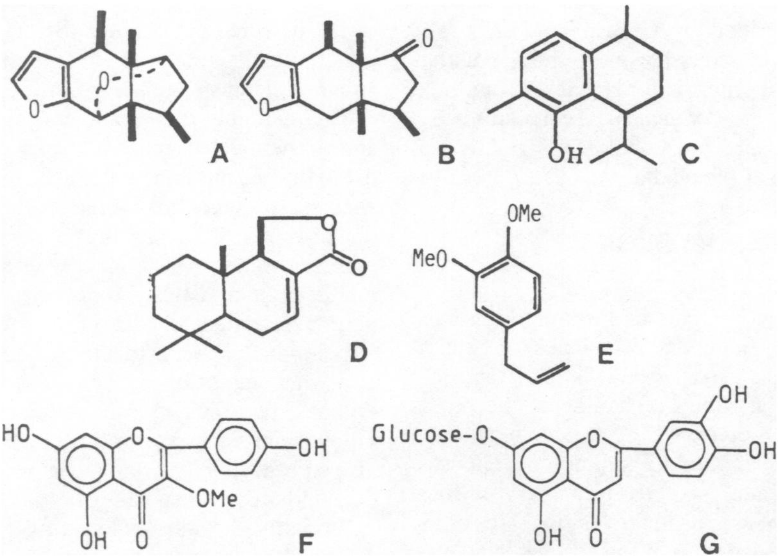

FIG. 8. Some taxonomically relevant terpenoids (A–E) and flavonoids (F–G) of the Lejeuneaceae. **A.** Pinguisanin. **B.** Pinguisone. **C.** 5-hydroxy-calamenene. **D.** Cinnamolide. **E.** Dimethyl-eugenol. **F.** Kaempferol-3-methylether. **G.** Luteolin-7-O-glucoside.

the pinguisanines, although it provides some support for the close relationship between three genera of the Ptychantheae postulated on mophological grounds.

Terpenoid data have also helped clarifying the taxonomic affinity between the genera *Ptychanthus* and *Tuzibeanthus*. On morphological grounds the two groups show many similarities but because of their very different leaf areolation they are sometimes classified far apart (Schuster, 1963; Gradstein, 1975). In chemical respects the two genera are remarkably similar, however. They share two unique, yet unidentified pinguisane-type sesquiterpenes and two unique labdane-type diterpenes. The four unique chemical markers shared by *Ptychanthus* and *Tuzibeanthus* clearly indicate that the two may be considered sister groups.

In other instances relationships postulated on morphological grounds are not corroborated by chemistry. *Lopholejeunea* and *Marchesinia*, for instance, are often considered sister groups, yet are completely different in chemical respects. *Lopholejeunea* species exclusively elaborate large amounts of the sesquiterepene 5-hydroxy-calamenene (Fig. 8C), whereas the aromatic dimethyl-eugenol (Fig. 8E) is the exclusive chemical markers of *Marchesinia* species. Study of the terpenoids of *Mastigolejeunea* and *Thysananthus* did not provide evidence in support of their morphological similarity. The two investigated species of *Mastigolejeunea* produced large quantities of pinguisane-type sesquiterpenes, but in the closely related genus *Thysananthus* (three species checked) no trace of pinguisanes could be detected.

Sesquiterpene lactones, characteristic of many species of *Frullania* and known for their toxicity, are rare in the Lejeuneaceae. Thus far they have only been detected in a few unrelated species of the Lejeuneoideae and in *Symbiezidium barbiflorum* (Brachiolejeuneae). In the Ptychantheae they are unknown. The drimane-type sesquiterpene lactone cinnamolide (Fig. 8D) is the chemical marker of *Lejeunea flava*. About 85% of the total gaschromatic yield of this species consisted of this single compound! Interestingly, this substance has never been discovered in any other species of Lejeuneaceae.

Flavonoids have been screened in 45 species of 22 genera (Kruijt et al., 1986; Mues, pers. comm.). As opposed to terpenoids, flavonoids are usually present in small amounts only in the Lejeuneaceae. Furthermore, considerable variation in flavonoid content was sometimes observed when more than one sample of a species was analyzed. For instance, in two samples each of *Brachiolejeunea laxifolia*, *B. phyllorhiza* and *Lopholejeunea evansiana*, one sample contained flavonoids whereas the other lacked them. Of five samples of *Archilejeunea fuscescens* analysed, only one yielded flavonoids. These findings are suggestive of the existence of chemical races in the species of Lejeuneaceae.

A few flavonoid compounds have thus far been isolated from Lejeuneaceae and identified. In *Marchesinia brachiata* Kruijt et al. (1986) detected two luteolin di-C-glycosides and from *Frullanoides densifolia* they isolated kaempferol-3-methylether (Fig. 8F), a free flavonol aglycone hitherto unknown in bryophytes. Gradstein et al. (1988) reported five different flavonoid structure types from Lejeuneaceae, all of which had also been detected in other liverwort families. They also analysed the flavonoid content of *Brachiolejeunea laxifolia* and *B. phyllorhiza*. The latter was usually considered a species of *Dicranolejeunea* but was recently transferred to *Brachiolejeunea* on morphological grounds. *Brachiolejeunea phyllorhiza* yielded luteolin-7-O-glycoside (Fig. 8G) and two closely related substances. Luteolin-7-O-glycoside is also the major flavonoid elaborated by *Brachiolejeunea laxifolia*. However, a study of flavonoids in *Dicranolejeunea* by Kruijt (1988) did not yield any luteolin-7-O-glycoside. The conclusion of these investigations was that the flavonoid chemistry is supportive of the transfer of *Dicranolejeunea phyllorhiza* to *Brachiolejeunea*.

FOSSILS

Fossil remains of Lejeuneaceae have been found in Tertiary amber deposits of central Europe, Mexico and the Dominican Republic (Grolle, 1988). Because of their occurrence on bark, species of Lejeuneaceae together with *Frullania* and *Radula* are the most frequently observed liverworts preserved in these fossil resins. The European fossils date from the late Oligocene, Eocene and the Miocene, those from the neotropics are probably from the Miocene (20–30 million years B.C.)

Recently, hepatics in amber have been studied in detail by Grolle (e.g., 1981, 1982, 1984, 1985). His excellent accounts include descriptions of eleven different species of Lejeuneaceae, most of them new to science. All of them are referred to extant genera but are different species. The fossil Lejeuneaceae from Europe show affinity to extant taxa from East Asia, those from Mexico and the Dominican Republic are elements of the current neotropical flora. The European species include *Cheilolejeunea latiloba*, *Nipponolejeunea europaea*, *Trocholejeunea contorta* and *Spruceanthus polonicus*. All of these are members of the subfamily Ptychanthoideae except for *Cheilolejeunea latiloba*. From the neotropics only one fossil species of Ptychanthoideae, *Bryopteris succinea* Grolle (1984), has been described. The species has diagnostic features of each of the two living *Bryopteris species* in the region, *B. diffusa* and *B. filicina*, but is apparently most closely related to the latter (see SYSTEMATIC TREATMENT).

Owing to the courtesy of Dr. R. Grolle and the curators of Haussknecht Herbarium, Jena and the Museum für Naturkunde, Berlin (BHU), I have been able to examine a small collection of holostipous Lejeuneaceae preserved in amber from the Dominican Republic. They are usually small stem fragments and are mostly sterile. Most of the specimens can be referred to extant genera and some even to extant species. The following three species, illustrated in Figs. 9 and 10, are elements of this fossil flora.

The fossil hepatic present in sample "1984–10" (BHU) has scattered ocelli in leaves and underleaves and is obviously a species of *Stictolejeunea* (Fig. 9A–B). Even though the specimen is only a small stem fragment with a few pairs of leaves and underleaves, I have been unable to find any difference with common neotropical *Stictolejeunea squamata* (Willd.) Schiffn. The robust stem, the large, deeply inserted underleaves and the peculiar, curved lobules of the fossil plant are features which are very characteristic of *S. squamata*.

The fossil hepatic in sample "1985–2" (BHU) has leaves with isodiametric cells and rounded apices, darkish pigmented cell walls, small underleaves with shallowly curved insertion lines, enlarged epidermis cells and a four cells wide ventral merophyte (Fig. 9C–E). This specimen may be referred to *Lopholejeunea*. Because of the small size of the underleaves and the acute distal ends of the lobules, the species resembles the common neotropical *L. nigricans* (= *L. muelleri-*

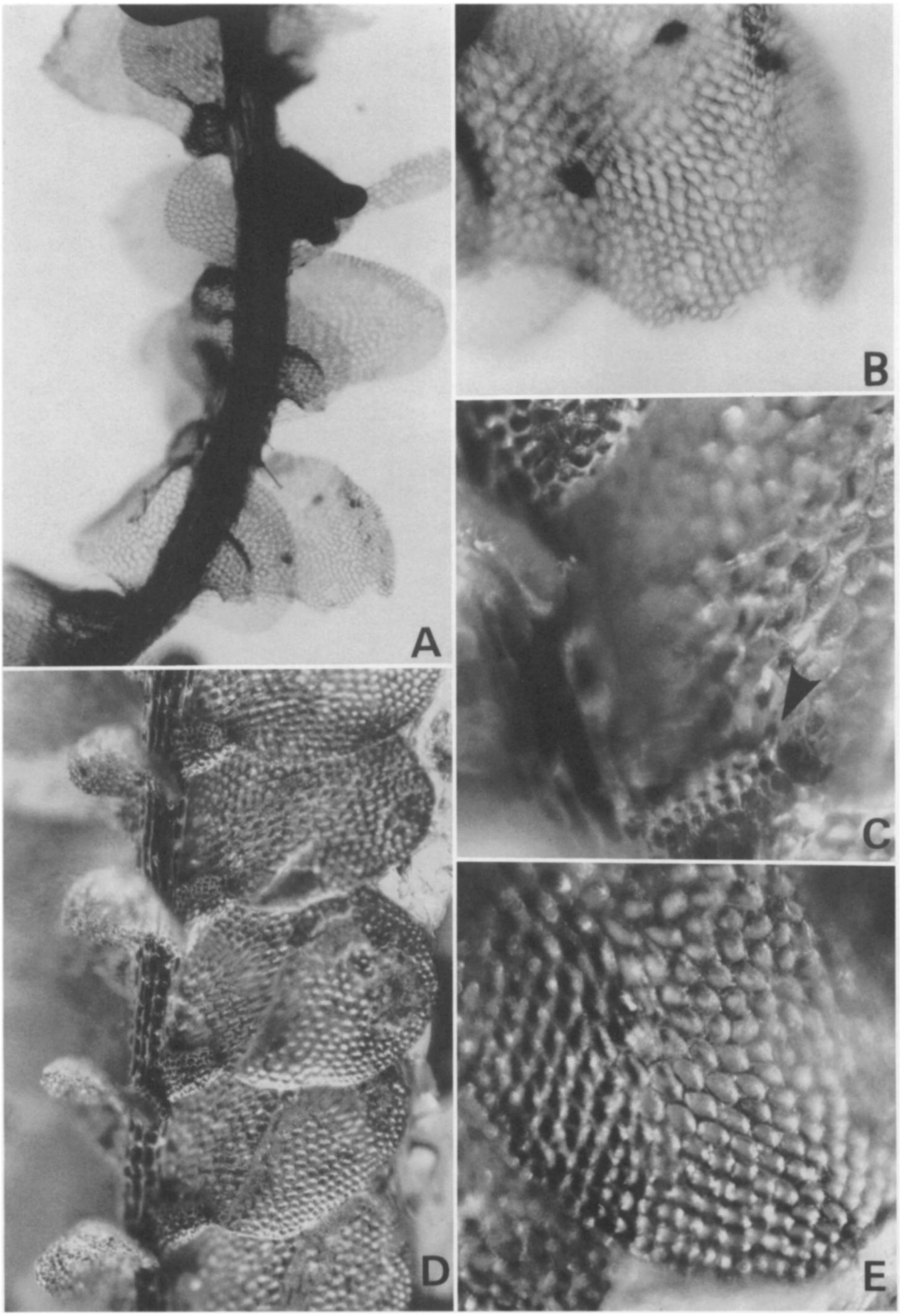

FIG. 9. Fossil Lejeuneaceae from Miocenic amber of the Dominican Republic. A–B. *Stictolejeunea squamata*. **A.** Habit, 90×. **B.** Portion of leaf showing ocelli, 230×. C–E. *Lopholejeunea sp.* **C.** Portion of stem and leaf, showing the sharp lobule tooth (arrow), 230×. **D.** Habit, 90×. **E.** Portion of leaf showing darkish cell walls, 230×.

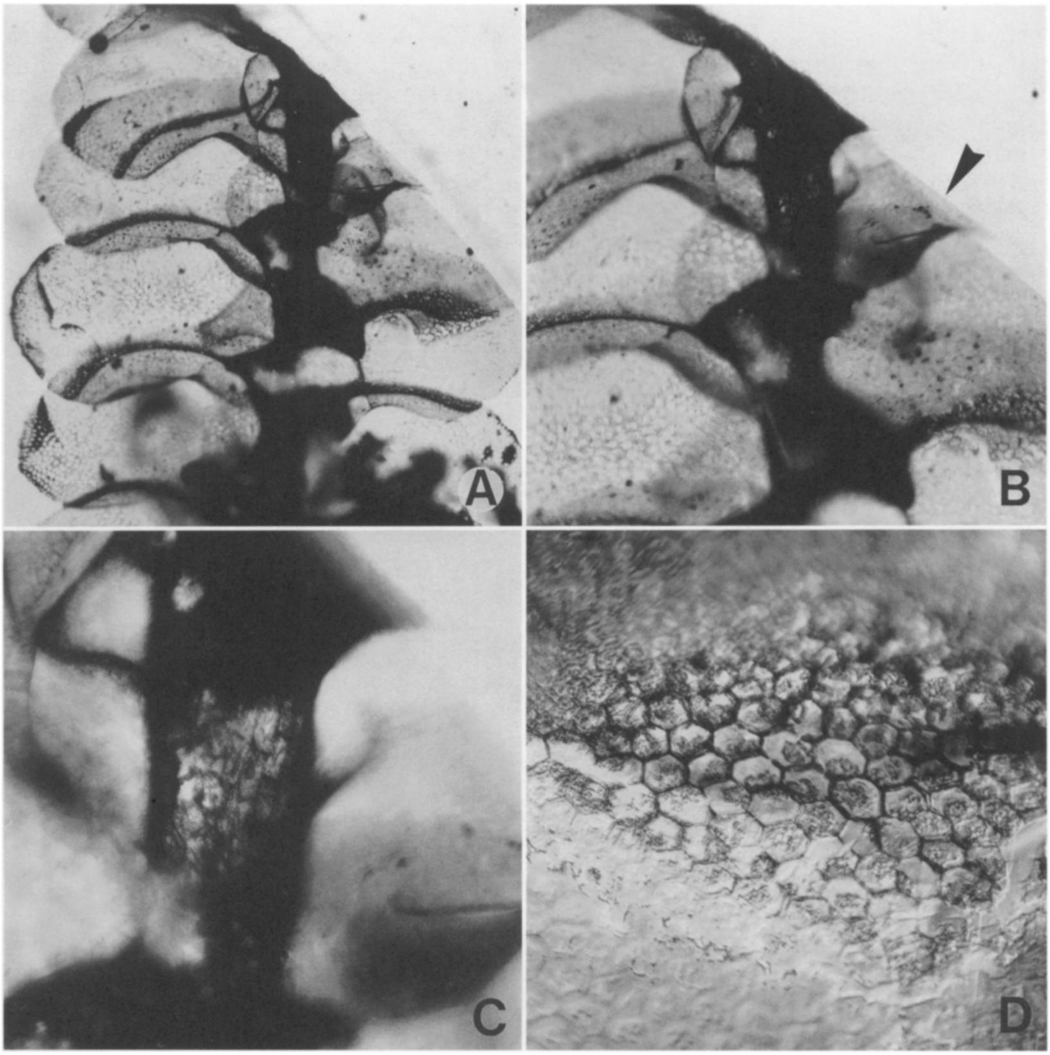

FIG. 10. Fossil Lejeuneaceae from Miocenic amber of the Dominican Republic: *Marchesinia brachiata*. **A.** Habit, 35×. **B.** Detail, showing lobule with teeth (arrow). **C.** Stem in ventral view, 230×. **D.** Mid-leaf cells, 230×.

ana). The latter, however, has more inflated lobules and a shorter, bluntish apical tooth. In the fossil *Lopholejeunea* species the lobules are very flat and the tooth is sharp and conspicuous, 1–2 cells long. A further peculiar feature are the squarrose underleaves. Although sterile, this fossil taxon may best be described as a new species (Gradstein, in press).

The third specimen in amber, sample "1985–1262" (BHU), is shown in Fig. 10. The plant is more robust that the other two fossil specimens and stands out by its elongated leaves with isodiametric cells, the large lobules with 2–3 small teeth regularly spatiated along the free margin, the decurrent underleaves with deeply arched insertion lines and the broad ventral merophytes (ca. 8 cells wide). This plant is in all respects similar to the common and highly variable neotropical *Marchesinia brachiata* (Sw.) Schiffn. The identification has been confirmed by Dr. E.P. Geissler, the specialist on the taxonomy of this genus.

The *Marchesinia brachiata* and *Stictolejeunea squamata* specimens are of considerable importance because they constitute the first records of extant species of liverworts in amber. They are the oldest fossil record of living liverwort species and show that these species are archaic taxa. The discovery of these fossils also lends support to the hypothesis, based on biogeographic and phylogenetic grounds, that the genera of Ptychantheae and Brachiolejeuneae are very old (see PHYTOGEOGRAPHY) and may have existed before the break-up of Gondwanaland. The data clearly corroborate the great evolutionary and biogeographic importance of these hepatics preserved in amber.

CLASSIFICATION

The Family Lejeuneaceae

The Lejeuneaceae are a very natural family whose circumscription has rarely been disputed. None of the numerous genera recognized in the Lejeuneaceae with the exception of *Bryopteris* have in the past been placed in other families. The characteristic lobule, the *Lejeunea*-type branches and, especially, the single archegonium per gynoecium (rarely two in *Nipponolejeunea*) are important morphological characters and separate Lejeuneaceae from the Jubulaceae (*Frullania* and its allies) which is the sister group of the Lejeuneaceae. Together they constitute the suborder Jubulineae, characterized by its unique sporophyte and shoot-sporophyte relationship (see MORPHOLOGY AND ADAPTATION).

Other features characteristic of the Lejeuneaceae are the dorsally interlocking merophytes and the modified epidermis cells, the so-called "superior central cells," by which leaves and underleaves are attached to the stem (Fig. 2E–F). These specialized attachment cells are apparently lacking in the Jubulaceae (but the anatomy of the underleaf base has been little investigated in that family). Also unique in Lejeuneaceae are the large rhizoid discs elaborated in epiphyllous plants.

Taxonomic knowledge of the family has advanced considerably in recent years due to monographic studies. Generic limits have become clarified, especially among "holostipous" Lejeuneaceae. The principles and problems of generic delimitation in the family have frequently been reviewed (e.g., Schuster, 1963; Gradstein, 1979) and will not be discussed here. In this chapter we will focus on the subfamilial and tribal classification, with particular reference to the above mentioned group of holostipous taxa. As many genera of Lejeuneaceae have not yet been revised, the conclusions presented here are preliminary.

Traditionally, the genera of Lejeuneaceae were classified into two rather artificial groups, the "Holostipae" and the "Schizostipae" (Spruce, 1884; Evans, 1935; Schuster, 1963). The two groups, variously classified as subtribes, tribes or subfamilies, are based principally on the presence of undivided or divided underleaves and the structure of the stem: rather robust and with 10 or more rows of epidermis cells (4 of which constitute the ventral merophyte) in the Holostipae and thinner and usually with only 7 rows of epidermis cells (2 of which constitute the ventral merophyte) in the Schizostipae. A separate group, the "Paradoxae" or Cololejeuneoideae Herz., has been created for a few genera of Schizostipae with unusual, pendulum-type leaf segmentation.

Holostipae and Schizostipae were not sharply defined by the above characters and consequently opinions differed as to the correct position of some of the genera (see Gradstein, 1975, 1985). The recognition of four additional subfamilies (Metzgeriopsidoideae Schust., Myriocoleoideae Schust., Nipponolejeunoideae Schust., Tuyamaelloideae Schust.) by Schuster (1963), based mainly on leaf insertion type, has not helped much to clarify the intrafamilial relationships. All of these subfamilies are small groups, split off to accomodate highly apomorphic, isolated genera with transverse leaf insertions, such as *Myriocolea*, *Nipponolejeunea*, and *Tuyamaella* and its relatives.

The publication of the treatment of the Japanese Lejeuneaceae by Mizutani (1961) marked a turning point in the classification of the Lejeuneaceae. Prior to that time, the genera were usually classified solely based on gametophytic traits. Mizutani found that the Japanese members of Holostipae and Schizostipae differed by many constant characters of the sporophyte. He treated the two groups as separate subfamilies, which he more appropriately named Ptychanthoideae (= Holostipae) and Lejeuneoideae (= Schizostipae). Already Spruce (1884) had observed that Ptychanthoideae and Lejeuneoideae usually have different setae, either with 16 longitudinal outer cell rows (Ptychanthoideae) or with only 12 rows (Lejeuneoideae). To this, Mizutani added many important characters of the capsules: wall thickening patterns, elater arrangement and morphology, spore shape, etc. (see MORPHOLOGY AND ADAPTATION).

Mizutani's subfamilies became soon widely adopted and authors began paying more attention to sporophyte characters (e.g., Stotler & Crandall, 1969; Gradstein, 1975; Geissler & Gradstein, 1982; Crandall-Stotler & Geissler, 1983; van Slageren & Berendsen, 1985). Van Slageren and Berendsen made a comprehensive study of the sporophyte of the Ptychanthoideae, using Scanning Electron Microscopy. They found new taxonomically important features of the spores (arrangement, sculpturing) and introduced the terms "fenestrate-type" and "nodular-type" for the capsule types found in Ptychanthoideae and Lejeuneoideae, respectively. Since nodular thickenings are not a unique feature of the capsule walls of Lejeunoideae, the term "nodular-type" seems less appropriate and may be replaced by *ptychanthoid* for the fenestrate-type capsule and *lejeunoid* for the nodular-type.

Van Slageren and Berendsen (1985) also found that nine genera of Ptychanthoideae had lejeuneoid instead of ptychanthoid capsules: *Acanthocoleus*, *Blepharolejeunea*, *Brachiolejeunea*, *Dicranolejeunea*, *Lindigianthus*, *Neurolejeunea*, *Odontolejeunea*, *Stictolejeunea*, *Symbiezidium*. These genera constitute the tribe Brachiolejeuneae van Slag. & Berends. They are mainly neotropical taxa (and had therefore not been studied by Mizutani). Van Slageren and Berendsen kept the genera of the Brachiolejeuneae in the Ptychanthoideae, in spite of their very different capsules. However, the numerous unique features of their lejeunoid capsules (non-recurving valves, lack of fenestrate thickening layer, margin-inserted elaters, rudimentary spirals, decussate tetrads, rectangular spores) indicate that the Brachiolejeuneae belong in the Lejeuneoideae rather than in the Ptychanthoideae. Brachiolejeuneae and Lejeuneoideae also share articulate setae, which are rare in the Ptychanthoideae (see MORPHOLOGY AND ADAPTATION).

Van Slageren and Berendsen (1985) argued that the holostipous nature of the gametophyte (robust stems, undivided underleaves) of the Brachiolejeuneae, in addition to the 16:4 seta, would be supportive of placement of this group in the Ptychanthoideae rather than in the Lejeuneoideae. None of the gametophytic characters are diagnostic, however. As shown by Gradstein (1985) and others, holostipous gametophytes are found in many genera of Lejeuneoideae, e.g. *Leucolejeunea, Omphalanthus, Lepidolejeunea, Pycnolejeunea, Calatholejeunea*, etc. This character state has apparently evolved several times within the family Lejeuneaceae and is not very useful for defining monophyletic groups. Other gametophytic character states shared with the Ptychanthoideae are (1) *Frullania*-type branches, in *Blepharolejeunea, Brachiolejeunea* and *Dicranolejeunea* and *Stictolejeunea* (lacking in other Lejeunoideae); (2) hyaline papilla entally displaced, in all genera of Brachiolejeuneae (in other Lejeuneoideae found in *Pictolejeunea*).

It should be noted that Brachiolejeuneae also have many gametophytic features which are common in the Lejeuneoideae and are not found in the Ptychanthoideae. As their occurrence in the Brachiolejeuneae is not constant, they are not diagnostic for the tribe. The following are typical lejeuneoid gametophyte characters of Brachiolejeuneae:

1. ventral merophyte 2 cells wide: in *Dicranolejeunea, Acanthocoleus* and *Odontolejeunea*;

2. epidermis cells thin-walled and much larger than medulla (very distinct hyalodermis): in *Odontolejeunea, Dicranolejeunea, Brachiolejeunea*, etc.;

3. underleaves in the androecia restricted to the base of the male spike: in *Symbiezidium, Neurolejeunea*, and *Stictolejeunea*;

4. antheridia occurring on specialized male spikes or paroicous: in almost all Brachiolejeuneae (specialized male spikes in Ptychanthoideae only in *Bryopteris* and *Mastigolejeunea innovata*; paroicous species very rare in Ptychanthoideae);

5. first lobule tooth reduced, hence hyaline papilla becoming distal in position: in *Neurolejeunea*;

6. presence of ocelli: in *Neurolejeunea* and *Stictolejeunea*;

7. pinguisane-type terpenoids ± lacking (common in Ptychanthoideae).

In conclusion, the placement of the Brachiolejeuneae in the Lejeuneoideae appears to be sup-

Table I

The sporophyte differences between Ptychanthoideae and Lejeuneoideae

PTYCHANTHOIDEAE	LEJEUNEOIDEAE
Capsule dehiscence explosive; valves widely spreading after dehiscence	Capsule dehiscence gently; valves remaining suberect after dehiscence
Inner capsule wall covered by an orange-brown, fenestrate sheeth of thickening	Inner capsule wall with pale trigones and intermediate thickenings, lacking sheeth of thickening
Elaters usually 72, upper ends attached to valve surface and margins; spiral band well-developed	Elaters 34 or less, upper ends attached to valve margins only; spiral band rudimentary
Spores isodiametrical, arranged in tetrahedral tetrads	Spores elongate-rectangular, arranged in decussate tetrads
(Seta made up of 16 or more outer rows of cells)	(Seta made up of 12 or 16 outer rows of cells)

ported by many sporophytic as well as gametophytic characters. The sporophyte characters, however, are the only constant, diagnostic features and therefore provide the main support for this classification (see Table I).

In many liverwort families sporophyte characters are more stable than gametophyte characters (Schuster, 1966). Liverwort sporophytes are always protected by gametophytic structures during their development and are much less exposed to environmental pressures than the gametophyte. Evolution through natural selection would therefore proceed much more slowly in the sporophyte and its characters could be expected to be less variable. Support for this hypothesis comes from the observation that spores are usually the only sporophytic structures in liverworts which show variation at the species level. They are the only sporophytic structures exposed to environmental pressures during longer periods of time. Natural selection may therefore act more strongly upon spores than on other parts of the liverwort sporophyte.

The above hypothesis provides an elegant explanation of the stability of sporophyte characters in the Lejeuneaceae. It does not explain, however, why some gametophytic traits which are well exposed to environmental pressures, may be very constant. An example are the two different lobule types which characterize the families Jubulaceae and Lejeuneaceae. Ontogenetically the two lobule types are closely related. Juvenile *Frullaniae* have lobules similar to those found in *Nipponolejeunea* and *Cololejeunea* (and other Lejeuneaceae with narrowly constricted lobule bases), but in the adult *Frullania* plant galeate lobules are produced. An occasional reversal to the lejeunoid lobule may occur, especially at the base of branches (Schuster, 1963a; VandenBerghen, 1977). In general, however, the lobule difference between the two families is very constant. It would be worthwhile to study the morphogenetic processes that control the development of the two lobule types in the Jubulinae.

As mentioned above, several subfamilies of Lejeuneaceae have been described in addition to Ptychanthoideae and Lejeuneoideae. They are mostly small groups characterized by a few highly apomorphic traits of their gametophytes. As argued elsewhere (Gradstein, 1991) I have chosen not to attribute subfamily rank to these groups. The Nipponolejeuneoideae Schust. (*Nipponolejeunea* only) have ptychanthoid capsules and may therefore be classified with the Ptychanthoideae. A separate tribe, Nipponolejeuneae Gradst., could be proposed for their accomodation. The Cololejeunoideae Herz., Metzgeriopsidoideae Schust., Myriocoleoideae Schust., Tuyamaelloideae Schust. have lejeuneoid capsules (but in some of the genera sporophytes remain unknown!) and should therefore be classified with the Lejeunoideae. I have tentatively placed them in a single tribe Lejeuneae, characterized by the 12:4 seta. An attempt to further classify the Lejeuneae would fall beyond the scope of this monograph and is therefore not attempted.

The tribal classification of the Lejeuneaceae proposed in this monograph is as follows:

1. Subfamily Ptychanthoideae Mizut.
   1.1. Tribe Nipponolejeuneae (Schust. & Kachroo) Gradstein *comb. nov.*
   (Nipponolejeuneoideae Schuster & Kachroo, Beih. Nova Hedwigia **9:** 90. 1963).
   Contains only the genus *Nipponolejeunea* Hatt.
   1.2. Tribe Ptychantheae Bischl.
   (including Bryopteridaceae Stotler = Bryopteridoideae Gradstein). Contains 18 genera. The position of *Phaeolejeunea* Mizut., known only from gametophytic material, remains uncertain.

2. Subfamily Lejeuneoideae Massal.
   2.1. Tribe Brachiolejeuneae van Slageren & Berendsen.
   Contains 9 genera.
   2.2. Tribe Lejeuneae Dum.
   (including Lejeuneoideae s.str., Cololejeuneoideae Herz., Metzgeriopsidoideae Schust., Myriocoleoideae Schust. and Tuyamaelloideae Schust.). Contains about 60 genera (Grolle, 1983 and updates).

The numerous characters diagnostic of Lejeuneoideae and Ptychanthoideae indicate that the two subfamilies are monophyletic groups. Ptychanthoideae share a common sporophyte with the Jubulaceae and may therefore be considered the more primitive subfamily of the two. There is some biogeographical and palaeobotanical support for the assumption that the Ptychanthoideae are the oldest group (Gradstein, 1991, 1992d). It appears that several endemic genera of Asiatic Ptychanthoideae (*Nipponolejeunea*, *Spruceanthus*, *Trocholejeunea*) occur as fossils in Eocenic amber of Europe (see FOSSILS). They were apparently widespread in the Holarctic during the early Tertiary, like Ginkgo and others. Presently two of the three genera (*Nipponolejeunea*, *Trocholejeunea*) are mainly restricted to the subtropical or temperate portions of continental East Asia. The third genus, *Spruceanthus*, occurs throughout Southeast Asia.

In contrast, none of the endemic genera of the Asiatic Lejeuneoideae are known as fossils. All of them occur in the tropical rain forests of the Malesian archipelago. It may therefore be assumed that they originated in more recent geological times in the tropical belt, synchronous with the evolution of the tropical rain forest. The contrasting evolutionary trends indicate that Ptychanthoideae are a more ancient group than Lejeuneoideae.

The Genera of the Ptychantheae and Brachiolejeuneae

The genera of the Ptychantheae and the Brachiolejeuneae have variously been grouped in informal taxonomic categories called "complexes" by Schuster (1963) and Gradstein (1975, 1987, 1991). These classifications were phenetic and based a rather limited number of characters. Gradstein (1975) used 15 characters, of which 13 were gametophytic features and 2 were derived from the sporophyte.

The various recent monographs and regional revisions of genera of Ptychantheae and Brachiolejeuneae have provided a better basis for determining generic relationships within the tribes. Much information on variation and distribution of characters and character states has been obtained and understanding of the natural limits of the genera has become much improved. The genera of Brachiolejeuneae have become particularly well known. All of them have been monographed on a world-wide basis (Gradstein, 1985, and this treatment; van Slageren, 1985; Kruijt, 1988; Teeuwen, 1989). As to the Ptychantheae, eleven genera have been revised on a world wide basis and regional revisions are available for the remaining eight genera. Taxonomic problems which remain to be solved in this group concern mostly the delimitation of some palaeotropical species, especially of *Lopholejeunea*, *Mastigolejeunea*, *Thysananthus*, *Caudalejeunea* and *Archilejeunea*.

Based on the available data, a cladistic analysis of the genera of Ptychantheae and Brachiolejeuneae has been undertaken. All 27 genera currently recognized in these groups were included in the analysis, except the genus *Phaeolejeunea* of which sporophytes remain unknown. The results of the analysis are the basis of the generic arrangement adopted in this treatment. Twenty-six characters have been included, totalling 58 character states (Table II). Arrangement of character states is unordered. The distribution of the character states in the two tribes is shown in Tables III and IV. Eighteen characters are relevant to the

Table II

Character state coding for cladistic analysis

1. Growth form	0 = dendroid; 1 = not dendroid
2. Vegetative branches	0 = mainly *Lejeunea* type; 1 = mainly *Frullania*-type
3. Flagellae	0 = produced; 1 = not produced
4. Epidermis cells	0 = larger; 1 = dorsal larger, ventral not larger; 2 = not larger than medulla cells
5. Subepidermis	0 = present; 1 = lacking
6. Epidermis walls	0 = thin; 1 = thickened
7. Ibid.	0 = colorless; 1 = brown
8. Ventral merophyte	0 = 2-3 cells; 1 = 4 or more cells wide
9. Median leaf cells	0 =isodiametrical; 1 = elongated
10. Ibid.	0 = more than 20 µm; 1 = less than 20 µm long
11. Trigones	0 = triangular-radiate; 1 = triangular-cordate; 2 = lacking
12. Dark cell walls	0 = present; 1 = lacking
13. Oil bodies	0 =segmented; 1 = homogeneous; 2 = lacking
14. Ocelli	0 = present; 1 = lacking
15. Lobules	0 = sometimes reduced; 1 = never reduced
16. Underleaf attachment	0 = bistratose; 1 = tristratose
17. Male bracteoles	0 = reduced; 1 = present throughout spike
18. Male bract lobules	0 =hypostatic; 1 = epistatic
19. Antheridia	0 = usually two; 1 = only one per bract
20. Gynoecial shoot	0 = elongated; 1 = abbreviated
21. Innovations	0 = lejeuneoid; 1 = pycnolejeuneoid; 2 = lacking
22. Female bracts	0 = winged; 1 not winged
23. Perianth ventral keels	0 = one; 1 = two; 2 = more than two; 3 = none
24. Perianth apex	0 = smooth; 1 = ciliate-laciniate; 2 = auriculate
25. Seta epidermis cells	0 = 20-25; 1 = more than 25 rows
26. Pinguisanines	0 = present; 1 = lacking.

genera of Ptychantheae and seventeen to the Brachiolejeuneae. Only shared generic characters or synapomorphies have been scored. Diagnostic features of individual genera or autapomorphies do not clarify phylogenetic relationships and are excluded from the analysis. The number of characters used is almost twice as many as in my previous, phenetic analysis (Gradstein, 1975). Moreover, the distribution of the character states is now much better known and can be scored more accurately. Some characters employed previously were excluded from the analysis because they show too much variation or are autapomorphic.

New characters not used previously are: 1. growth form (Gradstein, 1992), 4. flagellae, 6. subepidermis (Gradstein, 1992), 11. leaf cells size, 15. lobule reduction, 16. underleaf base anatomy, 17. male bracteoles, 19. antheridia, 20. gynoecial shoot, 21. innovation type (Thiers, 1985), 22. female bract wings, and 26. terpenoids (Gradstein et al., 1988). Characters employed previously whose state distributions had become better known include trigone morphology, oil bodies and sporophyte features. In my 1975 classification spores were unknown in nine genera and setae in seven. At present they remain unknown only in *Phaeolejeunea* and *Tuzibeanthus*. The genus *Tuzibeanthus* is the sister group of *Ptychanthus* on gametophytic grounds and is therefore included in the Ptychantheae. The systematic position of the Pacific genus *Phaeolejeunea* remains doubtful. This genus is therefore excluded from the analysis. Generic characters

Table III

Character state matrix for cladistic analysis of the Ptychantheae.

Outgroup: *Nipponolejeunea*; - = polymorphism; ? = missing data

	1	2	3	4	5	6	7	9	11	12	13	15	18	19	21	23	25	26
Nipponolejeunea	1	1	1	2	1	1	0	0	0	1	0	1	0	0	-	0	0	1
Acrolejeunea	1	0	1	0	1	0	0	1	1	1	1	1	1	1	2	2	0	0
Archilejeunea	1	0	1	2	1	1	0	0	0	1	0	-	0	0	-	1	0	1
Bryopteris	0	1	1	-	0	1	1	1	1	1	1	1	0	0	2	0	1	1
Caudalejeunea	1	0	1	0	1	0	0	1	1	1	1	1	0	0	2	-	0	?
Cephalolejeunea	1	0	1	0	1	0	0	0	0	1	?	0	0	0	0	2	0	?
Frullanoides	1	1	1	0	1	0	0	1	1	0	1	1	1	-	1	2	0	0
Dendrolejeunea	0	0	1	2	0	1	1	1	1	1	?	1	0	0	0	0	?	?
Fulfordianthus	0	0	1	2	0	1	1	0	2	1	2	1	0	0	1	0	0	?
Lopholejeunea	1	0	0	0	1	1	-	0	0	0	1	0	0	0	2	-	0	1
Marchesinia	1	0	1	1	1	1	1	0	0	0	1	0	0	0	1	3	1	1
Mastigolejeunea	1	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
Ptychanthus	0	1	1	2	0	1	1	1	1	1	0	1	0	0	0	2	0	1
Schiffneriolejeunea	1	0	1	1	1	1	1	1	1	1	0	0	0	0	2	-	0	1
Spruceanthus	1	0	0	2	1	1	1	-	0	1	1	0	0	0	0	2	0	1
Thysananthus	1	0	0	2	1	1	1	-	-	1	0	1	0	0	0	0	0	1
Trocholejeunea	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	2	1	0
Tuzibeanthus	0	1	1	2	0	1	1	0	0	1	0	1	0	0	0	2	?	1
Verdoornianthus	1	0	1	1	1	1	0	0	0	1	0	1	0	0	2	1	0	?

Table IV

Character state matrix for cladistic analysis of the Brachiolejeuneae.

Outgroup: *Leucolejeunea*; - = polymorphism

	2	4	7	8	10	11	13	14	15	16	17	18	19	20	22	23	24
Leucolejeunea	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0
Acanthocoleus	0	0	0	1	0	-	0	1	0	1	1	1	-	0	1	-	-
Blepharolejeunea	1	0	0	0	0	-	1	1	1	-	1	1	1	0	-	-	-
Brachiolejeunea	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	-
Dicranolejeunea	1	0	0	1	0	1	0	1	0	1	1	1	1	0	1	0	1
Lindigianthus	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	3	0
Neurolejeunea	0	2	1	0	1	2	0	-	1	0	-	0	0	0	-	0	2
Odontolejeunea	0	0	0	1	0	-	-	1	0	1	1	1	0	0	1	0	1
Stictolejeunea	1	2	1	0	1	2	2	0	0	0	0	0	0	1	1	0	2

which were excluded because they are too variable or are autapomorphies include the following:

a. *Position of dry leaves.* Leaf position in the dry state (convoluted or spreading) is usually correlated with the shape of the leaf cells and trigones (see MORPHOLOGY AND ADAPTATION) but varies much more than the cell characters and is therefore excluded from the analysis.

b. *Toothed leaves.* In *Dendrolejeunea*, *Fulfordianthus* and *Odontolejeunea* leaves are always toothed but in other genera it is usually a species character.

c. *Intermediate thickenings more than 1 per cell wall.* This feature is sometimes found in *Bryopteris* and *Caudalejeunea*. It is not constant and therefore not a good generic character.

d. *Underleaf insertion line deeply arched.* Deeply arched insertions are characteristic of some genera (especially *Brachiolejeunea* and its relatives). In others it is only a subgeneric (*Symbiezidium*, *Marchesinia*) or a species character (*Frullanoides densifolia*).

e. *Rhizoid discs.* These are an adaptation to epiphyllous growth and not a good taxonomic character.

f. *Number of female bract series.* Genera without innovations have 2–5 series of bracts, those with innovations only 1–2. The differences are gradual and are difficult to define.

g. *Asexual reproduction.* Specialized modes of asexual reproduction are autapomorphies of *Caudalejeunea* (gemmae), *Odontolejeunea* (cladia) and *Acrolejeunea* subgen. *Acrolejeunea* (caducous leaves).

h. *Specialized oil body types.* Most genera have homogeneous, *Massula*-type or segmented, *Calypogeia*-type oil bodies. The finely papillose *Jungermannia*-type oil bodies of *Neurolejeunea* and the large, homogeneous *Bazzania*-type oil bodies of *Symbiezidium* are autapomorphies.

i. *Distal hyaline papilla.* This common feature of *Cheilolejeunea* and its relatives (Lejeuneae) is an autapomorphy of *Neurolejeunea*.

j. *Vitta.* Restricted to *Dendrolejeunea* and two species of *Thysananthus*.

k. *Some branch features.* Except for innovations, flagellae and predominance of *Lejeunea* or *Frullania* type branches, branch characters are usually not constant at the generic level (Thiers, 1985). *Frullania*-type innovations are autapomorphies of *Trocholejeunea sandvicensis* and *Lopholejeunea evansiana* (Gradstein, 1991). *Bryopteris*-type branches are not recognized.

l. *Terpenoids.* Except for the occurrence of pinguisanines, chemical data have not been included in the analysis (see CHEMISTRY).

The cladistic analysis of the data (Tables III, IV) was performed using HENNIG86. The genera most closely related to the analysed tribes were chosen as outgroups. *Nipponolejeunea* is the outgroup of the Ptychanthea and *Leucolejeunea* (tribe Lejeuneae) was chosen as outgroup of the Brachiolejeuneae. The most parsimonious trees were determined using the *mh** option of HENNIG86 (the supposedly more superior *ie* option of this program did not give results even after several days of calculation on a much faster computer). The calculation resulted in one fully resolved shortest tree for Brachiolejeuneae; the consistency index of this cladogram is 71 and the number of steps 35. For the Ptychantheae two shortest trees were obtained, each with a consistency index of 53 and 48 steps.

The cladogram of the Brachiolejeuneae (Fig. 11) shows the existence of two basic clades which are described in this treatment as subtribes: the Stictolejeuninae (= *Stictolejeunea* complex sensu Gradstein, 1991) and the Brachiolejeuninae (*Symbiezidium* complex and *Brachiolejeunea* complex sensu Gradstein, 1991). The most significant result of the analysis is the association of *Symbiezidium* with the *Brachiolejeunea* complex. The taxonomic position of *Symbiezidium* has long been problematical. Most recently it was placed in a complex of its own, with closest affinity to the *Stictolejeunea* complex. The association of the genus with the *Brachiolejeunea* complex is based on four synapomorphies: enlarged epidermis, tristratose underleaf base (a new character), the homogeneous oil bodies, and the ciliate-laciniate perianth. The analysis confirms that *Symbiezidium* is the genus of Brachiolejeuninae nearest to the Stictolejeuninae. *Dicranolejeunea*, *Acanthocoleus* and *Odontolejeunea*, because of their narrow ventral merophytes and predominantly *Lejeunea*-type branching, are the end line of evolution of this tribe.

The topologies of the two most parsimonious trees of the Ptychantheae are very similar. They differ only in the position of the dendroid genera

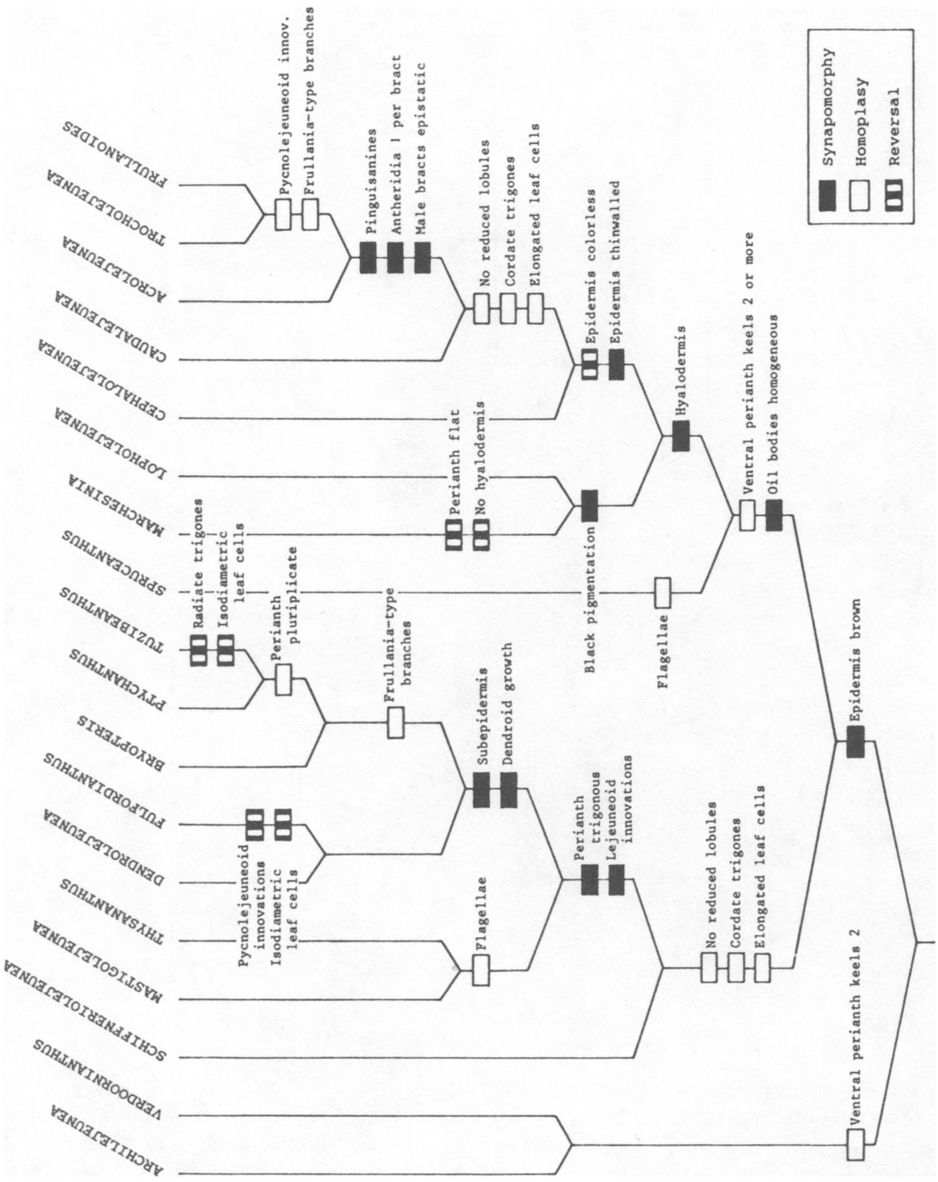

FIG. 11. Phylogenetic relationships of the genera of the Ptychantheae. For explanaiton see text.

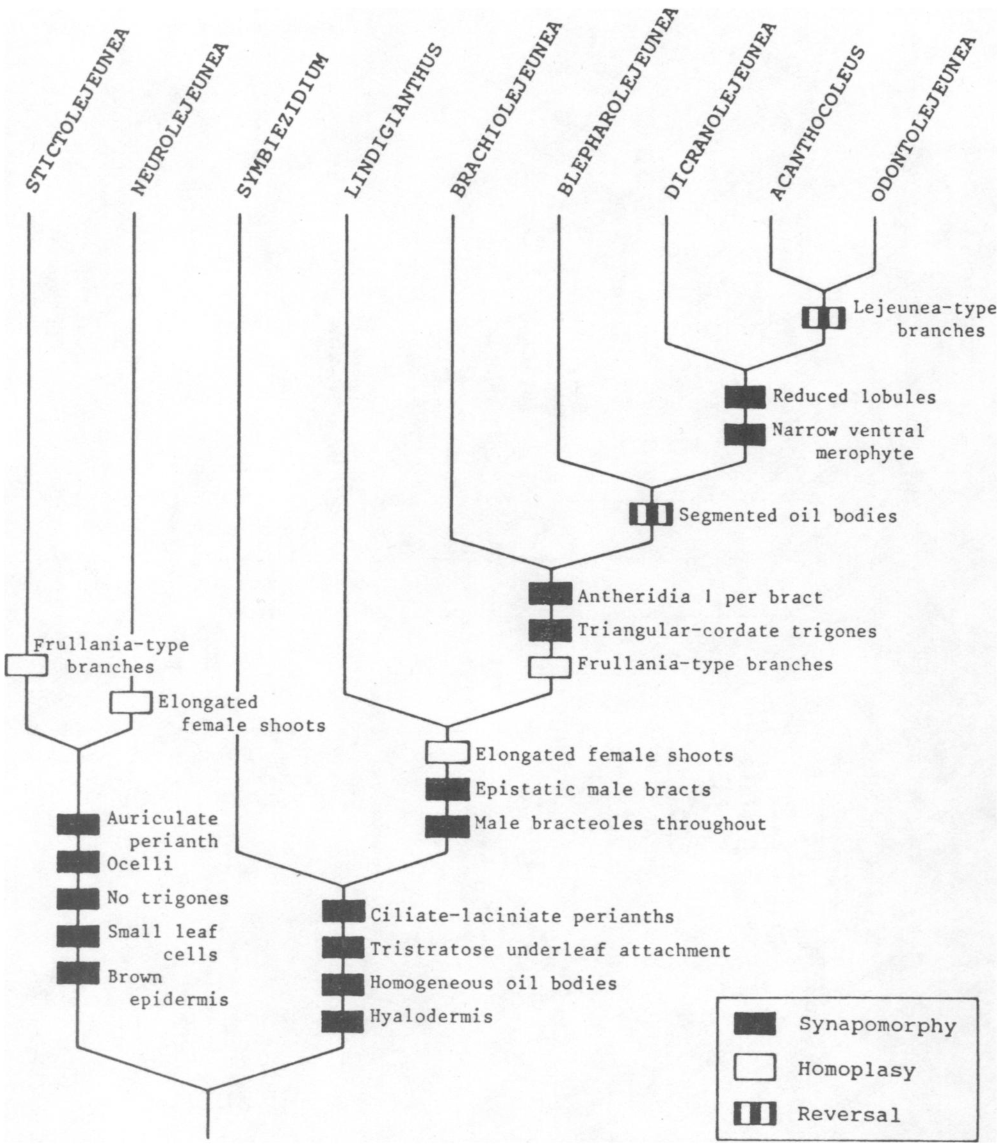

FIG. 12. Phylogenetic relationships of the genera of the Brachiolejeuneae. For explanation see text.

Bryopteris, *Fulfordianthus*, *Dendrolejeunea*, *Ptychanthus* and *Tuzibeanthus*. One tree recognizes *Ptychanthus* and *Bryopteris* as sister groups and positions *Tuzibeanthus* nearest to *Fulfordianthus*. The other recognizes *Tuzibeanthus-Ptychanthus* and *Fulfordianthus-Dendrolejeunea* as sister groups. Chemical data not included in the analysis have shown that *Ptychanthus* and *Tuzibeanthus* are much more similar to each other than to *Bryopteris* (see CHEMISTRY). Moreover, *Fulfordianthus* and *Dendrolejeunea* are usually considered sister groups on taxonomic grounds (Gradstein, 1991). Therefore, the second tree has been chosen (Fig. 12).

The basal nodes of the cladogram of the Ptychantheae indicate the existence of three different clades, which are described in this treatment as subtribes: the Archilejeuninae, the Ptychanthinae, and the Acrolejeuninae. The Ptychanthinae combine the *Bryopteris* complex and the *Pty-*

chanthus complex (Gradstein, 1991). All dendroid genera belong to this tribe. An isolated position of *Bryopteris* advocated previously (e.g., Stotler & Crandall-Stotler, 1974) is not supported. Synapomorphies of the Ptychanthinae are the cordate trigones, elongated leaf cells, the lobules which are never reduced and lejeuneoid innovations. A hyalodermis is lacking and most taxa have segmented oil bodies, a character shared with the Archilejeuninae. The latter subtribe is small and rather plesiomorphic. It is nearest to the *Nipponolejeuneae*, with which it shares the unspecialized stems, the presence of two different innovation types, leaf areolation, oil bodies, etc.

In the subtribe Acrolejeuninae genera of four different genus complexes are united: the *Acrolejeunea* complex, the *Caudalejeunea* complex, the *Lopholejeunea* complex and part of the *Archilejeunea* complex (Gradstein, 1991). Homogeneous oil bodies are the main synapomorphy of this tribe. A perianth with two or more keels is also shared by most of the genera of this group (except *Marchesinia*). *Spruceanthus* is the genus of this tribe nearest to the Ptychanthinae (this is also supported by taxonomy), whereas the members of the *Acrolejeunea* complex (*Acrolejeunea*, *Trocholejeunea*, and *Frullanoides*) are the end line of evolution of this subtribe. They are characterized by their unique terpenoids and androecia.

The cladogram of the Ptychantheae has more homoplasies and reversals than that of the Brachiolejeuneae, particularly in subtribes Ptychanthinae and Acrolejeuninae. Cordate trigones and elongated leaf cells have evolved at the root of the Ptychanthinae and at the branch giving rise to the genera of the *Acrolejeunea* complex. Dominance of *Frullania*-type branching, pycnolejeuneoid innovations and pluriplicate perianths have evolved at least twice (the latter character is also found in some *Mastigolejeunea* species). Many more homoplasies could probably be identified when autapomorphies would be included.

Another characteristic of the cladogram of the Ptychantheae is the weak support of some of the nodes. *Spruceanthus*, *Marchesinia* and *Lopholejeunea*, for example, are positioned on the basis of single synapomorphies only. One might therefore expect that slight changes of data matrix could result in a different cladogram. Tests have shown that this is indeed the case. A better supported cladogram might be achieved by inclusion of more characters in the analysis. To find new morphological characters relevant to the phylogeny of the group would probably be difficult. More promising data could be expected from chemical study. As shown in the CHEMISTRY section, species of Ptychantheae and Brachiolejeuneae elaborate many compounds with interesting taxonomic distributions. Unfortunately, many of these still remain unidentified. Another promising area of study would be the spore morphology and elater arrangement. Van Slageren (1985) preliminarily identified three different types of spore ornamentation in the Ptychantheae and showed that some genera have fewer elaters than others. As elaters break away easily after capsule dehiscence, this character can only be studied in undehisced capsules. Another method would be to count the number of elater attachement points on the capsule wall (Fig. 5).

In conclusion, the cladistic analysis has shown that different clades can be recognized in the Ptychantheae and Brachiolejeuneae based on shared synapomorphies of the genera. Some of these clades are more strongly supported than others. In the taxonomic treatment these clades will be ranked and formally described as subtribes.

PHYTOGEOGRAPHY

The Ptychantheae contain about 135 species world-wide, in eighteen or nineteen genera (the taxonomic position of *Phaeolejeunea* remains unknown). They are distributed throughout the tropics but the largest number of taxa are found in the Old World (Gradstein, 1991). Five genera of Ptychantheae are exclusively palaeotropical (*Cephalolejeunea*, *Dendrolejeunea*, *Ptychanthus*, *Trocholejeunea* and *Tuzibeanthus*) and an additional eight genera are Old World groups with only few species in the New World: *Acrolejeunea*, *Caudalejeunea*, *Lopholejeunea*, *Mastigolejeunea*, *Schiffneriolejeunea*, *Spruceanthus* and *Thysananthus*. As to the remaining genera, one is pantropical (*Archilejeunea*), one occurs in tropical Africa, tropical America and western Europe (*Marchesinia*), and four are strictly or predominantly neotropical: *Bryopteris*, *Frullanoides*, *Fulfordianthus*, and *Verdoornianthus*.

In all there are 37 species of Ptychantheae in the neotropics.

The genera *Archilejeunea* and *Frullanoides* are the most important neotropical genera of Ptychantheae in terms of number of species. Each has seven species and one subspecies in the neotropics; fewer taxa occur in the palaeotropics. Like many other members of the Ptychantheae, these genera are probably of Gondwanan origin (e.g., van Slageren, 1985). Another important neotropical genus is *Bryopteris*. Although previously believed to contain seven species (Stotler & Crandall-Stotler, 1974), I have been able to recognize only three species in *Bryopteris*: two in tropical America and one in Madagascar and the Mascarene islands. The distribution of the genus appears to be "peri-African" and is highly suggestive of a Gondwanan derivation (Stotler & Crandall-Stotler, 1974; Gradstein et al., 1983). Because of their large, fern-like fronds, the species of this genus are very conspicuous in the field and are frequently collected.

The two endemic neotropical genera of Ptychantheae, *Fulfordianthus* and *Verdoornianthus*, are small groups with limited ranges. *Fulfordianthus* has two species and occurs in Central America and northwestern South America (Fig. 24). The genus is most closely related to *Dendrolejeunea* from Asia and is a morphologically highly specialized taxon (Gradstein, 1992). *Verdoornianthus* (2 spp.) is a very rare Amazonian genus known from only few collections (Fig. 17). The species may have been overlooked because they grow mainly in the high canopy of the rain forest. The genus is probably a specialized off-shoot of *Archilejeunea* subgenus *Archilejeunea*, which is also Amazonian in distribution and is very common in the region.

The Brachiolejeuneae are a much smaller group than the Ptychantheae and have a very different distribution. There are 35 species in nine genera; all genera and about 80% of the species (28) occur in the New World. Four or five genera are endemic to the New World: *Brachiolejeunea* (?), *Blepharolejeunea*, *Dicranolejeunea*, *Lindigianthus*, *Neurolejeunea*. The species occur usually at low or middle elevations, except for *Brachiolejeunea laxifolia*, *Lindigianthus cipaconeus* and the species of *Blepharolejeunea* subgen. *Oreolejeunea* which are high-montane taxa adapted to life in cold tropical environments. A few species of *Brachiolejeunea* have established successfully in temperate South America.

The genera of Brachiolejeuneae occurring in the Old World are *Acanthocoleus*, *Odontolejeunea*, *Stictolejeunea*, *Symbiezidium*, and possibly *Brachiolejeunea* (the occurrence of *B. phyllorhiza* in Africa needs confimation). The genus most widely distributed in the palaeotropics is *Acanthocoleus*, which has three species in Africa and three in tropical Asia. Phylogenetic evidence suggests that *Acanthocoleus* originated in Gondwanaland (Kruijt, 1988). Its most primitive species are found in the New World. As to the other genera extending into the Old World, *Stictolejeunea* is pantropical (two species in Asia) and *Odontolejeunea* and *Symbiezidium* are Afro-American. The latter has three species in the neotropics and one in Madagascar and the Seychelles, hence has a "peri-African" distribution like *Bryopteris*.

The species diversity of Ptychantheae and Brachiolejeuneae is greatest in northwestern South America (northern Peru to Venezuela) and the Guianas (including eastern Guayana Highlands). Each of these areas has about 40 species (Fig. 13). Central America and the Greater Antilles are also rich in species of Ptychantheae and Brachiolejeuneae, though slightly less than in northern South America. The great altitudinal diversity coupled with very humid climates may be reasons for the relatively large numbers of species in northwestern South America and Central America. In the Greater Antilles and Guianas, where the mountains are usually lower, the high species numbers may to some extent be due to the rather advanced state of floristic exploration of the areas. The Greater Antilles have been collected rather intensively since the second half of the 18th century when Olof Swartz made the first neotropical hepatic collections on Jamaica and Hispaniola (Swartz, 1788). Parts of the Guianas have been explored rather intensively in recent years in the framework of the *Flora of the Guianas* project (Gradstein & Hekking, 1989) and this has yielded many species previously unknown to the region.

The vast Amazon and Orinoco basins, central and southern Brazil, the southern Andes and the lesser Antilles are regions poorer in species (Fig. 13) The absence of mountains in the Orinoco and Amazon basin and the dryer climates of large areas of Brazil and the southern Andes should be main reasons for the lower number of species. In

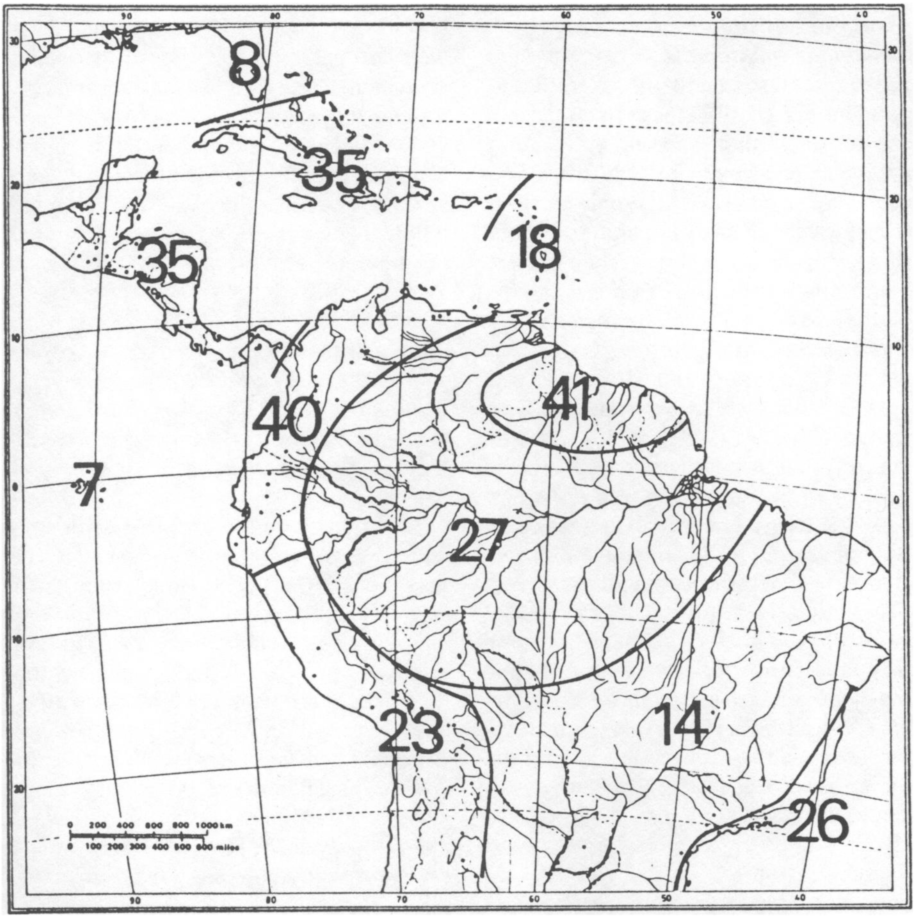

FIG. 13. Regional species richness of Ptychantheae and Brachiolejeuneae in the neotropics.

addition, insufficient exploration may also be a factor of importance here.

The ranges of the individual species vary from narrowly endemic to very widespread. They may be classified in twelve different categories or floristic elements.

Neotropical Species

Fifty species or almost 80% of the New World Ptychantheae and Brachiolejeuneae are restricted to the Neotropics. The following elements may be recognized:

1. **Amazonian element:** *Acrolejeunea torulosa* (Fig. 34), *Archilejeunea* (subgenus *Archilejeunea*) spp., *Mastigolejeunea innovans*, *M. plicatiflora* (Fig. 22), *Neurolejeunea seminervis* (Fig. 40), *Schiffneriolejeunea amazonica* (Fig. 20), *Thysananthus amazonicus* (Fig. 24), *Verdoornianthus* spp. (Fig. 18).

The region inhabited by the Amazonian species includes the Amazon River basin from the foot of the Andes to the Atlantic Ocean, as well as well as the Orinoco River basin and the Guianas. The liverwort flora of this vast area has been inventoried to a very limited extent only and this is reflected in the maps (e. g., Figs. 18, 20, 24, 31, 41). Most collecting has been done in central Amazonia around Manaus, along the Rio Negro and in the Guianas. Species common throughout the area and known from numerous collections are *Archilejeunea fuscescens*, *Acrolejeunea torulosa*, *Mastigolejeunea plicatiflora* and *Thysananthus amazonicus*. The remaining species are rarer and some are known from only a few specimens even though the collections may come from localities thousands of miles apart, e.g., *Mastigolejeunea innovans*, *Schiffnerriolejeunea amazonica* and *Verdoornianthus griffinii*. These are canopy dwellers of the high forest and their rarity may be due to neglect of their habitat.

Some Amazonean species exhibit rather remarkable disjunctions. *Archilejeunea fuscescens*, for instance, is disjunct between Colombian Amazonia and Cocos Island (Fig. 15) and *Neurolejeunea seminervis* is also found in Guatemala and southern Mexico (Fig. 40). As both species have rather limited, inner-Amazonian distributions, their occurrence in Central America (one record each) is certainly remarkable. They should be looked for in suitable habitats in intermediate areas. Worthy of mention, though certainly not unique, is the disjunct occurrence of *Thysananthus amazonicus* on Cuba. The island of Cuba is known for its rich liverwort flora and has many disjunct species including several from Amazonia (Pócs, 1988). The Amazonian taxa seem to be restricted to the eastern portion of the island where they occur in the remnants of the once more widespread lowlands rain forests of the island.

2. **Andean element:** *Blepharolejeunea incongrua* (Fig. 46), *B. securifolia*, *Brachiolejeunea laxifolia*, *Dicranolejeunea axillaris* (Fig. 49), *Frullanoides densifolia*, *F. laciniatiflora* (Fig. 36), *Lindigianthus cipaconeus* (Fig. 44).

The majority of the species belonging to the Andean element occur throughout the cordilleras, from Mexico to Bolivia. They may also occur elsewhere, e.g., on high peaks in SE Brazil (mainly Mt. Itatiaia) and in the Greater Antilles. As the localities outside the cordilleras are only few, I consider them Andean taxa. Two Andean species do not occur throughout the cordilleras. *Frullanoides laciniatiflora* is known only from northern Peru and *Lindigianthus cipaconeus* is a species confined to the humid "páramo region" (northern Peru to Costa Rica).

The Andean species usually occur between 1500–4000 m except *Frullanoides densifolia*, which ranges from almost sea level to the alpine belt and has the broadest altitudinal range of all species treated in this monograph. The vertical distribution of *F. densifolia* is to some extent correlated with latitude as the highest records are around the equator and the lowest records are from SE Brazil, at the southern limits of the tropical belt. On islands altitudinal ranges may also be lower. On the Galapagos Islands, *Dicranolejeunea axillaris* is very common and usually occurs between 200 and 1000 m (Gradstein & Weber, 1982).

3. **Caribbean element:** *Acanthocoleus juddii* (Fig. 53), *Frullanoides bahamensis*, *Frullanoides corticalis* (Fig. 36), *Lopholejeunea quelchii* (Fig. 31), *Neurolejeunea catenulata* (Fig. 40), *N. sastreana*.

The Caribbean element includes species which occur preferably in coastal areas; some may be tolerant of seasonal drought and salt spray (van Slageren, 1985). *Frullanoides bahamensis* and *Neurolejeunea catenulata* are restricted to the West Indian islands but the majority of the Caribbean species occur also on the adjacent mainland of Central and/or South America. *Frullanoides corticalis* is the most widely distributed species in this category and also occurs along the coast of southeastern Brazil, probably as the result of a long-range dispersal event (van Slageren, 1985).

4. **Central American element:** *Acrolejeunea heterophylla* (Fig. 34), *Fulfordianthus evansii* (Fig. 24), *Frullanoides mexicana* (Fig. 36).

Central America has many species of Ptychantheae and Brachiolejeuneae but only three are endemic to the area. Of these, *Acrolejeunea heterophylla* is the most widespread and occurs also in central Florida. All Central American species have been described rather recently which indicates that the area may be underexplored.

5. **Chocó element:** *Archilejeunea bischleriana* (Fig. 15), *A. porelloides* subsp. *chocoensis*, *Fulfordianthus pterobryoides* (Fig. 24), *Spruceanthus theobromae*, *Symbiezidium dentatum* (Fig. 41).

Many phanerogamic taxa are endemic to the very wet rain forests along the Pacific coast of northern South America, the Chocó phytogeographic province (Gentry, 1982). The bryophyte flora of the region is still poorly known, but recent evidence suggests that the area also has an unusual bryophyte flora (Gradstein, 1992, 1992c). Although floristic relationships with Central America (*Fulfordianthus*) and Amazonia (*Archilejeunea porelloides* subsp. *chocoensis*) are evident, the endemic taxa of the Chocó are often quite isolated taxa. Most of them are Lejeuneaceae, including the endemic genera *Luteolejeunea* and *Fulfordianthus*, and some seem to be very common in the area. During my 1992 exploration of the lowland rain forests of the Chocó Department, Colombia, I found the endemic *Fulfordianthus pterobryoides*, *Luteolejeunea herzogii* and *Symbiezidium dentatum* in almost every locality which I visited and on the island Gorgona, off the Pacific coast of Colombia, they seem to be common species of the coastal rain forest (Rudas & Aguirre, 1990). *Fulfordianthus pterobryoides* is also common in the Darien (Gradstein & Salazar, 1992).

Uncommon Chocó endemics include *Archilejeunea bischleriana* (two localities near Quibdo) and *Spruceanthus theobromae*, which is only known from the province Los Rios, Ecuador where it has been collected twice, lastly in 1947. *Spruceanthus theobromae* is one of the rarest species of neotropical Ptychantheae and is probably in danger of extinction (see below). Its continued existence is of considerable importance since it is the only neotropical species of the genus *Spruceanthus*.

6. Guyanan element: *Blepharolejeunea chimantaensis* (Fig. 47), *Brachiolejeunea conduplicata*, *Stictolejeunea balfourii* var. *bekkeri* (Fig. 38).

The Guianas have a rich liverwort flora due to the presence of vast areas of rain forest and numerous mountain ranges, belonging to the Guayana Highland. It is the richest area for Ptychantheae and Brachiolejeuneae in terms of number of species (Fig. 13). Endemism is rather low, however, probably due to the fact that the area is not sharply bounded by natural frontiers. Most of the species range well into the Amazon basin (Gradstein et al., 1990). Of the three taxa of Ptychantheae and Brachiolejeuneae endemic to the area, *Blepharolejeunea chimantaensis* is montane and the other two are lowland taxa.

7. Southern subtropical element: *Acanthocoleus trigonus* (Fig. 53).

The southern tropical and subtropical portions of South America (southern Peru, Bolivia, southern Brazil, Paraguay, northern Argentina and Chile) mostly have a rather dry climate and are rather poor in Lejeuneaceae (Gradstein, 1991, 1992a). Most of the taxa reported are widespread neotropical species. *Acanthocoleus trigonus* is the only species of Ptychantheae and Brachiolejeuneae endemic to this region. The rather poor Lejeuneaceae flora of subtropical South America should be due to the rarity in these areas of evergreen rain forests; most of these have disappeared due to deforestation (P. Geissler, pers. comm.).

8. Neotropical element: *Archilejeunea auberiana* (Fig. 15), *A. parviflora* (also Africa?), *Blepharolejeunea saccata*, *Brachiolejeunea leiboldiana*, *Bryopteris diffusa*, *B. filicica*, *Frullanoides liebmanniana*, *Neurolejeunea breutelii*, *Odontolejeunea decemdentata*, *O. rhomalea* (Fig. 54), *Stictolejeunea squamata*, *Symbiezidium barbiflorum* (Fig. 41), *S. transversale*.

The neotropical element includes species endemic to the neotropics and rather widespread in the region. Some are very common such as *Bryopteris filicina*, *Stictolejeunea squamata* and *Symbiezidium transversale*, others are scattered and known from only few collections, e. g., *Archilejeunea auberiana*, *Blepharolejeunea saccata*, *Brachiolejeunea leiboldiana*, *Frullanoides liebmanniana*. Their rarity may be due to insufficient inventory of the habitats where they occur. *Frullanoides liebmanniana*, for instance, is a species of forest canopies and isolated trees in areas with a pronounced dry season and should be much more common than the distributional data suggest.

The species of *Archilejeunea* listed here have close relatives in Africa and may prove to be Afro-American taxa. This matter needs further study.

Wide Tropical Species

This category includes transoceanic species which range into the palaeotropics. Fourteen species or about 20% of the neotropical Ptychantheae and Brachiolejeuneae fall in this category.

9. Afro-American element: *Acanthocoleus aberrans*, *Brachiolejeunea phyllorhiza*, *Caudalejeunea lehmanniana*, *Marchesinia brachiata*, *Odontolejeunea lunulata*.

All species listed here are common in the neotropics but rather rare in Africa. Thus, *Caudalejeunea lehmanniana* is known only from Nigeria and *Odontolejeunea lunulata* and *Brachiolejeunea phyllorhiza* are restricted to East Africa. The Afro-American element is the most common among the wide-tropical taxa. Gradstein et al. (1983) listed more than 50 liverwort species with this type of distribution.

10. Tricentric element: *Acrolejeunea emergens*, *Frullanoides tristis*, *Schiffneriolejeunea polycarpa*.

This element includes taxa occurring in America, Africa and the Indian subcontinent. The tricentric distribution type, which may indicate an old Gondwanan connnection, is uncommon among liverworts and is characteristic for *Acrolejeunea* subgenus *Acrolejeunea* and for the genus *Frullanoides*.

11. Pantropical element: *Lopholejeunea eulopha*, *Lopholejeunea nigricans*, *L. subfusca*, *Mastigolejeunea auriculata*, *Stictolejeunea balfourii*.

Prior to recent monographic work, all wide-tropical species were known from the various continents under different names. Thus, *Mastigolejeunea auriculata* was commonly known as *M. carinata* (Mitt.) Steph. in Africa and *M. humilis* (Gott.) Schiffn. in Asia. *Lopholejeunea nigricans*, described from Asia, was usually called *L. muelleriana* (Gott.) Schiffn. in the neotropics and *L. abortiva* (Mitt.) Steph. in Africa. *Lopholejeunea eulopha* was known in the New World as *L. cocosensis* Clark. *Stictolejeunea balfourii*, described from Rodrigues (Africa), was known as *S. africana* vandenBerghen in West Africa and as *S. richardii* Herz. in Asia. *Odontolejeunea lunulata* and *Marchesinia brachiata* were known from Africa as *O. tortuosa* (L. & L.) Steph. and *Marchesinia deslooveri* vandenBerghen, respectively.

The ranges of the widespread, disjunct bryophyte species have frequently been discussed (e.g., Grolle, 1969; Frahm, 1982; Gradstein et al., 1983; Reese, 1987; van Zanten & Gradstein, 1988). Most authors consider step-by-step overland dispersal prior to the separation of the land masses in the late Mesozoic or transoceanic long-range dispersal as the likely causes of the disjunction. Which of the two explanations is correct cannot usually be said, however; arguments in support of each of the two have been put forward. For Lejeuneaceae the following data are relevant (Gradstein, 1987):

a. Virtually all wide-tropical species are monoicous or polyoicous and may produce bisexual spores. Dioicous species, however, are as a rule restricted to single continents. This fact would lend support to the long-distance hypothesis.

b. The tricentric distribution of *Acrolejeunea emergens*, *Frullanoides tristis* and *Schiffneriolejeunea polycarpa* is also found in mesozoic conifers of the *Glossopteris* flora. The range is therefore suggestive of a Gondwanalandic origin of the species and subsequent step-by-step overland dispersal.

c. The fossil occurrences of *Marchesinia brachiata* and *Stictolejeunea squamata* in Miocenic amber of the Dominican Republic (see FOSSILS) indicate that these species are at least 20–30 million years old. It also indicates that the genera to which they belong are very old and may even have existed prior to the separation of the ancient Gondwananic landmasses at the end of the Cretaceous. If true, this would help explain the wide ranges of the genera. The fossil data would also furnish an explanation for the remarkably wide range of *Stictolejeunea balfourii*. This species is pantropical and grows in very sheltered habitats in dense lowland rain forests, on tree bases and roots close to the ground. These locations can hardly be considered as suitable for long-range dispersal. Moreover, the spores of *S. balfourii* have very poor frost- and drought resistance (less than a day, possibly less than a few hours) which would be prohibitive to effective long-range dispersal (van Zanten & Gradstein, 1988). Given the very old age of the genus *Stictolejeunea*, it may be argued that the species became widespread by the ancient migration of the land masses. Such a reasoning would indicate that the species must be at least 80-90 million years old.

d. van Zanten and Gradstein (1988) studied drought, frost and UV resistance of spores and sporelings in numerous tropical liverwort species, eight of which are treated in this monograph: the endemic neotropical *Blepharolejeunea incongrua*, *B. securifolia*, *Brachiolejeunea laxifolia*, *Dicranolejeunea axillaris* and *Frullanoides densifolia*, and the wide-tropical *Brachiolejeunea phyllorhiza*, *Marchesinia brachiata*, and *Stictolejeunea balfourii*. Drought resistance in the endemic species was less than a few days in *Blepharolejeunea*, *Brachiolejeunea axillaris* and *Stictolejeunea balfourii*, about two weeks in *Dicranolejeunea* and *Frullanoides densifolia*, 2–3 weeks in *Marchesinia brachiata* and about 2 months in *Brachiolejeunea phyllorhiza*. The results support the hypothesis that dispersal capabilities are usually better in the transoceanic species (except *S. balfourii*, see above), which have spore viability periods sufficiently long for allowing transoceanic transport via air currents.

e. The possibility that disjunct populations of widespread bryophytes may be chemically and genetically different, in spite of a lack of morphological differentiation, should not be ruled out (Gradstein, 1987; Shaw, 1991). In the widespread *Conocephalum conicum* five genetically well-defined strains have been detected using enzyme electrophoresis. Such strains might function as "sibling species" even though their genetic compatibility usually remains unknown. Several wide-tropical species treated in this monograph have been studied chemically (see CHEMISTRY) but a chemical comparison between disjunct populations has not been made. Careful chemical and genetic study of these species might be profitable for a better understanding of the biogeographic and evolutionary history of the taxa.

12. Temperate species: Three species treated in this monograph are restricted to temperate southern South America and do not occur in the neotropics. They are *Blepharolejeunea fuegiana*, *Brachiolejeunea fernandeziana* and *B. spruceana*. The genera to which they belong are adapted to growth in cool, temperate environments and are characteristic elements of the flora of the páramos of northern South America. Their occurrence at the southern tip of South America, far beyond the latitudinal limits of the tropical belt, does therefore not come as a surprise.

ECOLOGY

The species of Ptychanthoideae and Brachiolejeuneae usually grow as epiphytes on bark of trees and shrubs. Sometimes they occur as epiphylls on living leaves (*Caudalejeunea* and *Odontolejeunea* spp.). Epiphyllous growth is not very common in the Ptychantheae and Brachiolejeuneae and is much more characteristic of the tiny Lejeuneae. The leaf-inhabiting taxa of Ptychantheae and Brachiolejeuneae, moreover, are never obligatorily epiphyllous but may also grow on bark, particularly on twigs. They are typical pioneers adapted to growth on ephemerous substrates and are particularly common in the rain forest.

Many epiphytic species, especially the more common ones, may also grow on rocks when the environment is sufficiently humid, but terrestrial growth is very rare. Only two species of the genus *Acanthocoleus*, *A. juddii* and *A. trigonus*, seem to be exclusively saxicolous.

Like other Lejeuneaceae, most of the Ptychantheae and Brachiolejeuneae occur in rain forests at low or mid-elevations (Table V). The following are typical rain forest genera which lack or are rare in the dryer portions of tropical America: *Archilejeunea*, *Bryopteris*, *Fulfordianthus*, *Thysananthus*, *Verdoornianthus*, *Neurolejeunea*, *Odontolejeunea*, *Stictolejeunea* and *Symbiezidium*. The greatest numbers of species are found in humid, mixed rain forests. On 28 trees (belonging to 22 different species) in the mixed forest of French Guiana, Montfoort and Ek (1990) found 19 species of Ptychantheae and Brachiolejeuneae or about 30% of all neotropical taxa. A dry evergreen rain forest of Guyana, dominated by two species of trees (Cornelissen & ter Steege, 1989), yielded much fewer liverwort species. The large number of different host tree species characteristic of the mixed forest creates many niches and would thus be responsible for a rich epiphytic flora.

Few rain forest species are restricted to the understory of the forest and are specialized shade epiphytes: *Fulfordianthus*, *Lopholejeunea nigricans*, *Archilejeunea bischleriana*, *A. crispistipula*, *A. parviflora* and *Stictolejeunea balfourii*. The latter three species are particularly characteristic of periodically inundated forests. The other forest species are canopy taxa or have rather broad vertical ranges and occur in the understory as well as in the canopy. Some of them may also occur outside the forest, in secondary vegetations or plantations, in particular species of the Ptychantheae. *Archilejeunea auberiana*, *Frullanioides tristis*, *Mastigolejeunea auriculata*, *Schiffneriolejeunea polycarpa* and *Acanthocoleus* spp. are drought-tolerant taxa adapted to growth in semideciduous forests, the species of *Acrolejeunea* are particularly characteristic of savannah-type vegetations (but frequently grow in rain forest canopies as well), and *Frullanoides bahamensis* and *F. corticalis* occur mainly in coastal forests and swamps. *Lindigianthus cipaconeus*, *Blepharolejeunea* subgen. *Oreolejeunea* and *Brachiolejeunea laxifolia*, finally, are taxa adapted to life in the cool, high-montane environment and are frequently found in páramo vegetation.

CONSERVATION

The massive destruction of the tropical rain forest causes concern about the future survival of the biota of these forests. Studies of the rain forest bryophyte flora's in various tropical regions indicate that the bryophyte flora of secondary forests and plantations is usually much impoverished as compared with the virgin forest. Shade epiphytes of the forest understory seem more seriously affected than the canopy epiphytes although some canopy species may also become rare or disappear after disturbance. Depletion of the rich habitat diversity of the primary forest as well as the predominance in the disturbed habitats of fast-growing tree species, seem important reasons why bryophyte species of the primary forest are unable to reestablish in secondary growth (Gradstein, 1992b, 1992c).

Based on our current knowledge of their habitats, the following nineteen neotropical species of Ptychantheae and Brachiolejeuneae seem to be limited to undisturbed rain forest (Table V): *Archilejeunea badia*, *A. crispistipula*, *A. porelloides*, *Blepharolejeunea saccata*, *Fulfordianthus evansii*, *F. pterobryoides*, *Lopholejeunea eulopha*, *L. quelchii*, *Mastigolejeunea innovans*, *M. plicatiflora*, *Neurolejeunea catenulata*, *Neurolejeunea seminervis*, *Odontolejeunea semidentata*, *O. rhomalea*, *Stictolejeunea balfourii*, *Spruceanthus theobromae*, *Symbiezidium dentatum*, *Thysananthus amazonicus* and *Verdoornianthus griffinii*. Together these species constitute almost 30% of the neotropical species of Ptychantheae and Brachiolejeuneae. Conservation of their habitat would be of great importance for their continued existence.

An assessment of the status of these species as to the degree of endangerment is a hazardous affair because our knowledge of the distributions and habitats of the rain forest species are still very incomplete. In my review paper on the conservation of tropical rain forest bryophytes (Gradstein, 1992b) I presented a first and preliminary list of 14 mosses and 15 liverworts of the rain forest considered threatened. An updated list for the neotropics (Gradstein, 1992c) contained 48 threatened species (20 mosses, 28 hepatics). All of them are endemic species restricted to undisturbed rain forest. Some of them are very narrowly endemic, others are more widespread but rare thoughout their range. The very rare species occurring in areas undergoing rapid deforestation were classified in the category "Endangered" (IUCN Red Data Book Categories), the other species were classified as "Rare."

Seven species of Ptychantheae and Brachiolejeuneae were included in the list of threatened neotropical rain forest species:

1. Endangered Species: *Fulfordianthus evansii*, *Spruceanthus theobromae*.

Fulfordianthus evansii is a rare endemic species of very wet undisturbed rain forests on the Caribbean coast of Central America. A population of the species seems safeguarded in Costa Rica's Tortuguero National Park.

The continued existence of *Spruceanthus theobromae*, however, seems more threatened. The species is robust and habitually very distinct, yet is known only from the province Los Rios, coastal Ecuador where it has been collected in the mid 19th century and again in 1947 by Prof. Gunnar Harling. Since the 1960s most of that region has been deforested and it is unknown whether the species continues to exist in the area. *Spruceanthus theobromae* should certainly be regarded as one of the most critically endangered tropical bryophytes and has been included in the World Red List of Threatened Biota compiled by the IUCN. Its conservation is of particular importance because it is the only species of the genus *Spruceanthus* in the New World.

2. Rare Species ("at risk"): *Blepharolejeunea saccata*, *Lopholejeunea quelchii*, *Mastigolejeunea innovans*, *Neurolejeunea catenulata*, *Symbiezidium dentatum*.

Of the five taxa classified as "at risk," *Blepharolejeunea saccata* is rather widespread throughout the neotropics. Yet, it is a very rare taxon and known from only half a dozen collections. The others taxa are local endemics from the Chocó rain forest (*Symbiezidium dentatum*), the Caribbean (*Lopholejeunea quelchii*, *Neurolejeunea catenulata*) and inner Amazonia (*Mastigolejeunea innovans*). The most threatened species in the group of rare taxa may be *Neurolejeunea catenulata*. Until the beginning of this century this species had been collected on several Caribbean islands but since then it has only been found in Cuba. As rain forest destruction is very severe in the Caribbean, the species has probably become lost in most parts of its range.

SYSTEMATIC TREATMENT

LEJEUNEACEAE Casares Gil

Lejeuneaceae Casares Gil, Fl. Ibér. Brióf. Hepát. 703. 1919, *nom. cons.* Type. *Lejeunea* Libert. Named after L. S. Lejeune, a Belgian physician and amateur botanist.

Plants green, brown, black or whitish, never reddish, usually growing epiphytic on bark, wood or living leaves, also on rock, rarely on soil. *Branching* lateral, usually *Lejeunea*-type, sometimes *Frullania*-type or (innovations) *Radula*-type. *Stems* with or without enlarged epidermis cells, cell walls thin or thickened; ventral merophyte 2–6(–16) cells wide; lateral merophytes interlocking along dorsal midline of stem; leaves and underleaves attached to stem by U-shaped cells ("superior central cells"). *Rhizoids* in bundles from underleaf bases, loose or (in epiphyllous plants) connate and produced as large, circular discs. *Leaves* unequally complicated-bilobed, divided into an incubous dorsal lobe and a smaller ventral lobule attached to the lobe by an elongated keel; leaf insertion line elongated J-shaped or short, v-shaped; hyaline papillae associated with leaves three: one at dorsal lobe base of lobe, one at lobule base (= stylus), one at lobule apex; stylus usually not elaborated. *Cells*: walls normally with trigones and intermediate thickenings, oil bodies usually present, segmented or homogeneous, specialized oil cells (ocelli) sometimes present. *Underleaves* present or absent, when present bifid or undivided. *Androecia* normally with 1–2 antheridia per bract, antheridium globose, on a long 1–seriate stalk. *Gynoecia* normally with one archegonium surrounded by a beaked perianth and 1–5 series of bracts and bracteoles. *Sporophyte* foot rudimentary, not entering stem; seta short, few mm long upon maturity, usually made up 4 inner cell rows surrounded by 12 or 16 outer cells rows, occasionally cell rows more numerous; capsule globose, 4–valved for 3/4 of its length, wall normally 2-layered; elaters with or without distinct spirals, arranged vertically and attached to upper and lower portion of capsule wall, upper portion remaining attached to valve after capsule dehiscence; spores relatively large, several-celled due to intercapsular germination, spore coat variously ornamented, with or without rosettes. *Vegetative reproduction*, when present, by means of multicellular, flat gemmae, by caducous leaves or by caducous branchlets (cladia). *Chromosomes*: usually $n = 9$.

Distribution. The family Lejeuneaceae is widely distributed in the tropics, with hundreds of species in over 80 genera. In temperate areas the family is rather rare and represented with only few species. Most of the species are epiphytic and grow on bark, wood or living leaves, particularly in moist, evergreen tropical rain forests at rather low elevations. Many species may also grow on rock; few are found on soil.

The Lejeuneaceae have been variously subdivided into subfamilies and tribes (e. g., Schuster, 1963, 1980). In this treatment I recognize only two broad subfamilies, Ptychanthoideae and Lejeuneoideae, based on their fundamentally different capsules (see CLASSIFICATION). The two subfamilies are subdivided into tribes and subtribes as shown below.

Table V

Distribution and ecology of the neotropical species of Ptychantheae and Brachiolejeuneae.
Ama = Amazonian; And = Andean; CAm = Central American; Car = Caribbean; Cho = Chocó;
Guy = Guyanan; Neo = widespread Neotropical; Sub = southern Subtropical; WTr = Wide Tropical.
Species marked by an asterisk are restricted to undisturbed rain forest. Their continued existence may be threatened when the forest vanishes (see CONSERVATION)

species	range	alt/m	main habitat
PTYCHANTHEAE			
Acrolejeunea emergens	WTr	0-150	scrub, plantations
A. heterophylla	CAm	0-1000	scrub, evergreen forest
A. torulosa	Ama	0-800	savannah, scrub, rain forest (canopy), plantations
Archilejeunea auberiana	Neo	0-500	semi-deciduous forest, scrub, plantations
**A. badia*	Ama	0-600	rain forest
A. bischleriana	Cho	0-50	wet rain forest (understory)
**A. crispistipula*	Ama	0-500	periodically inundated rain forest (understory)
A. fuscescens	Ama	0-1000	rain forest
A. parviflora	Neo	0-1500	periodically inundated rain forest (understory)
**A. porelloides*	Ama	0-1200	low rain forest
Bryopteris diffusa	Neo	100-1500	evergreen forest
B. filicina	Neo	100-2500	rain forest, cloud forest
Caudalejeunea lehmanniana	WTr	0-1000	scrub, evergreen forest (canopy, margins)
Frullanoides bahamensis	Car	0-300	coastal forest, swamp
F. corticalis	Car	0-600	coastal forest, swamp, plantations
F. densifolia	And	100-3500	montane rain forest (canopy, margin), scrub
F. laciniatiflora	And	2000-3200	montane rain forest (canopy, margin), scrub
F. liebmanniana	Neo	200-1000	rain forest (canopy), plantations
F. mexicana	CAm	0-600	plantations, ? rain forest canopy/margins
F. tristis	WTr	0-2000	semi-deciduous forest, rain forest (canopy), plantations
**Fulfordianthus evansii*	CAm	0	coastal rain forest (understory)
**F. pterobryoides*	Cho	0-1500	rain forest (understory)
**Lopholejeunea eulopha*	WTr	0-100	rain forest
L. nigricans	WTr	0-1800	rain forest, scrub
**L. quelchii*	Car	100-1000	rain forest
L. subfusca	WTr	0-1200	rain forest (canopy, margin) scrub, plantations
Marchesinia brachiata	WTr	0-3000	rain forest, scrub, plantations
Mastigolejeunea auriculata	WTr	0-1500	scrub, evergreen forest (canopy), plantations
**M. innovans*	Ama	0-150	rain forest (canopy)
**M. plicatiflora*	Ama	0-700	rain forest

Table V

Continued

species	range	alt/m	main habitat
Schiffneriolejeunea amazonica	Ama	0-100	scrub, rain forest (canopy)
S. polycarpa	WTr	0-1600	scrub, semi-deciduous forest
**Spruceanthus theobromae*	Cho	100-300	rain forest
**Thysananthus amazonicus*	Ama	0-800	rain forest
**Verdoornianthus griffinii*	Ama	0-100	rain forest (canopy)
V. marsupiifolius	Ama	0-100	rain forest (canopy), scrub
BRACHIOLEJEUNEAE			
Acanthocoleus aberrans	Neo	150-2600	semi-deciduous forest, scrub
A. juddii	Car	800-2500	montane forest (on rock)
A. trigonus	Sub	1100-2600	semi-deciduous riparian forest
Blepharolejeunea chimantaensis	Guy	1850	montane scrub
B. incongrua	And	2000-4000	montane scrub, páramo
B. saccata	Neo	1200-1800	montane rain forest
B. securifolia	And	3000-4500	subalpine scrub, páramo
Brachiolejeunea conduplicata	Guy	0-150	rain forest (canopy), plantations
B. laxifolia	And	2000-3500	montane scrub, páramo
B. leiboldiana	Neo	800-1600	scrub, plantations
B. phyllorhiza	Neo	300-2000	scrub, plantations
Dicranolejeunea axillaris	And	500-3200	montane scrub
Lindigianthus cipaconeus	And	2000-3500	montane scrub, páramo
Neurolejeunea breutelii	Neo	0-3000	rain forest (canopy, margin) scrub
**N. catenulata*	Car	500-1200	rain forest
N. sastreana	Car	700-1400	rain forest (margin), scrub
**N. seminervis*	Ama	0-500	rain forest (canopy), scrub
**Odontolejeunea decemdentata*	Neo	0-1800	rain forest
O. lunulata	Neo	0-3000	rain forest
**O. rhomalea*	Neo	0-3200	rain forest
**Stictolejeunea balfourii*	WTr	0-800	rain forest (understory)
S. squamata	Neo	0-2400	rain forest
Symbiezidium barbiflorum	Neo	0-2800	rain forest
**S. dentatum*	Cho	0-800	rain forest (understory)
S. transversale	Neo	0-1700	rain forest

Synoptic Key to Subfamilies and Tribes of Lejeuneaceae (tribes treated in this volume in **bold**)

1. Capsule valves spreading after dehiscence, inner walls brownish, covered by a fenestrate thickening layer; elaters usually 72 per capsule (sometimes less), upper ends attached to valve surface and margins, spiral band well-developed, brown; spores isodiametric, tetrads tetrahedral; seta with 16 or more outer rows of cells; underleaves usually undivided; ventral merophyte 4 or more cells wide . . . . **Ptychanthoideae.**
   2. Leaf insertion elongated J-shaped; underleaves undivided or emarginate; leaf margins entire or toothed, lacking cilia; throughout the tropics . . . . **Ptychantheae.**
   2. Leaf insertion very short, almost transverse; underleaves narrowly bifid; leaf margins with long cilia; East Asia . . . . Nipponolejeuneae.
1. Capsule valves remaining suberect after dehiscence, pale-colored, lacking a thickening layer; elaters 34 or less per capsule, upper ends attached to valve margins only, spiral band rudimentary, pale-colored; spores elongated-rectangular, tetrads decussate; seta with 12 or 16 outer rows of cells; underleaves bifid or undivided; ventral merophyte 2–4 or more cells wide . . . . Lejeuneoideae.
   3. Seta epidermis consisting of (14-)16 longitudinal rows of cells; underleaves undivided; mainly neotropical . . . . **Brachiolejeuneae.**
   3. Seta epidermis consisting of only 12 longitudinal rows of cells; underleaves bifid, undivided or lacking; world-wide . . . . Lejeuneae s.l..

Artificial Key to the Genera of Ptychantheae and Brachiolejeuneae and other neotropical holostipous Lejeuneaceae

The classification of the Lejeuneaceae into taxa with undivided underleaves ("Holostipae") and with bifid underleaves ("Schizostipae") is an artificial one (see CLASSIFICATION). For identification purposes, however, this subdivision remains very useful because all genera of the Ptychantheae and the Brachiolejeuneae are holostipous whereas the Nipponolejeuneae and the majority of the Lejeuneae are schizostipous (a few genera of Lejeuneae have no underleaves at all and are "astipous"). The presence of bifid or undivided underleaves can usually be easily ascertained and remains a most practical means to make a first separation of collections of Lejeuneaceae into groups. For that reason, I have included in this generic key all "Holostipae" recorded from the New World. Thus, the key provides access to the twenty-two genera of the Ptychantheae and the Brachiolejeuneae treated in this monograph as well as to the following (holostipous) members of the Lejeuneae: *Amblyolejeunea, Amphilejeunea, Anoplolejeunea, Aureolejeunea, Ceratolejeunea* subgen. *Ceratophora, Cheilolejeunea fragrantissima, Cyclolejeunea convexistipa, Cyrtolejeunea, Lejeunea reflexistipula, Lepidolejeunea spongia, Leucolejeunea, Luteolejeunea, Omphalanthus,* and *Physantholejeunea.* Some members of Lejeuneae (*Lepidolejeunea eluta, Taxilejeunea sulphurea*) have very shallowly bifid underleaves and may easily be taken as holostipous; these are also included in the key.

In all, more than half of the New World genera of Lejeuneaceae are accessed in this key. Emphasis is on vegetative characters, to facilitate the identification of sterile material. Taxa treated in this monograph are numbered and in **bold face**, those not treated are unnumbered and in *italics*. For identification of the latter groups my *Key to the New World species of holostipous Lejeuneaceae* (Gradstein, 1990) may also be consulted.

For an explanation of the terminology used in this key see MORPHOLOGY AND ADAPTATION.

1. Leaf margins toothed, at least near apex.
   2. Ventral merophyte four or more cells wide.
      3. Leaf cells with evenly thickened walls, trigones lacking; lobules with a very long (5–10 cells), curved tooth; underleaves toothed, deeply emarginate; northwestern South America and Central America . . . . 6. **Fulfordianthus.**
      3. Leaf cells with trigones, walls not evenly thickened; lobules without or with a short tooth (less than five cells long), or with several teeth; underleaves entire or toothed.
         4. Median leaf cells elongated; trigones cordate.
            5. Underleaves toothed.
               6. Plants pinnate or forked, branches predominantly of the *Frullania*-type; innovations lacking; throughout tropical America . . . . 7. **Bryopteris.**

6. Plants irregularly branched, branches *Lejeunea*-type; innovations present; northern South America, Cuba . . . . 5. **Thysananthus.**

5. Underleaves entire.

7. Lobules with 7–9 teeth; plants turning black on age; underleaf apex rounded, the bases auriculate; perianths 8–10-keeled, with innovations; high Andes of Peru . . . . 13.4 **Frullanoides laciniatiflora.**

7. Lobules with 1–3 teeth; plants turning pale brown on age, branches *Lejeunea*-type; underleaf apex emarginate, the bases not auriculate; perianths 3-keeled, without innovations; throughout tropical America . . . . 11. **Caudalejeunea.**

4. Median leaf cells isodiametrical; trigones various, not cordate.

8. Underleaf insertion line straight; plants 1.5–2 mm wide; perianth with two ventral keels; innovations lacking; throughout tropical America . . . . 10.3 **Lopholejeunea nigricans.**

8. Underleaf insertion line deeply arched; plants usually more than 2 mm wide; perianth without ventral keels; innovations present or lacking.

9. Apical portion of leaf broadly recurved; ventral merophyte four cells wide, epidermis cells thin-walled; plants glossy brown; northern Andes, Costa Rica, above 2000 m . . . . 17. **Lindigianthus.**

9. Leaf plane; ventral merophyte more than four cells wide, epidermis cells thick-walled; throughout tropical America.

10. Lobules plane, with (1–)2–4 distinct teeth; perianths terminal on main stem or elongated branches, with two innovations; throughout tropical America . . . . 9. **Marchesinia.**

10. Lobules strongly inflated-rounded, very small and hidden behind the underleaves, without distinct teeth; perianths on a very short branch, appearing lateral on the stem, without or with one short innovation; Pacific coastal lowlands of Ecuador and Colombia . . . . 16.2 **Symbiezidium dentatum.**

2. Ventral merophyte only 2(–3) cells wide.

11. Underleaves very large, 6–10 × stem width, at apex short bifid or notched; perianths terete, smooth; throughout tropical America, montane . . . *Taxilejeunea sulphurea* (Lehm. & Lindenb.) Schiffn.

11. Underleaves smaller, apex undivided; perianths keeled.

12. Lobules large, ca. 1/2 × leaf length, truncate; leaves strongly falcate; small (up 1.2 mm wide) creeping, brown plants; lower montane, rare . . . . 19. **Blepharolejeunea subgen. Blepharolejeunea.**

12. Lobules less than 2/5 × leaf length, not truncate; leaves not falcate.

13. Leaves with ocelli: scattered, in a short row or 1–2 near leaf base.

14. Plants pale-green; discoid gemmae usually produced on dorsal leaf margins; perianth apex toothed; throughout tropical America, often epiphyllous . . . . *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans

14. Plants brown; discoid gemmae lacking; perianth apex not toothed, with four bulbiform extensions; Andes . . . . *Ceratolejeunea* subgen. *Ceratophora* Schust.

13. Ocelli lacking

15. Leaves with (5-)7–25 teeth; underleaves toothed or entire; on living leaves or bark; throughout tropical America . . . . 22. Odontolejeunea.

15. Leaves with 1–5 teeth; underleaves entire; on bark or rock, not on living leaves.

16. Branches predominantly *Frullania*-type; epidermis cells strongly bulging outwards (stem cross section); female bracteoles toothed; common in the Andes and Central America, rare in the West Indies, montane . . . . .20. **Dicranolejeunea.**

16. Branches predominantly *Lejeunea*-type; epidermis cells not bulging outwards; female bracteoles entire; throughout tropical America, mainly submontane-montane . . . . 21. **Acanthocoleus.**

1. Leaf margins entire.

17. Underleaves toothed 6

17. Underleaves entire.

18. Leaves with ocelli: scattered or in a row.

19. Ocelli arranged in a row.

20. Row of ocelli up to 5 cells long; ventral merophyte 2(-3) cells wide; lobule tooth 1 cell long; northern South America . . . . *Ceratolejeunea desciscens* (Sande Lac.) Schiffn.

20. Row of ocelli 7–22 cells long; ventral merophyte 4–6 cells wide; lobule tooth 3–5 cells long; northern South America and West Indies . . . . 15. **Neurolejeunea** sect. **Neurolejeunea.**

19. Ocelli scattered.

21. Ventral merophyte four cells wide.

22. Leaf apex rounded; underleaf apex undivided; *Frullania*-type branches frequently present; stem without hyaloderm; throughout tropical America . . . . 14. **Stictolejeunea.**

22. Leaf apex acute; underleaf apex notched; *Frullania*-type branches lacking; stem with a distinct hyaloderm; northern South America . . . . *Lepidolejeunea eluta* (Nees) Schust.

21. Ventral merophyte 2(–3) cells wide.

23. Plants tiny, less than 1 mm wide; underleaves orbicular, 2–3x stem width; leaf apex often with a whitish border of dead cells; West Indies . . . . *Physantholejeunea* Schust.

23. Plants more than 1 mm wide; underleaves reniform, 6–10x stem width; leaf apex without whitish border.

24. Leaf cells thick-walled, with large trigones; ocelli conspicuous, usually larger than green leaf cells; epidermis cells thick-walled; lobules curved downward; Panama, Pacific side of northern South America. . . . . *Luteolejeunea* Piippo

24. Leaf cells very thin-walled, with minute trigones; ocelli rather inconspicuous, equal in size to or smaller than other leaf cells; epidermis cells thin-walled; lobules straight or somewhat curved upwards; northern Andes, Cuba . . . . *Lepidolejeunea spongia* (Spruce) B. Thiers

18. Leaves without ocelli.

25. Ventral merophyte four or more cells wide.

26. Leaf cells with cordate trigones; median leaf cells elongated; leaves mostly convoluted when dry, occasionally plane.

27. Underleaf apex distinctly emarginate; leaves oblong, obliquely spreading-falcate, usually not convoluted; stems pale-colored, flaccid, with distinct hyalodermis; lobules with 1–3 teeth; perianth 3-keeled, without innovations; plants green to pale brown, growing in small tufts on leaves or twigs; throughout tropical America . . . . 11. **Caudalejeunea.**

27. Underleaf apex rounded or truncate, not emarginate.

28. Lobules with 3–10 teeth (the teeth sometimes inflexed).

29. Plants blackish in older stem portions; perianths with 5–10 keels, with innovations; common throughout tropical America . . . . 13. **Frullanoides.**

29. Plants becoming yellowish-brown, never blackish; perianths with 3–10 keels, innovations present or lacking; throughout tropical America but very rare in the West Indies.

30. Underleaf insertion line slightly curved, underleaf bases plane; perianths with 5–10 keels; innovations lacking; flagelliform branches (producing caducous leaves) frequently present; tropical America, lowlands only . . . . . 12. **Acrolejeunea.**

30. Underleaf insertion line deeply arched, underleaf bases folded; perianths with 3(–4) keels; innovations present; flagelliform branches lacking; tropical and southern temperate America, usually montane . . . . 18. **Brachiolejeunea.**

28. Lobule teeth 1–2 or lacking.

31. Medulla cells thick-walled; ventral epidermis cells not or scarcely larger than medulla cells (stem cross section).

32. Leaf apex acute; female bracts and bracteoles toothed; northern South America, Cuba . . . . 5. **Thysananthus.**

32. Leaf apex rounded; female bracts and bracteoles without teeth.

33. Plants turning olive- to reddish brown on age; innovations lacking; female bract apices acute-acuminate; leaves when dry strongly wrapped around the stem; throughout tropical America but mainly on islands and in coastal areas, rare inland . . . . 3. **Schiffneriolejeunea.**

33. Plants turning dark-brown to black on age; innovations present; female bract apices rounded; leaves when dry rather flat appressed to the stem,

not wrapped around the stem; common throughout tropical America . . . . 4. **Mastigolejeunea.**

31. Medulla cells thin-walled; ventral epidermis cells distinctly larger than medulla cells.

34. Leaf lobules mostly reduced . . . . 21. **Acanthocoleus.**

34. Leaf lobules well-developed, never reduced, with two teeth.

35. Lobule teeth dissimilar, the first lobule tooth rather inconspicuous, incurved and blunt, the second tooth pointing outwards, sharp; lobules truncate; leaves not squarrose; tropical and southern temperate America, in tropical America above 2000 m . 19. **Blepharolejeunea** subgen. **Oreolejeunea.**

35. Lobule teeth equal or the first tooth more conspicuous; lobules oblique or truncate; leaves squarrose when moist; tropical and southern temperate America, lowland or montane . . . . 18. **Brachiolejeunea.**

26. Trigones various but not cordate; median leaf cells isodiametrical (elongated: *Spruceanthus* [36], *Neurolejeunea* [44]); leaves when dry spreading and plane, curved down or somewhat folded but not convoluted.

36. Median leaf cells about 2 × longer than wide; plants robust, ventral merophyte more than ten cells wide; lobules often reduced; perianth with 5–8 keels; coastal lowland region of Ecuador, very rare . . . . 8. **Spruceanthus.**

36. Median leaf cells isodiametrical or slightly elongated only.

37. Lobules with 2–4 teeth.

38. Epidermal cells distinctly larger than medulla cells, medulla cells thin-walled 34

38. Epidermal cells not or hardly larger than medulla cells, medulla cells thick-walled.

39. Insertion line of underleaves deeply arched (more than 100 µm deep); ventral merophyte 6–12 cells wide; plants more than 2 mm wide, often black; perianths without ventral keels; throughout tropical America, predominantly montane, at higher latitudes also at sea-level . . . . 9. **Marchesinia.**

39. Insertion of underleaves straight or shallowly curved; ventral merophyte four cells wide; plants smaller, never black; perianths with two ventral keels; lowland and submontane, below 1000 m.

40. Plants whitish or gray in color; second lobule tooth much larger than the first tooth; androecia on short-specialized branches, male bracteoles reduced . . . . *Leucolejeunea unciloba* (Lindenb.) Evans

40. Plants pale green to brown; teeth identical or the first tooth larger than the second tooth; androecia on elongated shoots, male bracteoles not reduced . . . . 1.5 **Archilejeunea auberiana.**

37. Lobules with only one tooth or teeth lacking.

41. Branches predominantly *Frullania*-type 34

41. Branches predominantly *Lejeunea*-type.

42. Underleaf insertion line straight or shallowly curved; ventral merophyte 4–6 cells wide.

43. Plants whitish, pale yellowish or grayish; scattered throughout tropical America, usually montane . . . . *Leucolejeunea* Evans

43. Plants darker in color: green, brown or black.

44. Median leaf cells small, 10–20 µm in diameter; trigones confluent, the cell walls almost evenly thickened; lobules flask-shaped, often darker than the lobe; plants usually black; throughout tropical America . . . . 15.2 **Neurolejeunea** subgen. **Aneurolejeunea.**

44. Median leaf cells larger; trigones not confluent, cell walls not evenly thickened; lobules not flask-shaped, not darker than the lobe; plants green, brown or black.

45. Epidermis cells distincly larger than medulla cells (stem cross section); perianth keels ciliate-laciniate; innovations lacking; plants glossy black or dark-brown (rarely green in shade); oil bodies homogeneous; common throughout tropical America . . 10. **Lopholejeunea.**

45. Epidermis cells not or little larger than medulla cells; perianth keels smooth or denticulate; innovations present, rarely lacking; plants green or brown (black: *Archilejeunea parviflora*); oil bodies segmented.
  46. Innovations present; lobule free margin plane; leaves when moist widely spreading, ± squarrose; throughout tropical America, common . . . . 1. **Archilejeunea.**
  46. Innovations lacking; free margin involuted, at least near apex; leaves when moist obliquely spreading, squarrose; inner Amazonia and Guianas, rare . . . . 2. **Verdoornianthus.**

42. Underleaf insertion line deeply arched, over 100 μm deep; ventral merophyte 4-16 cells wide.
  47. Leaf apex strongly and broadly recurved, acute; epidermis cells thin-walled; ventral merophyte only four cells wide; plants glossy brown; northern Andes, Costa Rica, above 2000 m . . . . 17. **Lindigianthus.**
  47. Leaf apex ± plane, rounded or acute-acuminate; epidermis cells thick-walled.
    48. Lobules small, less than 1/4 × leaf length, inflated-rounded; leaf cells with radiate trigones; perianths on a very short branch (appearing lateral on the stem), keels ciliate-laciniate; throughout tropical America, mostly lowland and lower montane . 16. **Symbiezidium.**
    48. Lobules larger, 1/4–1/2 × leaf length, truncate; leaf cells usually with large bulging trigones; perianths on an elongated shoot, keels smooth; montane.
      49. Lobules subquadrate-trapezioid, up to 1/3 × lobe length; plants green to yellowish-brown, growth usually pendent; throughout the mountains of tropical America, common . . . . . *Omphalanthus* Nees
      49. Lobules rectangular, 2/5–1/2 × lobe length; plants usually dark brown or reddish brown, growth creeping or ascending; above 2000 m, uncommon . . . . *Aureolejeunea* Schust.

25. Ventral merophyte two cells wide.
  50. Lobules uniformly swollen and strongly involuted, the free margin inrolled 2–3 times; throughout tropical America, submontane-montane . . . . Anoplolejeunea (Spruce) Schiffn.
  50. Lobules not or only weakly involuted.
    51. *Frullania*-type branches present, sometimes only few; lobules when well-developed with two teeth; plants usually brown 16
    51. *Frullania*-type branches entirely lacking; lobules with one tooth only; plants pale green, rarely brown.
      52. Lobules more than 1/3 × lobe length.
        53. Underleaves large, more than 3 × stem width; plants 1–2 mm wide; plants pale green (when brown: *Aureolejeunea* Schust.); northern Andes, above 1500 m only . . . . *Amphilejeunea* Schust.
        53. Underleaves smaller, less than 3 × stem width; plants tiny, up to 1 mm wide; mainly at lower elevations.
          54. Apex of lobule with enlarged margin cells; hyaline papilla proximal of the apical tooth; perianths terete, without keels; underleaves undivided; Guadeloupe . . . . *Amblyolejeunea* Jovet-Ast
          54. Margin cells of lobule not enlarged; hyaline papilla distal of the apical tooth; perianths keeled; underleaves undivided or short bifid; throughout tropical America, lowland-lower montane . . . . *Cyrtolejeunea* Evans
      52. Lobules small, less than 1/3 × lobe length.
        55. Leaf cells with large trigones; hyaline papilla of the lobule distal of the apical tooth; northern South America, montane . *Cheilolejeunea fragrantissima* (Spruce) Schust.
        55. Leaf cells with minute trigones; hyaline papilla proximal of the apical tooth.

56. Underleaf apex recurved; lowland and lower montane, up to 1500 m . . . . *Lejeunea reflexistipula* (Lehm. & Lindenb.) Gott. et al.
56. Underleaf apex plane.
    57. Plants brownish; underleaves reniform, emarginate; leaf apex broadly rounded; ocelli present in leaves and underleaves but often rather inconspicuous in herbarium material; northern Andes, Cuba, montane . . . . *Lepidolejeunea spongia* (Spruce) B. Thiers
    57. Plants pale green; underleaves orbicular, bifid but incision sometimes narrow and inconspicuous; leaf apex narrowly obtuse to acuminate; ocelli lacking; throughout tropical America . . . . *Taxilejeunea* spp.

PTYCHANTHOIDEAE Mizutani

PTYCHANTHEAE Bischler emend.

Lejeuneaceae tribe Ptychantheae Bischler, Revue Bryol. Lichénol. **33:** 400. 1965; Ptychanthoideae Mizut. p.p.; *Lejeuneae Holostipae* Spruce p.p. Type. *Ptychanthus* Nees.

Bryopteridaceae Stotler, Bryophyt. Biblioth. **3:** 57. 1974; Lejeuneaceae subfam. Bryopteridoideae (Stotler) Gradstein, Bryophyt. Biblioth. **4:** 139. 1975. Type. *Bryopteris* (Nees) Lindenberg.

Plants creeping, ascending or pendent; sometimes dendroid. Vegetative branching Lejeunea-type or Frullania-type; flagelliform branches present or lacking. Stem with 4–20 cells wide ventral merophyte. Leaf insertion long, J-shaped. Hyaline papilla at lobule apex usually entally displaced. Underleaves undivided. Male bracts epistatic or hypostatic. Perianth with 0–5 ventral keels. Sporophyte: seta usually not articulate, made up of 16 or more outer rows of cells and 4 or more inner rows; capsule valves widely spreading after dehiscence, inner walls brownish, covered by a fenestrate sheeth of thickening, outer wall colorless, with nodulose cell thickenings; elaters usually 72 per capsule, sometimes fewer, upper ends attached to valve surface and margins, spiral 1(–2), well-developed, brown; spores isodiametric, arranged in tetrahedral tetrads, spore coat densely and finely spinose and with rosettes on each facet. Terpenoid chemistry: pinguisane-type sesquiterpenes frequently produced.

Distribution. Pantropical, a few representatives in temperate areas.

The tribe Ptychantheae includes all the genera of the subfamily Ptychanthoideae as defined in this treatment, except *Nipponolejeunea* which constitutes a tribe of its own. There are about 135 species in 18 or 19 genera world-wide (the systematic position of the Pacific genus *Phaeolejeunea*, known only from gametophytic material, remains unresolved). The majority of the species of Ptychantheae occur in tropical Asia. In the New World 37 species in 13 genera are recognized.

The cladistic analysis (see CLASSIFICATION) indicates that there are three generic lines of evolution. These are classified as subtribes. The differences between the subtribes are exclusively based on characters of the gametophyte and are not very sharp.

Key to the Subtribes of Ptychantheae

1. Oil bodies segmented (except *Bryopteris*); stems usually without enlarged epidermis; plants dendroid or not dendroid.
    2. Epidermis cells colorless; leaf cells usually isodiametrical and with simple-triangular trigones; perianth sharply 4–5–keeled. . . . . Subtribe Archilejeuninae.
    2. Epidermis cells brown; leaf cells usually elongated and with cordate trigones; perianth sharply 3-keeled or pluriplicate (except *Schiffneriolejeunea*). . . . . Subtribe Ptychanthinae (p. 70).
1. Oil bodies homogeneous; stems with enlarged epidermis (except *Spruceanthus* and *Marchesinia*); plants never dendroid. . . . Subtribe Acrolejeuninae (p. 100).

ARCHILEJEUNINAE Gradstein emend.

Ptychantheae subtribe Archilejeuninae Gradstein, Bryologist **90:** 338. 1987; tribe Archilejeuneae Gradstein, Bryophyt. Biblioth. **4:** 146. 1975. Type. *Archilejeunea* (Spruce) Schiffn.

Plants creeping or ascending, not dendroid. Stem epidermis cells colorless, not or little larger than medullary cells. Median leaf cells isodiametrical, with simple-triangular to radiate trigones; oil bodies segmented. Innovations lejeuneoid or pycnolejeuneoid, or lacking. Perianth usually with two sharp ventral keels.

Distribution. Pantropical. The subtribe Archilejeuninae consists of two genera, both of which occur in the neotropics: *Archilejeunea* and *Verdoornianthus*.

The subtribe is morphologically rather plesiotypic and approaches the tribe Nipponolejeuneae.

1. **Archilejeunea** (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; Gradstein & Buskes, Beih. Nova Hedwigia **80:** 89. 1985; *Lejeunea* subgen. *Archilejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 88. 1884. Lectotype (Evans 1908). *Archilejeunea porelloides* (Spruce) Schiffner.

Plants 1–10 cm long × 1–3.5 mm wide, dull or glossy green to brown to black, loosely creeping to ascending or forming dense mats, on bark or rock. *Branching* predominantly *Lejeunea*-type, occasionally *Frullania*-type, flagelliform branches lacking. *Stems* epidermis cells similar in size to medullary cells, rarely epidermis cells somewhat enlarged (*Archilejeunea bischleriana, parviflora*), walls colorless and somewhat thickened; ventral merophyte 4–6(–8) cell rows wide. *Leaves* widely spreading when dry, apex rounded to obtuse, usually plane, margins entire, rarely dentate (Asiatic species); leaf cells isodiametric-hexagonal to slightly elongate, averaging 25–35 μm in diam., trigones simple-triangular or radiate, intermediate thickenings 0–3 per cell, one per wall, oil bodies coarsely segmented, *Calypogeia*-type, ocelli lacking. *Lobules* 1/3–1/2 × lobe length, sometimes reduced in subgen. *Dibrachiella*, flat or slightly inflated, with 1–2 teeth; hyaline papilla positioned on or below the free margin at the proximal base of the apical tooth. Underleaves (2)3–6(7) × stem width, apex rounded to truncate, margins entire, bases cuneate, insertion line weakly curved; underleaf base at the rhizoid disc bistratose, with four superior central cells. *Androecia* on elongated branches, bracts smaller than leaves, subequally bilobed, lobule hypostatic, underleaves present throughout; antheridia two per bract. *Gynoecia* with 1–2 lejeuneoid or pycnolejeuneoid subfloral innovations, bracts in one series, about as large as leaves, with rounded to obtuse apex and entire margins (sometimes dentate in Asiatic species), lobules usually large, bracteoles as long as bracts, undivided or short bifid. *Perianths* exserted, with 4–5 sharp, irregularly crenate-denticulate (rarely smooth) keels: 2 lateral, 2 ventral and 0–1 dorsal, ventral keels rarely reduced. *Sporophyte*: seta not articulate; elaters 72 per capsule; otherwise as in the tribe. *Vegetative reproduction* by regeneration from leaf cells.

Distribution. The genus *Archilejeunea* is pantropical and contains about twelve species. In their revision of the neotropical taxa, Gradstein and Buskes (1985) accepted four species, in two subgenera. Their treatment has proven to be too conservative, however. In the course of this study, I have seen many additional specimens and was able to collect all species in the field and study their ecology. These data have allowed me to recognize seven species in tropical America, including one species new to science (*A. bischleriana*) and one new subspecies (*A. porelloides* subsp. chocoensis). The new taxa were already present among the specimens studied by Gradstein and Buskes but had not been distinguished by lack of adequate material.

The genus *Archilejeunea* is common throughout the neotropics, especially in the Amazon basin, and occurs in lowland and submontane regions from sea level up to 1000(–1500) m in the Andes. The species are usually epiphytic; one species (*A. parviflora*) also occurs on rock.

Archilejeunea is recognized by its greenish or brownish (rarely blackish) color, the usual lack of enlarged epidermis cells (except *A. bischleriana*), the isodiametric leaf cells without secondary pigmentation in the cell walls, the perianths which are usually 4–5-keeled and are subtended by 1–2 subfloral innovations, and by the segmented oil bodies. Branching is mainly of the *Lejeunea*-type and innovation leaf sequence is either lejeunoid or pycnolejeuneoid.

Based on differences in innovation leaf sequence, plant color and lobule reduction, *Archilejeunea* is subdivided into two subgenera: subgen. *Archilejeunea* and subgen. *Dibrachiella* (Spruce) Schiffner (Gradstein & Buskes, 1985). Subgenus *Archilejeunea* is limited to the neotropics and contains four species. Subgenus *Dibrachiella* is pantropical and contains two species in the neotropics.

Archilejeunea is related to the rare Amazonian genus *Verdoornianthus* Gradst. Differences are discussed under the latter.

Key to the Subgenera of *Archilejeunea*

1. Plants glossy yellow-brown to dark brown; underleaves (3)4–7 x stem width, imbricate; lobules never reduced; innovations pycnolejeuneoid (first appendage an underleaf); dioicous, rarely paroicous; common in northern South American lowland forests, very rare elsewhere. . . . . 1. *A. subgen. Archilejeunea.*
1. Plants pale-green to greenish-brown to black; underleaves 2–4x stem width, distant to subimbricate; lobules tending to become reduced; innovations lejeuneoid (first appendage a lateral leaf); autoicous; throughout tropical America but rare in Amazonia, 0–1500 m . . . . 2. *A.* subgen. *Dibrachiella.*

1. **Archilejeunea** subgenus **Archilejeunea**; *Lejeunea* subgen. *Archilejeunea* Spruce sect. *Monotropella* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 98. 1884; *Archilejeunea* subgen. *Monotropella* (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893.

Dioicous, rarely paroicous. Stem epidermis cells similar in size to medullary cells. *Plants* glossy yellow-brown to dark brown. *Leaves* margins entire; trigones well-developed, triradiate and sometimes confluent. *Lobules* never reduced, short rectangular with truncate apex and 0–1 teeth. Underleaves imbricate, rarely distant (etiolated plants), (3)4–7 x stem width. *Androecia* terminal or intercalary on branches or below gynoecia, bracts in (1-)6–14 series. *Gynoecia* usually with a single, repeatedly fertile pycnolejeuneoid innovation, only in *Archilejeunea porelloides* a pair of innovations below and repeatedly fertile single innovations above (as in subgen. *Dibrachiella*), bracts as large as vegetative leaves or slightly longer, lobe apex rounded or obtuse, lobules usually lanceolate-acuminate and about 2/3 x lobe length, never reduced; bracteoles ovate-oblong, apex rounded to very short bifid. *Perianths* with (0-)2 ventral keels, the ventral keels sometimes reduced in *A. fuscescens.*

Distribution. Lowland rain forests of northern South America; rare elsewhere (Panama, Costa Rica).

Key to the Species of *Archilejeunea* subgenus *Archilejeunea*

1. Underleaf margins undulate; ventral leaf margin usually auriculate at the junction with the keel; inner Amazonia and Guianas, usually in periodically inundated forests. . . . . 2. *A. crispistipula.*
1. Underleaf margins not undulate; ventral leaf margin never auriculate.
    2. Plants creeping; leaves suborbicular, ca. 1.2 x longer than wide; northern South America, common. . . . . 3. *A. fuscescens.*
    2. Plants growing away from the substrate, erect; leaves ovate-oblong, more than 1.2 x longer than wide.
        3. Leaves less than 2 mm long; lobules strongly swollen, lobule tooth long, the uniseriate tip (2-) 3–5 cells long; innovations always singly; paroicous, growing on fine twigs; inner Amazonia, Guyana. . . . . 1. *A. badia.*
        3. Leaves more than 2 mm long; lobules rather flat, lobule tooth lacking or short, with a 1–2 cells long uniseriate tip; oldest gynoecium with two innovations, younger ones with single innovations; dioicous; inner Amazon and Orinoco basin, Chocó, Panama. . . . . 4. *A. porelloides.*

1. **Archilejeunea badia** (Spruce) Stephani, Spec. Hep. **4:** 711. 1911; *Lejeunea badia* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 92. 1884. Type. Brazil. Rio Vaupés, *Spruce L104* (holotype, MANCH).

Lejeunea recurvans Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 93. 1884; *Archilejeunea recurvans* (Spruce) Stephani, Spec. Hep. **4:** 718. 1911. Type (Gradstein & Buskes, 1985). Brazil. Rio Negro, São Gabriel, *Spruce L462* (lectotype, MANCH).

Archilejeunea fuscescens (Hampe) Fulf. var. *paroica* Gradstein, in sched.

Paroicous. *Plants* 1–3 cm long x 2 mm wide, glossy brown, little branched, growing away from twigs, always fertile. *Leaves* subimbricate, dorsal lobe ovate-oblong, ca. 1.2–1.5 x 0.8–1 mm, apex rounded, plane or recurved, margins plane, ventral margin curved, forming a wide angle with the keel, not auriculate at keel junction; median cells about 30–40 μm in largest diam., trigones rather thick, intermediate thickenings 1–3 per cell, one per wall; oil bodies not observed. *Lobules* rectangular, 1/3–1/2 x lobe length, usually rather strongly inflated, apex with a sharp and often curved tooth, the uniseriate tip

(2–)3–5 cells long; hyaline papilla positioned at the proximal base of the tooth on the inner surface of the lobule. Underleaves imbricate, orbicular or wider than long, 4–6× stem width, apex rounded, recurved or plane, margins plane or recurved, not undulate. *Androecia* immediately below the gynoecium, the male bracts in 1–2(–3) series. *Gynoecia* as in *A. fuscescens*; perianths always with two sharp ventral keels. *Sporophyte* not observed.

Illustration. Gradstein and Buskes, Beih. Nova Hedwigia **80:** 93, Fig. 1b, e–f. 1985.

Distribution. Brazil (inner Amazonia), Guyana, from almost sea level to about 550 m in Guyana. *Archilejeunea badia* grows on small twigs in rather open primary rain forest (terra firme or várzea) and in scrub.

Specimens examined. GUYANA. Upper Mazaruni District, along Waruma river, *Gradstein 5022* (U).

BRAZIL. AMAZONAS: Manaus, campus INPA, *Griffin et al. 1-84a* (FLAS, U); Rio Lages, 130 km along the Manaus–Caracarai road, *Griffin et al. 426* (FLAS, U); Campina forest, km 60 along the Manaus-Caracarai road, *Griffin et al. 591* (FLAS, U); along Igarapé Santa Luzia, just off Rio Uatumã, *Buck 2893* (NY, U); Rio Negro, *Spruce several colls.*, annotated as *A. juliformis* by G. Buskes (MANCH); Rio Negro, along Rio Cariua from Rio Curicuriari to Cachoeira Piraiauara, *Schuster 79-16-855* (NY), Igarapé Foibará at first cachoeira, *Schuster 79-21-1105* (NY), Serra de Jacumin NW of Santa Isabel, *Buck 2290* (NY). PARÁ: Serra do Cachimbo, near cataracts on Rio Curuá, *Reese 16587* (NY).

Archilejeunea badia is closely related to A. fuscescens but differs by its erect growth on fine twigs, its more elongated leaves, the strongly swollen lobules with a rather long, often curved tooth, and the paroicous sex distribution. The plants are always copiously fertile but the androecia, which are located just below the gynoecia, are rather inconspicuous and are easily overlooked (they were not observed by Spruce). The antheridia develop in the axils of the somewhat enlarged and swollen, hypostatic lobules of subinvolucral leaves and are usually decayed in herbarium materials. Gradstein and Buskes (1985) treated *A. badia* as a paroicous form of *A. fuscescens.*

2. Archilejeunea crispistipula (Spruce) Stephani, Spec. Hep. **4:** 712. 1911; Gradstein and Buskes, Beih. Nova Hedwigia **80:** 98. 1985; *Lejeunea crispistipula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 93. 1884. Type (Gradstein & Buskes, 1985). Brazil. Amazonas: Rio Negro, Uanauaca, *Spruce L60* (lectotype, MANCH, 2 colls.).

Dioicous. *Plants* rather small and brittle, up to 3 cm long × 1.2 mm wide, glossy yellow brown to golden brown, creeping. Stems in cross section on average composed of 12 epidermal cells surrounding 15 similar medullary cells; ventral merophyte four cell rows wide. *Leaves* subimbricate, dorsal lobe ovate-orbicular, 0.6–0.8 × 0.5–0.6 mm, apex rounded, plane, margins sometimes undulate especially ventrally, ventral margin curved, forming a sharp angle (90°) with the keel and auriculate at junction with keel, the auricle often touching the lobule or even covering part of the upper portion of the lobule; median cells about 25 µm in largest diam., trigones rather thin, intermediate thickenings 1–2 per cell; oil bodies coarsely segmented, *Calypogeia*-type, 3–5 in median leaf cells, more numerous in basal leaf cells. *Lobules* (sub)rectangular, 1/3–2/5 × lobe length, apex with one sharp, erect or outwardly pointing tooth of 2–3 cells long, hyaline papilla positioned near the proximal base of the tooth on the inner surface of the lobule. *Underleaves* imbricate, suborbicular-obtrapezioid or broadly ovate, wider than long, 4–5 × stem width, apex rounded or truncate, sometimes emarginate, margins undulate-crispate. *Androecia* with 5–12 series of bracts. *Gynoecia* with only one subfloral innovation, bracts slightly longer than vegetative leaves, lobe apex obtuse, lobules oblong-lanceolate, about 1/2–2/3 × lobe length, apex rounded to acuminate; bracteoles ovate-oblong, apex very short bifid (to 0.07 mm deep). *Perianths* with two ventral keels, all keels irregularly crenate-denticulate. *Sporophyte* not observed.

Illustration. Gradstein and Buskes, Beih. Nova Hedwigia 80: 97, Fig. 2g–j. 1985.

Distribution. Northern South America: upstream regions of the Amazon, Essequibo and Orinoco rivers and their tributaries. *Archilejeunea crispistipula* occurs on bark in the understory of moist primary forest: in periodically inundated rain forests or in low forest on white sand.

Specimens examined. COLOMBIA. AMAZONAS: Río Apoporis, Cachivera de Jirijirimo, *Schultes & Cabrera*

42046 (FLAS, U).

VENEZUELA. **AMAZONAS:** Upper Orinoco, Temblador I., *Mägdefrau 154* (U); San Carlos del Río Negro, *Spruce s.n.* (MANCH); Cerro Neblina, *Buck 11609* (NY), *Halling 4219, 4358* (NY).

GUYANA. **UPPER MAZARUNI DISTR.:** Kamarang, *Robinson 85-63* (U, US).

PERU. **SAN MARTÍN:** Mt. Guayrapurina, *Spruce s.n.* (MANCH); road Yurimaguas-Tarapoto km 56, *Frahm et al. 1332*, 1446, 1984 (B, U).

BRAZIL. **ACRE:** Cruzeiro do Sul, *Prance et al. 11860* (NY, U). **AMAZONAS:** Rio Negro, Panuré, *Spruce s.n.* (MANCH), Tapuruquara, *Prance et al. 15292* (NY, U), Ilha Acarabu, *Buck 2346* (NY), near São Gabriel, *Schuster 965, 998, 1013* (NY); Rio Urubu, *Griffin et al. 843, 848, 854, 901* (FLAS, U); road Manaus-Caracarai km 60, *Griffin et al. 584, 971* (FLAS, U); road Manaus-Itacoatiara, Ducke forest reserve, *Griffin 328, 349* (FLAS, NY); Manaus, Ponta Negra, *Prance et al. 11700, 11712* (NY, U). **PARÁ:** Rio Trombetas, *Prance et al. 22187* (NY, U).

Archilejeunea crispistipula is the smallest species of the subgenus *Archilejeunea* and is easily recognized by its undulate underleaf margins. The plants grow appressed on bark and are usually rather brittle.

3. **Archilejeunea fuscescens** (Hampe ex Lehmann) Fulford, Bryologist **45:** 174. 1942; *Lejeunea fuscescens* Hampe ex Lehmann, Nov. Min. Cogn. Stirp. Pug. **7:** 16. 1838; *Marchesinia fuscescens* (Hampe ex Lehmann) Kuntze, Revis. Gen. Pl. **2:** 837. 1891. Type. Peru (?). "in cortic. Chinae reg.," ex hb. Hampe (holotype, BM; isotype, W). Fig. 14.

Phragmicoma juliformis Nees, Syn. Hep. 298. 1845; *Ptychocoleus juliformis* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. **3 (4):** 405. 1877; *Lejeunea juliformis* (Nees) Stephani, Hedwigia **29:** 133. 1890; *Marchesinia juliformis* (Nees) Kuntze, Revis. Gen. Pl. 2: 837. 1891; *Acrolejeunea juliformis* (Nees) Schiffner, Hedwigia **33:** 183. 1894; *Archilejeunea juliformis* (Nees) Gradstein, Bryophyt. Biblioth. **4:** 126. 1975. Type. Araracoara, *Martius s.n.* (holotype, STR; isotypes, FH, M, PC, S, W).

The basionym of *Archilejeunea juliformis* has sometimes been cited as *"Jungermannia juliformis"* Nees *in* Martius, Fl. Bras. **1 (1):** 351. 1833 (Gradstein, 1975; Gradstein & Buskes, 1985), a name which would antedate *Lejeunea fuscescens* Hampe. *Jungermannia juliformis* Nees was misspelled *J. "filiformis"* in the original publication, however, and should therefore be rejected (even though it was referred to as J. juliformis on p. 321).

Lejeunea rufa Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 94. 1884; *Archilejeunea rufa* (Spruce) Stephani, Spec. Hep. **4:** 719. 1911. Type. Brazil. Pará: Santarem, *Spruce L91, L250* (syntype, MANCH), Obidos, *Spruce L57* (syntype, MANCH, NY).

Marchesinia extensa (Stephani) Stephani, Spec. Hep. **5:** 143, 151. 1912; *Homalolejeunea extensa* Stephani, Hedwigia **35:** 99. 1896. Type. Peru. Unknown Collector, Hb. Meissner s.n. (holotype, G), *syn. nov.*

Archilejeunea spruceana Stephani, Spec. Hep. **4:** 720. 1911; *Lejeunea unciloba* sensu Spruce 1884.

Archilejeunea juliformis (Nees) Gradstein var. *unicarinata* (Spruce) Gradstein in Gradstein & Buskes, Beih. Nova Hedwigia **80:** 95. 1985; *Lejeunea unciloba* Lindenberg var. *unicarinata* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 92. 1884. Type. Brazil. Pará, *Spruce s.n.* (holotype, MANCH).

Dioicous. *Plants* 1–4(-6) cm long × 1–2 mm wide, glossy yellow brown to reddish brown to dark brown, creeping, the shoot tips somewhat ascending when fertile. *Stems* in cross section on average composed of 15 epidermal cells surrounding 18 similar medullary cells; ventral merophyte 4–6 cell rows wide. *Leaves* imbricate, dorsal lobe suborbicular, 0.8–1.1 × 0.7–0.9 mm, apex rounded to obtuse, plane or recurved, margins plane, ventral margin curved or almost straight forming a sharp or wide angle (90–150°) with the keel, not auriculate at keel junction; median cells about 25–35 μm in largest diam., trigones rather thick, intermediate thickenings 1–3 per cell, one per wall; oil bodies coarsely segmented, *Calypogeia*-type, bluntly ellipsoid, 8–16 × 4–6 μm, 4–6 in median leaf cells, up to 9 in basal leaf cells. *Lobules* subrectangular, 1/4–1/2 × lobe length, apex with a sharp, erect or outwardly pointing tooth, the uniseriate tip 2–3 cells long, hyaline papilla positioned at the proximal base of the tooth on the inner surface of the lobule or, when tooth very short, at the free margin. *Underleaves* imbricate, rarely distant, orbicular or wider than long, 0.5–1 × 0.4–0.6 mm, (3-)4–7 × stem width, apex rounded, recurved or plane, margins plane or recurved, not undulate. *Androecia* with 6–12 series of bracts. *Gynoecia* with only one subfloral innovation, bracts about as large as vegetative leaves, lobe apex rounded, lobules lanceolate-acuminate, about 2/3 × lobe length; bracteoles ovate, apex rounded to very short bifid (to 0.07 mm deep). *Perianths* usually with two ventral keels, sometimes the ventral keels weakly developed or even reduced (var.

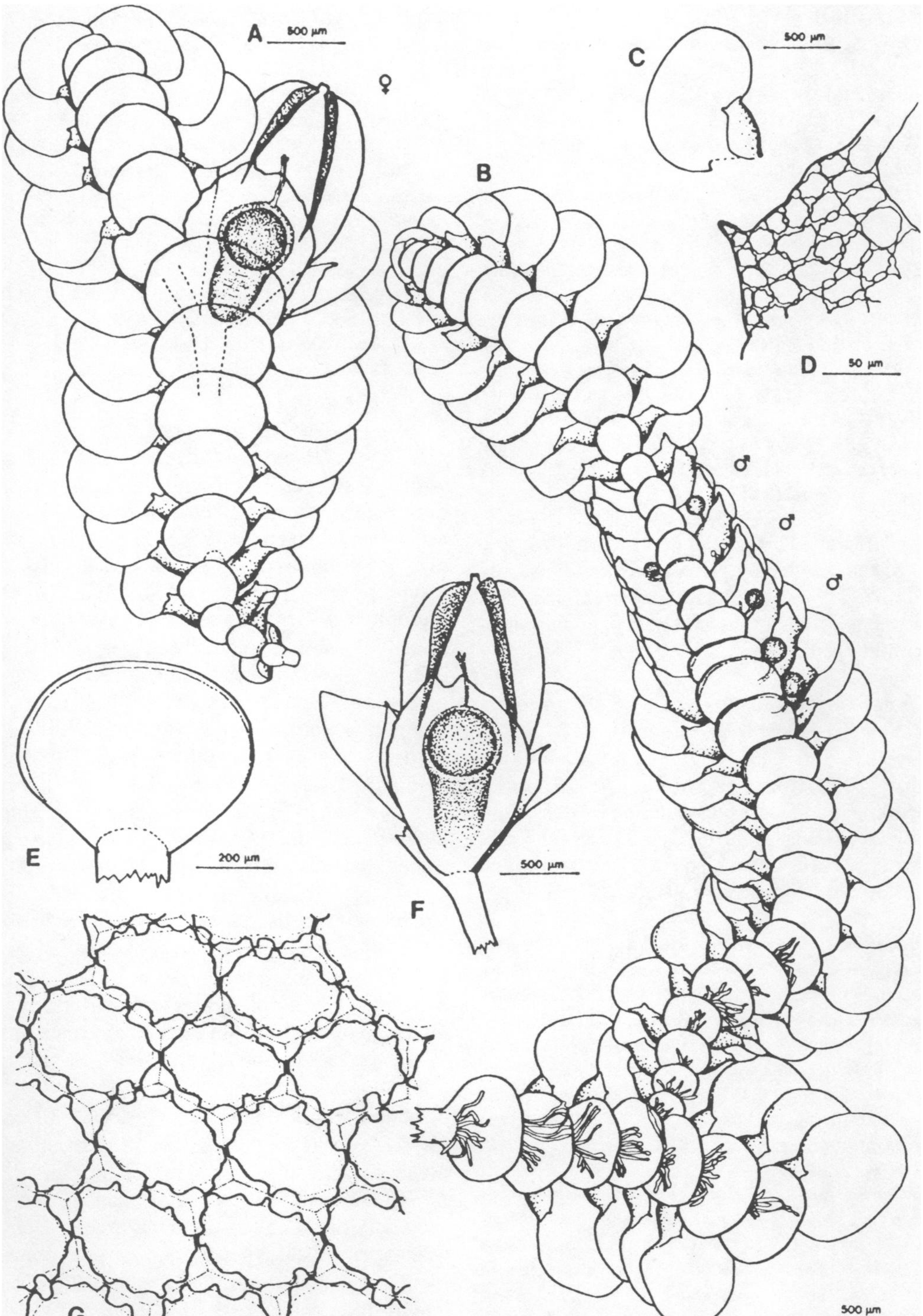

FIG. 14. *Archilejeunea fuscescens*. **A.** Gynoecial shoot, with one innovation. **B.** Elongated androecial branch; note hypostatic lobules of maled bracts. **C.** Leaf **D.** Lobule apex. **E.** Underleaf. **F.** Gynoecium. From Colombia, *Bischler 1595*.

FIG. 15. Distribution of *Archilejeunea auberiana* (small stars), *A. bischleriana* (large star) and *A. fuscescens* (dots).

unicarinata), keels irregularly crenate-denticulate to almost smooth. *Sporophyte* as in the genus.

Distribution (Fig. 15). Northern South America, particularly in the Amazonia and the Guianas where the species is very common; also collected on Cocos Island (Costa Rica). *Archilejeunea fuscescens* grows on tree trunks and branches in moist or mesic, primary or secondary rain forests, in the understory and the canopy; occasionally on rotten logs.

Selected specimens examined. COSTA RICA. COCOS ISLAND: *Weber 589* (COLO, U).

COLOMBIA. CASANARE: near Sácama, *VanderHammen 1717* (COL, U). **META:** Río Gayabero, *Bischler 1595, 1626* (COL, PC, U).

VENEZUELA. AMAZONAS: Upper Orinoco, between Maricapure and Isla Quiritare, *Mägdefrau 164* (U); Casiquiare, mouth of Río Paciba, *Mägdefrau 224* (U); Cerro Neblina, *Buck several colls.* (NY). **APURÉ:** Paez, *vanderWerff & Gonzales 4787* (MO, U). **FALCÓN:** Santa Ana, *Steyermark & Braun 94573* (US). **TACHIRA:** Uribante, road La Siberia-Las Cuevas Represa, vanderWerff & Gonzales 5286 (MO, U); W of El Pinal, *Steyermark & Rabe 96669* (US).

TRINIDAD. Valencia, Toco Rd., *Britton et al. 1883* (NY, YU); Sangre Grande, *Britton 2878* (NY).

GUYANA. Pomeroon river, *Bartlett 8052* (BM); near Bartica, *Richards 189, 201, 439, 473, 494, 515, 812* (YU); Timehri, *Cornelissen & Gradstein 7, 27, 31* (U), *Gradstein 4708, Bryoph. Neotrop. Exsicc. 81* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL); Mabura Hill, *Cornelissen & ter Steege 15 colls.* (U); Upper Mazaruni, Jawalla, *Gradstein 4863, 4881* (U); Kanuku Mts., Nappi Mt., *Jansen-Jacobs 766* (U).

SURINAME. Brownsberg, *Gradstein 4647, 4659* (U); Kabalebo Dam Project area, *Bekker 33 colls.* (BBS, U).

FRENCH GUIANA. Cayenne, *Moen s.n.* (MANCH); Montsinery near Cayenne, *Gradstein 5789* (U); Kourou, *Gradstein 5830* (U); Sinnamary, Piste de St. Elie, *Cremers 5291* 9CAY, U); Mts. de Kaw, *Gradstein 5881, 5910* (U); Saül, *Montfoort 835-841* (U).

PERU. **LORETO:** Iquitos, Laguna Quistrococha, *Hegewald 630* (U), Río Momon, *McDaniel 13646* (NY).

BRAZIL. **ACRE:** road Rio Branco–Brasileia km 33, *Reese & McPherson 13246* (NY, U); Cruz do Sul, *Prance et al. 11868, 11870, 11900, 11901, 11905, 11951* (NY, U). **AMAZONAS:** Manaus, Ponta Negra, *Griffin et al. 194, 197, 299* (FLAS, U); campus INPA, *Griffin et al. 1-69, 1-100* (FLAS, U); road Manaus–Itacoatiara km 27, Ducke forest reserve, *Griffin et al. 168, 210, 313, 327, 340, 354* (FLAS, U), *Prance et al. 11307, Bryoph. Neotrop. Exsicc. 80* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL); road Manaus-Caracarai km 60, *Griffin et al. 20, 21, 88, 89, 585, 587, 941, 977, 982* (FLAS, U), ibid. km 130, Rio Lages, *Griffin et al. 361, 364, 371, 414* (FLAS, U); road Manaus–Porto Velho km 240, *Lieras et al. P19575, P19580* (NY, U); along Rio Negro between Manaus and São Gabriel, *Schuster many colls.* (NY). **PARÁ:** Santarem and Obidos, type of *A. rufa.* **PERNAMBUCO:** Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). **RORAIMA:** Mucajai airstrip, *Prance et al. 10951* (NY, U).

BOLIVIA. **BENI:** Guayaramerín, *Reese 12771, 12791, 12926, 13100* (NY, U); Prov. Vaca Diez, vicinity of Chácobo village Alto Ivon, *Boom 4156* (NY).

Local names and uses. Chácobo Indians (Bolivia, Dept. Beni) call the species "nihibimi" and prepare a decoction which is drunk against chest pains (Boom, in sched.).

Archilejeunea fuscescens is one of the most common species of Ptychanthoideae in northern South America and is recognized by its glossy brownish color, appressed growth and suborbicular leaves. The species has been confused with *A. porelloides* and *A. badia* but the latter two have more elongated leaves and erect growth.

Archilejeunea fuscescens varies considerably in size; small plants have been described as *A. rufa* Spruce. The perianth in *A. fuscescens* normally has 2 sharp ventral keels, but one or both of these keels may occasionally be reduced. Plants with only one broad ventral keel have been described as var. *unicarinata* (Spruce) Gradst. & Buskes (see Gradstein & Buskes, 1985, Fig. 1c) and are rare. I am not sure whether they merit distinction as a separate taxon.

4. Archilejeunea porelloides (Spruce) Schiffner, Hedwigia **33:** 181. 1894.[1]

Within this species, two different subspecies can be recognized based on their different lobules and geographical ranges.

Key to the Subspecies of *Archilejeunea porelloides*

1. Lobule apex without discrete tooth; inner Amazonia.
. . . . 4a. *A. porelloides* var. *porelloides.*
1. Lobule apex with a sharp, 1–5 cells long tooth; northwestern South America, Panama.
. . . . 4b. *A. porelloides* subsp. *chocoensis.*

4a. Archilejeunea porelloides (Spruce) Stephani subspecies **porelloides**; *Lejeunea porelloides* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 90. 1884. Type (Gradstein & Buskes, 1985). Venezuela. Amazonas: San Carlos del Río Negro, *Spruce L44* (lectotype, MANCH, 2 colls.; isolectotype, NY, W).

Lejeunea porelloides var. *andina* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 91. 1884. Type (Gradstein and Buskes, 1985). Peru. San Martín: Mt. Guayrapurina, *Spruce L180* (lectotype, MANCH, 2 colls.).

Lejeunea porelloides var. *longiflora* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 91. 1884. Type (Gradstein and Buskes, 1985). Venezuela. Amazonas: San Carlos del Río Negro, *Spruce s.n.* (lectotype, MANCH).

Dioicous. *Plants* 4–10 cm long × 2.5–3.5 mm wide, glossy yellow brown to dark brown, ascending to erect, largely growing free from the substrate. *Stems* in cross section composed of 20–30 epidermal cells surrounding 28–40 similar medullary cells; ventral merophyte 6–8 cell rows

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[1] Geissler and Gradstein (in press) have shown that the correct name for this species is *Archilejeunea ludoviciana* (De Notaris ex Lehmann) Geissler & Gradstein (basionym: *Phragmicoma ludoviciana* De Notaris ex Lehmann, Nov. Stirp. Pug. **10:** 11. 1857). The type material of the latter (Tropical America, "in cortice Cinchonae," *L. Dufour s. n.* [holotype, S]) belongs to *A. porelloides* subsp. *chocoensis* Gradst. The correct names of the two subspecies of *A. porelloides* are as follows: **Archilejeunea ludoviciana** (De Notaris ex Lehmann) Geissler & Gradstein subsp. **ludoviciana** (*A. porelloides* subsp. *chocoensis* Gradstein); **Archilejeunea ludoviciana** (De Notaris ex Lehmann) Geissler & Gradstein subsp. **porelloides** (Spruce) Gradstein **comb. nov.** (Lejeunea porelloides Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 90. 1884).

wide. Leaves subimbricate, dorsal lobe ovate-oblong, ca. 1.5 × 0.9 mm, apex (narrowly) rounded, margins plane, ventral margin almost straight, forming a wide angle with the keel and not auriculate at keel junction; median cells about 30 µm in largest diam., trigones rather thick, intermediate thickenings 0–1 per cell; oil bodies not observed. *Lobules* subrectangular, 1/3–1/2 × lobe length, apex triangular, obtuse or acute, without discrete tooth, apical margin truncate, angle between apical margin and ventral leaf margin at junction usually less than 90°; hyaline papilla long cylindrical, positioned on the free margin proximal of the apex. *Underleaves* large, imbricate, rarely distant, gibbose, longer than wide to orbicular, 4 × stem width, apex rounded, plane or slightly recurved, margins not undulate. *Androecia* with 6–14 series of bracts. *Gynoecia* with 1–2 subfloral innovations, a paired innovation below and repeatedly fertile single innovations above, bracts slightly longer than vegetative leaves, lobe apex rounded to obtuse, lobules lanceolate-acuminate, about 3/4 × lobe length; bracteoles oblong, apex narrowly bifid, incision to 0.3 mm deep. *Perianths* with two ventral keels, sometimes one ventral keel less well developed, keels irregularly crenate-denticulate to smooth. *Sporophyte* as in the genus.

Illustration. Gradstein and Buskes, Beih. Nova Hedwigia **80:** 97, Fig. 2a–f. 1985.

Distribution. Inner Amazonia (below 500 m); very common along the upstream portion of the Rio Negro. *Archilejeunea porelloides* subsp. *porelloides* grows on small trunks and twigs in lowland rain forest and in scrub.

Specimens examined. COLOMBIA. AMAZONAS: Araracuara, *Sipman & Duivenvoorden 27849, 28350* (B, U); near Leticia, *Churchill et al. 16197* (NY).

VENEZUELA. AMAZONAS: Casiquiare, Capiguara, *Mägdefrau 207* (U); Río Guarnia, *Mägdefrau 277* (U); San Carlos del Río Negro, *Delascio et al. 9453* (FLAS, U), *Liesner 3325, 3378* (MO, U); Cerro Neblina, along Río Mawarinuma, *Buck 10853, 11040, 11102, 11315 11331, 11375* (NY), *Halling 4136, 4179, 4213* (NY).

ECUADOR. Bomboiza, Gualayuir, *Allioni 600* (U).

PERU. LORETO: near Iquitos airport, *Timme 4758* (NY). SAN MARTÍN: Moyabamba, Mt. Pingullu, *Spruce s.n.* (MANCH, YU).

BRAZIL. AMAZONAS: Rio Panuré, *Spruce s.n.* (MANCH); Rio Negro, Morro Ximaio, *Schuster 477, 481, 490, 514* (NY), Serra Curicuriari, *Schuster 748, 752, 765, 767, 833* (NY); road Manaus-Caracarai km 130, Rio Lages, *Griffin et al. 418* (FLAS, U); Rio Uatumã, *Buck 3031* (NY).

Archilejeunea porelloides subsp. *porelloides* is the largest taxon of the genus. It is easily distinguished by its large size, its distinctly elongated, ovate-oblong leaves, its underleaves which are usually longer than wide (sometimes orbicular, however) and the lack of a discrete lobule tooth. The hyaline papilla is unusually long, narrow cylindrical and stands away from the free margin proximal to the apex (Gradstein & Buskes, 1985: p. 97, fig. 2c).

Characteristically, the apex of the lobule is usually extended distad and the angle between apical margin of lobule and ventral leaf margin is usually less than 90°. In *Archilejeunea fuscescens*, which has sometimes been confused with *A. porelloides*, the lobule apex is not extended; moreover, the apex of the lobule is always sharply toothed. *Archilejeunea fuscescens* is also a much smaller plant than *A. porelloides*, with shorter, suborbicular leaves and shorter underleaves. Moreover, the growth form and the gynoecial branching system of the two species are quite different. *Archilejeunea fuscescens* grows appressed to the substrate whereas *A. porelloides* has erect growth. Innovations in *A. fuscescens* are always singly whereas in *A. porelloides* the gynoecial branching system is made up of a pair of innovations below and repeatedly fertile single innovations above (like in *Archilejeunea* subgenus *Dibrachiella*).

4b. Archilejeunea porelloides subspecies **chocoensis** Gradstein *subsp. nov.*[1] A subsp. *porelloides* differt lobulis conspicue unidentatis. Type. Colombia. Chocó: Mun. Nuqui, El Amargal 5 km SW of Arusi, high up trunk of fallen tree in wet coastal rain forest, alt. ca. 40 m, 5 Aug 1992, *Gradstein 8870*, male specimen (holotype, COL; isotype, U).

Marchesinia longistipula Steph., Spec. Hep. **5:** 150. 1912. Type. Ecuador. Azuay: Gualaquiza, "in silva secus rivum Sapotilla," *Allioni 6569 (holotype, G; isotype, FI), syn. nov.* I am grateful to Dr. P. Geissler, Geneva, for calling my attention this synonym.

Dioicous. Plants up to 5 cm long × 3 mm wide, glossy yellow brown, ascending to erect, standing away from the substrate. *Stems* in cross sec-

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[1] See footnote p. 58

tion composed of 20–25 epidermal cells surrounding 28–35 similar medullary cells; ventral merophyte 6–8 cell rows wide. *Leaves* subimbricate, dorsal lobe oblong, ca. 1.1–1.3 × 0.6–0.7 mm, sometimes falcate, apex rounded, margins plane, ventral margin gradually curved, forming a wide angle with the keel, not auriculate at keel junction; cells as in ssp. *porelloides*. *Lobules* subrectangular, 1/5–1/3 × lobe length, rather flat and with a discrete, 1–5 cells long tooth, the tooth 1–3 cells wide at the base, the uniseriate tip 1–2 cells long, apical margin truncate, angle between apical margin and ventral leaf margin at junction more than 90°, distal end of the free margin acute or connate with the lobe surface across 1–2 cells. *Underleaves* imbricate, concave, orbicular-obtrapezioid to transversely ovate, rarely longer than wide, 3.5–5 × stem width, apex truncate, plane or slightly recurved, margins not undulate, bases decurrent, insertion line arched. *Gametoecia* as in subsp. *porelloides*. *Sporophyte* not observed.

Distribution. Panama, Colombia, Ecuador; mainly found along the Pacific side of the Andes in the Chocó Department, from sea level to about 500 m. *Archilejeunea porelloides* subsp. *porelloides* is a typical sun epiphyte of wet rain forests and grows high up on the trunks of large canopy trees and on trees at forest margins.

Specimens examined. PANAMA. VERAGUAS: slopes of Cerro Tuti, *Gentry 6272A* (MO, NY, U).

COLOMBIA. CHOCÓ: road St. Cecilia–Tado km 40, *Gradstein 8729* (COL, U); road Quibdo-Istmina, near Certegui, *Gradstein 8786* (COL, U); Mun. Nuqui, El Amargal 5 km SW of Arusi, *Gradstein 8870, 8909* (COL, U); road Tutunendo-El Carmen at point 20, *Gradstein 8909* (COL, U). META: Cordillera La Macarena (extreme NE), between Río Guejar and Caño Guapayita, *Schultes 11184* (FLAS, U).

ECUADOR. Type of *Marchesinia longistipula*.

Archilejeunea porelloides subspecies *chocoensis* is habitually similar to subsp. *porelloides* but the plants are usually somewhat more slender, the leaves are slightly smaller and more falcate, the lobules are smaller (often less than 1/3 × lobe length) and the underleaves are usually not elongated. An unusual morphological trait of subsp. *chocoensis* is the fact that in some lobules the distal end of the free margin is truncate and connate with the surface of the leaf lobe across 1–2 cells. I have never observed this feature in other species of Archilejeunea but in *Lopholejeunea* this is an excellent species character, e.g., of *Lopholejeunea subfusca*.

The most significant morphological character of subspecies *chocoensis* is the presence of a discrete lobule tooth, a feature which lacks in the typical populations of *A. porelloides* from inner Amazonia. However, in a specimen of *A. porelloides* from Ecuador, described by Stephani as *Marchesinia longistipula* Steph., lobules with or without teeth are present. Since the majority of the lobules were clearly toothed, I have identified this material as *A. porelloides* subsp. *chocoensis*. The Ecuadorian specimen shows that the two subspecies are very closely related and that morphologically intermediate populations may occur. The two subspecies of *A. porelloides* are of considerable biogeographic interest and illustrate a case of vicariant speciation on either side of the Andes.

2. **Archilejeunea** subgenus **Dibrachiella**

(Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; *Lejeunea* subgen. *Archilejeunea* Spruce sect. *Dibrachiella* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 90. 1884. Lectotype (Gradstein & Buskes, 1985). *Lejeunea florentissima* Spruce (= *Archilejeunea auberiana* (Montagne) Evans).

Mastigolejeunea sect. *Paradoxae* Verdoorn, Ann. Bryol. Beih. **4:** 118. 1934. Type. *Mastigolejeunea paradoxa* Verdoorn (= *Archilejeunea planiuscula* (Mitten) Stephani).

Autoicous, usually fertile. *Stem* epidermis cells similar in size to medullary cells or slightly larger. *Plants* light green to green brown to black, dull or glossy. *Leaves* margins entire or (in the Asiatic *A. polymorpha*) toothed; trigones simple-triangular to short radiate, sometimes lacking and cells entirely thin-walled (hygromorphic forms). *Lobules* often reduced, when well-developed with 1–2 teeth. *Underleaves* distant or (robust plants) subimbricate, 2–4(4.5) × stem width. *Androecia* usually terminal on branches or innovations close to the gynoecium, bracts in 3–10 series. *Gynoecia* with 1–2 lejeuneoid innovations, usually a pair of innovations below and repeatedly fertile single innovations above, occasionally the innovations short and sterile in *A. parviflora*, bracts about as large as vegetative leaves or smaller, lobe apex rounded, lobules ovate-lanceolate with obtuse to acuminate apex, up to 2/3 × lobe length, sometimes reduced; bracteoles usually much shorter than the perianth, ovate-oblong or orbicular, apex rounded to very short bifid. *Perianths* always with two ventral keels, the keels smooth or rough, sometimes narrowly winged.

Distribution. Pantropical.

Key to the Species of *Archilejeunea* subgenus *Dibrachiella*

1. Lobules 1/3–1/2x lobe length, rectangular, with 2 teeth; plants glossy light green; in rather dry woodlands and open habitats. . . 5. *A. auberiana.*

1. Lobules smaller, to 1/3x lobe length (sometimes reduced), with 0–1 teeth; plants green to brown to blackish; in the understory of humid rain forest.

2. Lobules ovate with oblique apex and a blunt tooth, frequently reduced; ventral leaf margin forming an almost straight line with the keel; underleaves distant or subimbricate, (sub)orbicular; throughout tropical America. . . . . 7. A. parviflora.

2. Lobules short rectangular with truncate apex and a sharp tooth, not reduced; ventral leaf margin curved, forming a rather sharp angle of ca. 120° with the keel; underleaves distant, reniform; Chocó. 6. *A. bischleriana.*

5. **Archilejeunea auberiana** (Montagne) Evans, Bull. Torrey Bot. Club **35:** 168. 1908; *Lejeunea auberiana* Montagne *in* de la Sagra, Hist. Phys. Nat. Cuba (Bot. Pl. Cell.) 483. 1842. Type. Cuba. *Auber s.n.* (holotype, PC-MONT; isotypes, W, YU).

Lejeunea florentissima Spruce var. *monotropa* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 95. 1884; *Archilejeunea florentissima* (Spruce) Herzog, Rev. Bryol. Lichénol. **20:** 130. 1951; *Archilejeunea parviflora* var. *florentissima* (Spruce) Gradstein & Buskes, Beih. Nova Hedwigia **80:** 104, Fig. 3. 1985. Type (Gradstein & Buskes, 1985). Peru. San Martin: Tarapoto, *Spruce L152* (lectotype, MANCH).

Lejeunea florentissima Spruce var. *calliandra* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 96. 1884. Type. Ecuador. Near Guayaquil, *Spruce s.n.* (MANCH).

Autoicous. *Plants* 1.5–4 cm long × 1–2 mm wide, glossy light green to brown green, never becoming black, usually ascending and sometimes pendent when growing on twigs. *Stems* in cross section on average composed of 12–18 epidermal cells surrounding ca. 15–30 similar medullary cells; ventral merophyte 4–6 cell rows wide. *Leaves* imbricate, dorsal lobe ovate, 0.8–1 × 0.6–0.7 mm, apex rounded, plane, margins plane or slightly recurved, ventral margin curved, forming a wide angle with the keel; median cells about 20–40 µm in largest diam., trigones usually well-developed, intermediate thickenings 0–2 per cell, one per wall; oil bodies coarsely segmented, 3–6 in median leaf cells. *Lobules* occasionally reduced, when well-developed rectangular, 1/3–1/2 × lobe length, apex truncate, with two teeth separated from each other by a narrow sinus, the first tooth 2-5 cells long and 2 cells wide at base, the second tooth as large as the first tooth or (usually) shorter, the teeth erect or curved outwards, hyaline papilla positioned at the free margin in the sinus between the two teeth. *Underleaves* imbricate or distant, orbicular to broadly ovate-reniform, 3–4(4.5) × stem width, apex rounded, margins plane. *Androecia and gynoecia* as in the genus/subgenus. *Sporophyte* as in the genus.

Illustration. Evans, Bull. Torrey Bot. Club **35:** 179, Pl. 8. 1908 (as *Archilejeunea viridissima*); Gradstein and Buskes, Beih. Nova Hedwigia **80:** 103, Fig. 3d. 1985 (as *Archilejeunea parviflora* var. *florentissima*).

Distribution (Fig. 15). Scattered throughout tropical America but almost lacking in Amazonia; at low elevations. *Archilejeunea auberiana* is a drought-tolerant species and grows on bark of trees and shrubs in rather dry locations: at the edges of rain forest, in seasonal forest, in open, secondary vegetation and on isolated trees.

Selected specimens examined. MEXICO. CHIAPAS: Nuntuntun, 3 km S of Palenque, *Gradstein 8241, 1992* (U). **OAXACA:** W of Tuxtepec, *Sharp s.n.* (US).

NICARAGUA. Escondido rivet, *unknown collector* (US, YU).

CUBA. MATANZAS: El Grillo, *Britton et al. 793* (NY, YU). **ORIENTE:** Guantanamo, Baracoa, *Pócs & Reyes 9063* (HAC, U).

TRINIDAD. *Thaxter s.n.* (hb. Fulford).

SURINAME. Kabalebo Dam project area, *Bekker 1120d* (U).

FRENCH GUIANA. Saül, *Gradstein 6085, 6185* (U), *Montfoort 834* (U).

ECUADOR. GUAYAQUIL: Daule, *Spruce s.n.* (MANCH). **PICHINCHA:** Río Palenque Forest Reserve, *Gradstein et al. 6969* (U).

PERU. LORETO: Iquitos, Río Momón, *Timme 4781* (NY). **SAN MARTÍN:** road Yurimaguas–Tarapoto km 112, *Frahm et al. 2133* (B, U).

BRAZIL. PARÁ: Caripi, Spruce s.n. (MANCH, W, YU); highway Transamazon Altamira-Itaituba, branch road to Santarem km 20, Prance et al. 24718a (MG, NY, U). RIO GRANDE DO SUL: Parque Flor. do Turvo, Lindeman 6593 (ICN, U). SÃO PAULO: Barra do Turvo, Vital 2791e (SP, U).

BOLIVIA. BENI: Guayaramerín, *Reese 13115* (NY, U). SANTA CRUZ: Prov. Ichilo, 15 km S of Buena Vista, *Gradstein 7735* (LPB, U).

PARAGUAY. ALTO PARANÁ: 35 N of Hernandarías, *Geissler 14523* (G); 80 km N of Hernandarías, *Geissler 1642, 1675* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993). Material from Colombia (Chocó, *Bischler 177*) identified as *Archilejeunea auberiana* by Gradstein and Buskes (1985) belongs to *A. bischleriana.*

Archilejeunea auberiana occurs in dryer habitats than *A. parviflora*, grows more free from the substrate (appressed in *A. parviflora*), is lighter green in color and has a larger, less frequently reduced lobule with two distinct teeth. Otherwise the two species are very similar.

6. Archilejeunea bischleriana Gradstein *spec. nov.* Ab *Archilejeunea auberiana* differt lobulis minoribus unidentatisque. Type. Colombia. Chocó: road Quibdo-Istmina, near Certegui, on dead twigs, alt. 50 m., 2 Aug 1992, *Gradstein 8789* (holotype, COL; isotype, U).

Autoicous, copiously fertile. *Plants* 1.5–3 cm long × 1.5 mm wide, glossy green to brown green, not becoming black, creeping to ascending to erect on twigs. *Stems* in cross section on average composed of 12–14 epidermal cells surrounding 25 smaller medullary cells, epidermis cells subrectangular, 25–30 × 18–25 μm, medullary cells 13–20 μm in diam., all cell walls slightly thickened; ventral merophyte four cell rows wide. *Leaves* ± imbricate, dorsal lobe ovate-oblong, ca. 0.75 × 0.5 mm, apex rounded, plane, margins plane or slightly recurved, ventral margin curved, forming an angle of ca. 120° with the keel; median cells about 25–40 μm in largest diam., trigones small, simple or irregularly radiate, intermediate thickenings scarce, 0–1 per wall; oil bodies coarsely segmented, 3–7 in median leaf cells. *Lobules* almost invariably well-developed (a few reduced lobules may be present at branch bases and on innovations), short rectangular, ca. 1/3 × lobe length, apex truncate, with one sharp, 2 cells long, outwardly pointing tooth, free margin weakly bordered by elongated, thin-walled cells. *Underleaves* distant, small, reniform, 2–3 × stem width, apex truncate, margins plane. *Androecia* terminating elongated vegetative branches or occupying specialized branches, bracts in 4–10 series, bracteoles distinctly smaller than underleaves, becoming almost reduced near the apex of the spike. *Gynoecia* with only one lejeuneoid innovation, sometimes with an additional "pseudo-innovation" of the *Lejeunea*-type, innovations usually repeatedly fertile, bracts smaller than leaves, suberect, with reduced lobules; bracteole elongated, rather small, about 1/4–1/3 × perianth length. *Perianths* long exserted, cylindrical-obpyriform, short-stalked at base, ca. 1.2 mm long, 5-keeled over most of their length, the keels narrowly winged and crenulate, apex truncate; beak short, 3–4 cells long. *Sporophyte* not observed.

Distribution (Fig. 15). Chocó, Colombia, ca. 50–80 m. *Archilejeunea bischleriana* is only known from two localities in the very wet lowland forests (rainfall about 12000 mm per year or more!) near Quibdo, in the central region of the Chocó Department. The species grows on rotten twigs and cyperaceous leaves in the understory of primary and secondary rain forest.

Specimens examined. COLOMBIA. CHOCÓ: along road Quibo–Tutunendo, *Bischler 177*, April 1957 (COL, PC, U); along road Quibdo-Istmina, near Certegui, *Gradstein 8788* (COL, U).

Archilejeunea bischleriana is named in honor of Dr. Helène Bischler, Paris who first collected the species. The species shows affinities to both *A. auberiana* and *A. parviflora* but is different from either of them. The outstanding characters of *A. bischleriana* are the small, truncate lobules, which show hardly any tendency for reduction and have one sharp tooth and a more or less bordered free margin, and small, reniform underleaves. Unlike the other species of the subgenus *Dibrachiella*, innovations in *Archilejeunea bischleriana* are invariably singly.

With *A. parviflora* the species shares occurrence in the shaded understory of moist forests, although those in which *A. bischleriana* grows are considerably wetter than any of the forests in which *A. parviflora* has been found. The species also shares with *A. parviflora* the somewhat enlarged stem epidermis, a character unusual for *Archilejeunea*. In other respects (lobules, underleaves) the two species are quite different, however.

7. **Archilejeunea parviflora** (Nees) Schiffner, Hedwigia **33:** 181. 1894; Gradstein and Buskes, Beih. Nova Hedwigia 80: 101, Fig. 3. 1985; *Jungermannia parviflora* Nees *in* Martius, Fl. Bras. **1 (1):** 353. 1833; *Phragmicoma parviflora* (Nees) Nees, Naturgesch. Eur. Leberm. **3:** 248. 1838; *Lejeunea parviflora* (Nees) Gottsche, Lindenberg & Nees, Syn. Hep. 318. 1845; *Symbiezidium parviflorum* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. **3 (4):** 402. 1877. Type. Brazil. "Flumen Amazonum," *Martius s.n. (holotype, STR; isotypes, G, W).* Fig. 16.

Jungermannia leprieurii Montagne, Ann. Sci. Nat., Bot. (sér. 2) **3:** 213. 1835; *Lejeunea leprieurii* Montagne, Ann. Sci. Nat., Bot. (sér. 2) **3:** 213. 1835, nom. inval.; *Symbiezidium leprieurii* (Montagne) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 402. 1877; *Archilejeunea leprieurii* (Montagne) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893. Type. French Guiana. *Leprieur s.n.* (holotype, PC-MONT; isotype, G).

Lejeunea cruegeri Lindenberg, Syn. Hep. 319. 1845; *Symbiezidium cruegeri* (Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 402. 1877; *Archilejeunea cruegeri* (Lindenberg) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; *Marchesinia cruegeri* (Lindenberg) Stephani, Spec. Hep. **5:** 151. 1912. Type. Trinidad. *Crüger s.n.* (holotype, W; isotypes, G, W).

Lejeunea viridissima Lindenberg, Syn. Hep. 320. 1845; *Archilejeunea viridissima* (Lindenberg) Evans, Bull. Torrey Bot. Club **35:** 169. 1908. Type. Venezuela. Caracas, ex hb. Hampe (holotype, W).

Archilejeunea parviloba Stephani, Spec. Hep. **4:** 717. 1911. Type. French Guiana. *Leprieur s.n.* (holotype, G).

Autoicous, usually fertile. *Plants* 1.5–4 cm long × 1–2 mm wide, dull green to brown green, the older parts usually turning blackish, sometimes entirely black (hygromorphic forms, these with fully reduced lobules), creeping to slightly ascending when fertile. *Stems* in cross section on average composed of 12–18 epidermal cells surrounding ca. 15–30 similar or slightly smaller medullary cells; ventral merophyte 4–6 cell rows wide. Leaves imbricate to contiguous, at opposite sides of the stem sometimes of different length, dorsal lobe ovate-suborbicular, 0.7–1 × 0.5–0.7 mm, apex rounded to obtuse, plane, margins plane or slightly recurved, ventral margin straight, forming an almost straight line with the keel; median cells about 20–40 µm in largest diam., trigones rather small or lacking altogether (in hygromorphic forms), intermediate thickenings 0–2 per cell, one per wall; oil bodies segmented with 10–20 segments of about 1 m in diam., bluntly ellipsoid to globose, 4–10 × 4–5 µm, 3–8 in median leaf cells, up to 12 in basal leaf cells. *Lobules* often reduced, when well-developed ovate, 1/3 × lobe length, apex oblique, without or with one short, 1–2 cells long tooth, hyaline papilla positioned at the free margin. *Underleaves* subimbricate or distant, (sub)orbicular, plane or squarrose, 2–3.5 × stem width, apex rounded, margins plane. Androecia and gynoecia as in the subgenus/genus. Sporophyte as in the genus.

Terpenoids: bicyclogermacrene, various sesquiterpene alcohols, pinguisanines, furanoditerpenes, a diterpene alcohol, etc.; the terpenoid content of this species is variable (Gradstein et al., 1985).

Distribution. Throughout tropical America, from sea level up to 1500 m; rather rare in inner Amazonia. *Archilejeunea parviflora* grows in the understory of humid lowland and submontane rain forests on trunk bases, roots, rotten logs or on rocks. The species is particularly common in periodically inundated habitats, along creeks or rivers. It very rarely grows on twigs (e.g. Jamaica, *Britton 824*); this is the main habitat of the sister species *A. auberiana* and *A. bischleriana*.

Selected specimens examined. MEXICO. CHIAPAS: Lacandon forest reserve along Río Lacantun, near Chajul Biological Station, *Gradstein 7919, 7947, 8152* (U); Palenque, *Gradstein 8232* (U). VERACRUZ: near Catemaco, *den Held & van Rijn HH17* (U).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley 55342* (US).

PANAMA. DARIÉN: base of Cerro Pirre, *Salazar & Gradstein 9227* (PMA, U). PANAMÁ: Barro Colorado I., *Chung & Aranda 238, 243* (NY).

BAHAMA ARCHIPELAGO. Eight Mile Rocks, *Britton & Millspauch 2605* (YU).

CUBA. GUANTÁNAMO: La Prenda, *Hioram 5113* (HAC, YU).

JAMAICA. Union Hill, *Britton 824* (YU).

PUERTO RICO. Luquillo Mountains, El Yunque, *Evans 140* (YU).

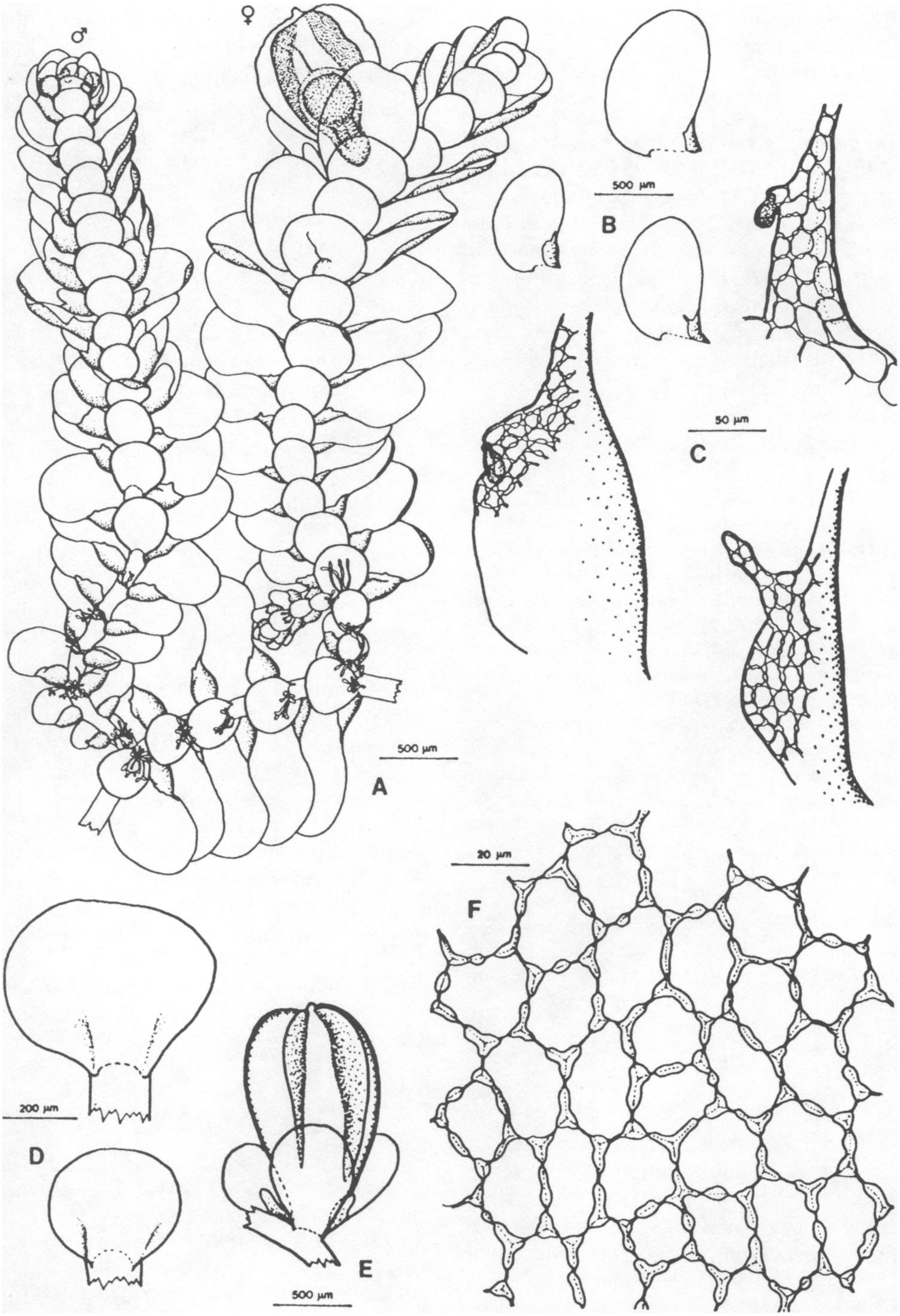

FIG. 16. *Archilejeunea parviflora*. **A.** Habit, with androecia and gynoecia. **B.** Leaves. **C.** Lobules; note reduction of lobule and modification of the apex. **D.** Underleaves. **E.** Gynoecium. **F.** Leaf cells. A, D from Brazil, *Yano 451*. B–C, E–F from Brazil, *Vital 6681*.

COLOMBIA. CAUCA: Gorgona I., *Santana et al. 734* (COL). META: Serranía la Macarena, Río Guayabero, *Bischler 1658* (COL, PC, U). NORTE DE SANTANDER: Catatumbo, *Bischler 2520, 2650* (COL, PC, U). RISARALDA: **Santa Rosa de Cabal, *Gradstein 3607* (COL, U), *van Reenen et al. 1854, 1858* (COL, U).**

VENEZUELA. AMAZONAS: Upper Orinoco, Isla Cangrejo, *Mägdefrau 161* (U).

TRINIDAD. Type of *Lejeunea cruegeri.*

GUYANA. Georgetown, *Quelch s.n.* (G); Bartica, First Falls, *Richards 366b* (YU); Mabura Hill, *Cornelissen & ter Steege 35, 196, 199, 203* (U); Kako river, *Gradstein 4966* (U).

SURINAME. Kabalebo Dam project area, *Bekker numerous colls.* (U).

FRENCH GUIANA. Kourou, *Gradstein 5829* (U); near Cayenne, *Gradstein 5845, 5857* (U); Mana river, *Cremers 7598* (CAY, U); Tampoc, *Cremers 4694* (CAY, U); Saül, *Cremers 4066* (CAY, U), *Bekker 2145* (U), *Gradstein 6123, 6152, 6156, 6196* (U), *Montfoort 842-845* (U).

ECUADOR. PICHINCHA: Río Palenque Forest Reserve, *Gradstein et al. 6953, 6954* (U).

PERU. LORETO: road Pucallpa–Lima km 80, *Spichiger s.n.* (G); Maynas, between Río Napo and Río Amazonas, *Timme 4854, 4858* (NY). SAN MARTÍN: road Yurimaguas–Tarapoto km 112, *Frahm et al. 1791* (B, U).

BRAZIL. AMAZONAS: Rio Negro, *Spruce s.n.* (YU), Serra de Jacumin, *Schuster 245, 252* (NY), above and below junction Rio Negro-Rio Branco, *Schuster 79-2-32* (NY); Rio Uatuma, *Buck 2779, 3063, 3235* (NY, U). PARÁ: Obidos, *Spruce s.n.* (MANCH, YU); Serra do Cachimbo, *Reese 16795* (NY). PERNAMBUCO: Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). RONDONIA: Alto Condeias, Mun. Ariquemes, *Fife et al. 4208, 4126* (NY). RORAIMA: road Manaus–Venezuela km 517, S of Igarapé Dias, *Buck et al. 1915* (NY, U). SÃO PAULO: Cananeia, Casca I., *Vital 6688, 6689* (SP, U); Barra do Turvo, *Vital 2790a* (SP, U).

BOLIVIA. BENI: Ballívian, Serranía del Pilón Lagas, *Gradstein 7122* (LPB, U).

PARAGUAY. GUAIRA: S of Colonia Independencia, Cordillera del Ybytyruzú, *Geissler 15101* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Lobule reduction is common in *Archilejeunea parviflora* and plants from very moist habitats, e.g., from rocks along streams, may be entirely devoid of lobules. Such elobulate forms are often blackish in color and have tiny, widely spatiated underleaves, which are often strongly squarrose. The leaf cells of these hygromorphic forms are very thin and without discrete trigones. When sterile, these blackish plants can easily be confused with *Lopholejeunea* from which they can be distinguished by the lack of an enlarged epidermis and the segmented oil bodies.

Excluded Species

(see Gradstein & Buskes, 1985: 107–111)

Archilejeunea clypeata (Schweinitz) Schiffner
= *Leucolejeunea clypeata* (Schweinitz) Evans

Archilejeunea cognata (Nees) Stephani
= *Anoplolejeunea conferta* (Meissner) Evans

Archilejeunea conchifolia Evans
= *Leucolejeunea conchifolia* (Evans) Evans

Archilejeunea conferta (Meissner) Schiffner
= *Anoplolejeunea conferta* (Meissner) Evans

Archilejeunea germana Stephani
= *Leucolejeunea cf. unciloba* (Lindenberg) Evans (Gradstein & Buskes, 1985: 109)

Archilejeunea herminieri Stephani
= ? *Amblyolejeunea fulfordiae* Jov.-Ast.

When this synonymy proves to be correct, the epithet "*herminieri*" has priority.

Archilejeunea huanucensis (Gottsche) Stephani
= *Omphalanthus huanucensis* (Gottsche) Gradstein

Archilejeunea involuta Stephani
= *Leucolejeunea xanthocarpa* (Lehmann & Lindenberg) Evans

Archilejeunea negrensis Stephani, Spec. Hep. 4: 716. 1911. Type. Brazil. Manaus, Rio Negro, *Spruce s.n.* (holotype, G) = ?

"Probably not *Archilejeunea* but the specimen is too poor to permit proper identification" (Gradstein & Buskes, 1985: 110).

Archilejeunea ovata Herzog, Rev. Bryol. Lichénol. 20: 130. 1951. Type. Honduras. *Standley 55669* (holotype, JE, n.v.) = ?

The material could not be located. Judging from the original description and illustration, which was based on a sterile stem fragment, this plant belongs to *Lopholejeunea* (*L. nigricans* or *L. subfusca*).

Archilejeunea pabstii Stephani
= *Leucolejeunea xanthocarpa* (Lehmann & Lindenberg) Evans

Archilejeunea praetermissa Stephani
= *Omphalanthus* cf. *filiformis* (Stephani) Nees

Archilejeunea pseudocucullata Stephani
= *Cyrtolejeunea holostipa* (Spruce) Evans

Archilejeunea saccatiloba Stephani
= *Cyrtolejeunea saccatiloba* (Stephani) Gradstein

Archilejeunea sellowiana Stephani
= *Leucolejeunea unciloba* (Lindenberg) Evans

Archilejeunea subinermis Stephani
= *Cyrtolejeunea saccatiloba* (Stephani) Gradstein
Archilejeunea tonduzana Stephani
= *Omphalanthus* cf. *platycoleus* Herzog
Archilejeunea unciloba (Lindenberg) Schiffner
= *Leucolejeunea unciloba* (Lindenberg) Evans
Archilejeunea xanthocarpa (Lehmann & Lindenberg) Stephani
= *Leucolejeunea xanthocarpa* (Lehmann & Lindenberg) Evans

2. **Verdoornianthus** Gradstein, Bryologist **80:** 607, Figs. 1–9. 1978 "1977." Type. *Verdoornianthus marsupiifolius* (Spruce) Gradstein. Genus named after Frans Verdoorn, well-known Dutch hepaticologist.

Autoicous. *Plants* up to 2 cm long × 1.2-1.8 mm wide, dull olive to dark brown when dry, loosely creeping on bark. *Branching Lejeunea*-type, flagelliform branches lacking. *Stems* with asymmetric epidermis, dorsal epidermal cells larger and slightly thinner-walled than medullary and ventral epidermal cells, all cell walls colorless and thickened; ventral merophyte 4–8 cell rows wide. *Leaves* obliquely spreading and weakly convoluted when dry, when moist curved upwards, somewhat falcate and squarrose and not spreading widely, apex rounded, plane, margins entire; leaf cells isodiametric-hexagonal to slightly elongate, averaging 25–30 µm in diam., trigones radiate, intermediate thickenings 0–3 per cell, one per wall, oil bodies segmented, *Calypogeia*-type; ocelli lacking. *Lobules* 1/2 × lobe length, not reduced, inflated along the keel, free margin usually incurved proximally, with 1 teeth; hyaline papilla not observed. *Underleaves* 4–6× stem width, apex truncate, margins entire, often recurved, bases straight to rounded, insertion line weakly curved; underleaf base at the rhizoid disc tristratose, with four superior central cells, rhizoid disc elongated. *Androecia* terminal or intercalary on elongated branches, bracts smaller than leaves, in 3–6 series, subequally bilobed, lobules hypostatic, underleaves present throughout; antheridia two per bract. *Gynoecia* without subfloral innovations, bracts in 1–2 series, slightly larger than leaves, lobe obovate, with rounded to obtuse apex and entire margins, lobule slightly shorter than lobe, ligulate, apex rounded, margins incurved, keel short; bracteoles as long as bracts, obovate, apex rounded or retuse, margins plane or recurved, entire. *Perianths* obcuneate, short exserted, in the upper half with 4(–5) sharp, irregularly crenate-denticulate keels: 2 lateral, 2 ventral and 0–1 dorsal; beak ca. 6 cells long. *Sporophyte*: seta not articulate (?); elaters 72 (?) per capsule; otherwise as in the tribe. *Vegetative reproduction* lacking.

Distribution (Fig. 18). *Verdoornianthus* is a rare Amazonian genus of two species occurring at low elevations, up to 200 m, in the Amazon basin and the Guianas. The species are always epiphytic and apparently rather xerotolerant. They grow on twigs and branches, and occasionally on leaves, in the canopy of primary and secondary rain forest and campina forest. The genus is only known from half a dozen collections and has probably been overlooked.

Verdoornianthus is recognized by its dull brownish color, the lack of subfloral innovations, the large lobules of leaves and female bracts, the swollen, usually tristratose rhizoid discs, the autoicous inflorescence, and the leaves, which are weakly spreading only when dry and somewhat falcate and squarrose when moist. The stem epidermis is asymmetric and the dorsal epidermis cells are somewhat larger than the medullary cells, whereas the ventral epidermis cells are similar in size to the medullary cells. The free margin of the lobule is usually somewhat involuted and in *V. marsupiifolius* it is folded inwards at the apex, obscuring the apical tooth.

Verdoornianthus is closely related to Archilejeunea, especially to A. subgen. *Archilejeunea.* The two groups have a similar leaf areolation and perianth, but the lack of innovations in *Verdoornianthus* and other diagnostic characters mentioned above separate the two. The species of *Archilejeunea* subgen. *Archilejeunea* are very common in the general area where *Verdoornianthus* occurs but seem to prefer moister habitats. They are particularly common in the understory of the rain forest, whereas *Verdoornianthus* seems restricted to branches or twigs of the forest canopy.

Color and leaf position of *Verdoornianthus* are reminiscent of *Schiffneriolejeunea*, which also lacks innovations. *Schiffneriolejeunea*, however, has distinctly elongated leaf cells with cordate trigones, whereas in *Verdoornianthus* the leaf cells are isodiametric and the trigones radiate.

Key to the Species of *Verdoornianthus*

1. Leaf lobule ovate, ca. 1.2x longer than wide, the apex folded inwards and the tooth therefore invisible without dissection; northern Amazonia, on bark. . . . . 2. *V. marsupiifolius.*
2. Leaf lobule rectangular, ca. 2x longer than wide, the apex plane, the tooth clearly visible; Amazonia, Guianas, in tree crowns and on shrubs. . . . . 1. *V. griffinii.*

1. Verdoornianthus griffinii Gradstein, Bryologist 80: 609, Figs. 1-2. 1978 "1977." Type. Brazil. Amazonas: Manaus, campus INPA, in secondary terra firme forest, *Griffin et al. 1-70-A* (holotype, FLAS; isotypes, hb. Grolle, U) Fig. 17.

Autoicous. Leaf cells with segmented, *Calypogeia*-type oil bodies (observed in dry material). Lobule rectangular, ca. 0.5 × 0.2 mm, entirely inflated, not flattened towards free margin, keel slightly curved, free margin incurved proximally, at distal edge short continuing into the ventral leaf margin, lobule apex truncate and plane, not folded, apical tooth clearly visible, slender, 2–3 cells long, 1 cell wide; hyaline papilla not observed. Underleaves ca. 1.0 mm wide, rhizoid disc up to 100 μm long. Other characters as in the genus.

Distribution (Fig. 18). *Verdoornianthus griffinii* is known from three widely separated localities: Iquitos (Peru), Manaus (Brazil) and coastal French Guiana. The species occurs on branches and leaves of trees in the canopy of undisturbed lowland rain forest (terra firme). The vast range of *V. griffinii* and its growth high up in tree crowns suggest that the species has been under-collected and should be more common.

Specimens examined. FRENCH GUIANA. Trail St. Laurent–Apatou km 65, *Cornelissen & ter Steege C269* (U).

PERU. LORETO: Requena, reserva forestal de Jenaro Herrera, *J. Meroz s.n.* (G).

BRAZIL. AMAZONAS: type of *Verdoornianthus griffinii.*

Verdoornianthus griffinii is distinguished from *V. marsupiifolius* by the characters mentioned in the key. The species might be confused with *Archilejeunea fuscescens*, one of the most common liverwort species of Amazonian rain forests. When sterile or male the latter can be recognized by its glossy appearance, the widely spreading leaves, the plane free margin of the lobule (incurved in *V. griffinii*), the dioicous inflorescence (autoicous in *V. griffinii*) and the dorsal epidermis cells, which are not or hardly larger than the medullary cells. When perianths are present, *A. fuscescens* is recognized by the presence of subfloral innovations.

2. Verdoornianthus marsupiifolius (Spruce) Gradstein, Bryologist **80:** 609. 1978 "1977"; *Lejeunea marsupiifolia* Spruce, Trans. Proc. Bot. Soc. Edinburgh **15:** 118. 1884; *Ptychocoleus marsupiifolius* (Spruce) Steph., Spec. Hep. **5:** 35. 1912. Type. Brazil/Venezuela. Upstream Rio Negro, *Spruce* (holotype, MANCH; isotype, FH).
The locality and country of origin of the type material are questionable. The original publication mentions "S. Gabriel" [Brazil] as type locality whereas the handwritten herbarium label reads "S. Carlos" [Venezuela].

Autoicous. Oil bodies unknown. Leaf lobule ovate-suborbicular, ca. 0.5 × 0.4 mm, inflated along the keel and flattened towards free margin, flattened portion rather wide, on stem leaves sometimes as wide as the inflated portion, keel strongly arched, free margin plane or somewhat incurved proximally, at distal edge rather longly continuing into the ventral leaf margin, lobule apex folded, free margin and apical tooth projecting into the sac at fold, apical tooth not visible without dissection, rather blunt, ca. 3 cells long and 2 cells wide; hyaline papilla not observed. Underleaves ca. 0.75 mm wide, rhizoid disc conspicuous, up to 150 μm long. Other characters as in the genus.

Illustration. Gradstein, Bryologist **80:** 608, Figs. 3–9. 1978.

Distribution (Fig. 18). Northern Amazonia: Brazil, Venezuela (?). On bark of trees.

Specimen examined. BRAZIL. AMAZONAS: Rio Uatumã, Iguarapé Caititu, *Buck 2956* (NY).

Verdoornianthus marsupiifolius is readily recognized by the peculiar, folded apex of the lobule. The apical tooth of the lobule is curved inwards into the watersac and can only be observed after dissection.

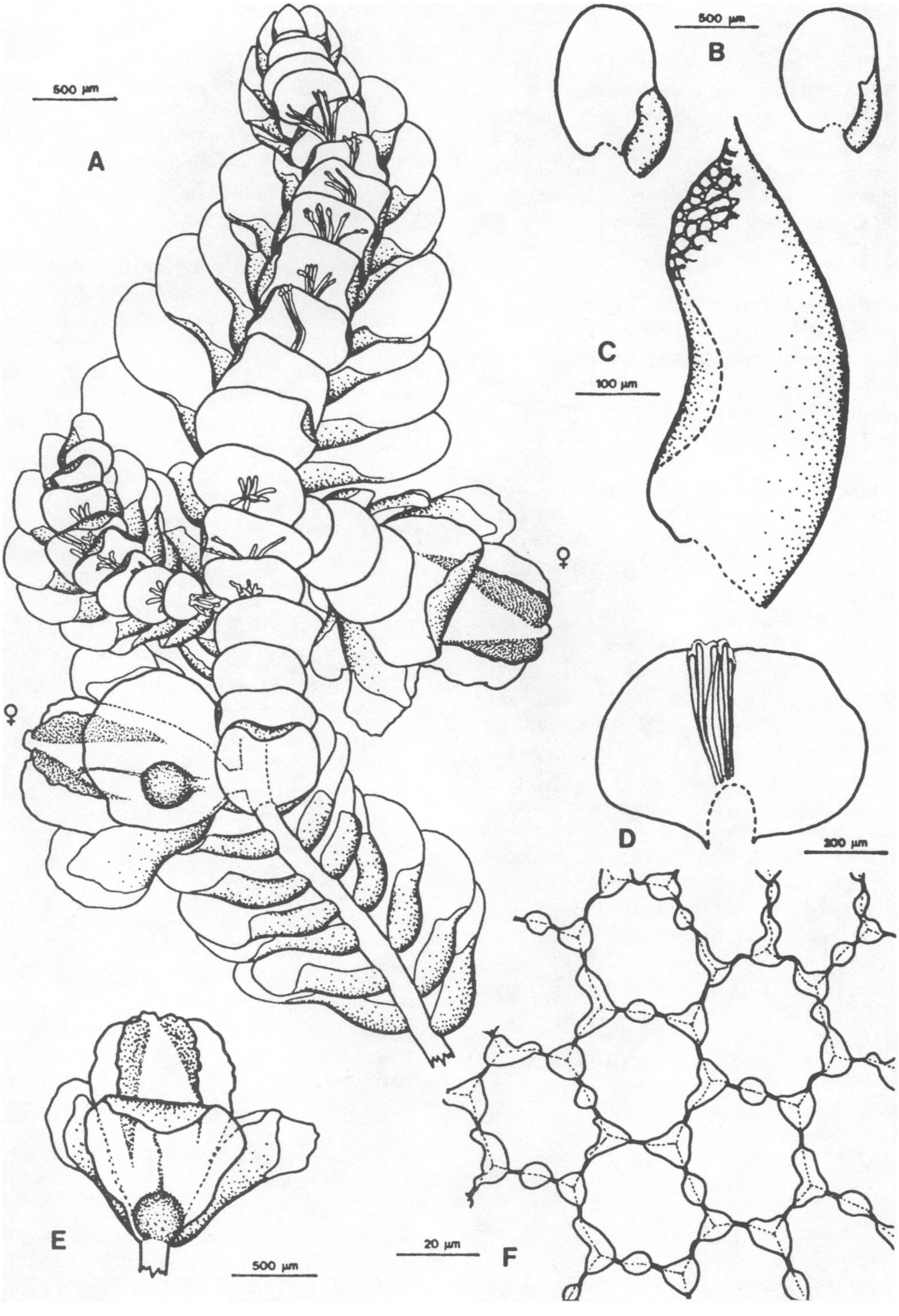

FIG. 17. *Verdoornianthus griffinii.* **A.** Habit, with two gynoecial branches. **B.** Leaves. **C.** Lobule. **D.** Underleaf. **E.** Gynoecium. **F.** Leaf cells. From the type.

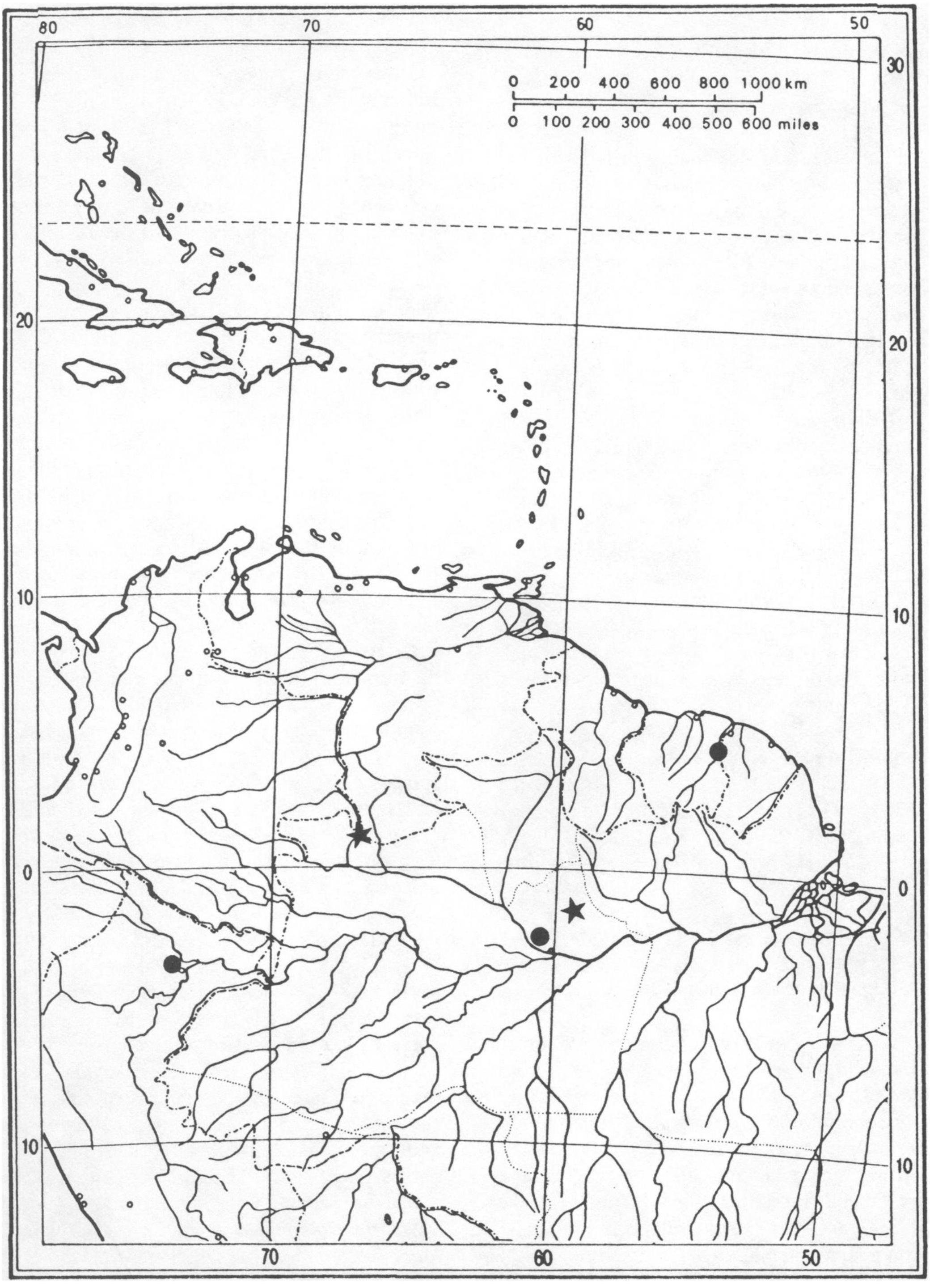

FIG. 18. Distribution of *Verdoornianthus griffinii* (dots) and *V. marsupiifolius* (stars).

PTYCHANTHINAE
Gradstein emend.

Ptychantheae subtribe Ptychanthinae Gradstein, Bryologist **90:** 338. 1987. Type. *Ptychanthus* Nees.

Plants creeping, ascending or pendent, sometimes dendroid. Stem epidermis cells brown, not larger than medullary cells or enlarged dorsally. Median leaf cells usually elongated and with cordate trigones; oil bodies segmented, rarely homogeneous (*Bryopteris*) or lacking (*Fulfordianthus*). Innovations usually lejeuneoid, or lacking. Perianth with one sharp ventral keel or pluriplicate, rarely 4–5-keeled (*Schiffneriolejeunea*).

Distribution. Pantropical. The subtribe Ptychanthinae consists of eight genera, five of which occur in the neotropics: *Schiffneriolejeunea*, *Mastigolejeunea*, *Thysananthus*, *Fulfordianthus* and *Bryopteris*. Other members of this subtribe are *Dendrolejeunea* (Asia), *Ptychanthus* (palaeotropics) and *Tuzibeanthus* (Asia).

The rather robust stems without or with scarcely enlarged epidermis cells, the elongated leaf cells with cordate trigones, the segmented oil bodies and the lejeunoid innovations are the most distinctive features of this group.

3. Schiffneriolejeunea Verdoorn, Ann. Bryol. **6:** 89. 1933; Gradstein, J. Hattori Bot. Lab. **38:** 333. 1974. Type. *Schiffneriolejeunea omphalanthoides* Verdoorn. Genus named after Victor Schiffner, well-known Austrian hepaticologist.

Phragmilejeunea Schuster, J. Hattori Bot. Lab. **11:** 27. 1954. Type. *Phragmilejeunea pappeana* (Nees) Schuster (= *Schiffneriolejeunea pappeana* (Nees) Gradst.).

Plants 1–4 cm long × 1–2 mm wide, green to glossy brown when alive, usually brown when dry, creeping or ascending (rarely pendent: *S. omphalanthoides* from Asia). *Branching Lejeunea*-type, occasionally *Frullania*-type, flagelliform branches lacking. *Stems* rigid, dorsal epidermal cells larger than medulla and ventral epidermal cells, all cell walls thickened, with brownish pigmentation in the epidermis, medulla colorless; ventral merophyte 4–8 cell rows wide. *Leaves* convoluted when dry, apex rounded, margins entire; leaf cells elongate, trigones cordate, intermediate thickenings scarce to frequent, one per wall, oil bodies coarsely segmented, *Calypogeia*-type, ca. 3–8 per cell, ocelli lacking. *Lobules* 1/3–2/3× lobe length, sometimes reduced, inflated along the keel, flattened towards the free margin, with 1–2(–3) teeth; hyaline papilla positioned on the inner side of the lobule near the proximal base of the first tooth. *Underleaves* with entire margins, bases usually decurrent, insertion line curved; underleaf base at the rhizoid disc bistratose. *Androecia* on elongated shoots with 5–25 series of bracts, bracts slightly smaller than leaves, lobules enlarged and saccate, hypostatic, underleaves present throughout; antheridia 2–3 per bract. *Gynoecia* without subfloral innovations, pseudo-innovations lacking, bracts in 2–3 series, larger than leaves, keel unwinged, lobes usually with acute-acuminate apex, margins entire, lobules large, more than 1/2× lobe length, bracteoles undivided or short bifid, margins entire. *Perianths* with 4–6 smooth or slightly notched keels. *Sporophyte:* seta articulate; elaters 34 (?) per capsule; otherwise as in the tribe. *Vegetative reproduction* by regeneration from leaf cells.

Distribution. The genus *Schiffneriolejeunea* is pantropical in distribution and contains fourteen species, two of which occur in the neotropics (Gradstein, 1985a). Tropical Africa is the center of diversity with eight species. The neotropical species of *Schiffneriolejeunea* occur in lowland and submontane areas, up to 700(–1300) m. They are usually epiphytic and grow on bark or rotten wood in rather mesic or dry woodlands and scrub, at forest edges and on shrubs in savannas.

Schiffneriolejeunea is a well-defined genus, recognized by its brown color, lack of innovations, absence of a stem hyaloderm, coarsely segmented oil bodies, and a perianth with usually two short, rounded ventral keels. The perianth keels vary somewhat in this genus. In *S. amazonica* and its African relative *S. occulta* they are long and sharp; in the species of the section *Pappeanae* (Africa) they are reduced and perianths are cylindrical-eplicate (Gradstein & VandenBerghen, 1985). The articulate seta is another unusual feature of *Schiffneriolejeunea*.

Schiffneriolejeunea is most closely related to *Mastigolejeunea*, from which it differs mainly by its gynoecium. The stiffly suberect rather than convoluted leaves of the latter in the dry state, is a good character to separate the two when gynoecia are lacking. Moreover, plant color in *Mastigolejeunea* is usually different (see discussion under *S. polycarpa*).

Key to the Species of *Schiffneriolejeunea*

1. Leaf lobule narrow rectangular, 1/2–3/5x lobe length, with 2 teeth; perianth with 4 sharp keels extending over more than 1/2 of perianth length; beak of perianth 7–10 cells long; lobule of inner female bract as long as lobe; Amazonia, Guianas, in the canopy of lowland rain forest and in scrub. . . . . 1. *S. amazonica.*
1. Leaf lobule ovate, 1/3–1/2x lobe length, with 1(–2) teeth; perianth near apex with 4–5 short, broadly rounded keels; beak of perianth 2–3 cells long; lobule of inner female bract shorter than lobe; ventral merophyte 5–8 cell rows wide; widespread (but mainly in coastal areas). . . . . 2. *S. polycarpa.*

1. Schiffneriolejeunea amazonica Gradstein, Beih. Nova Hedwigia **80:** 25. 1985. Type. Bolivia. Beni: 22 km NW of Guayaramerín, along road to Cachuela Esperanza Forest, *Reese 12815* (holotype, U; isotypes, INPA, LAF, NY).

Autoicous. *Plants* 1–2 cm long x 1–1.5 mm wide, dull brown to blackish when dry, creeping. *Branching* irregularly pinnate, *Lejeunea*-type. *Stems* up to 0.1 mm in diam.; ventral merophyte four cell rows wide. *Leaves* subimbricate, when dry suberect and appressed to the stem (not convoluted), when moist obliquely spreading, dorsal lobe plane, ovate-oblong, up to 0.9 x 0.55 mm, apex rounded, ventral margin plane, forming a very wide angle with the keel; leaf cells in midleaf ca. 30–40 x 20 μm, trigones well-developed, intermediate thickenings rare; oil bodies not observed. *Lobules* large, never reduced, 1/2–3/5x lobe length, narrow rectangular, up to 0.55 x 0.2 mm, apex truncate, with 2 teeth, first tooth 2–3 cells long, second tooth similar or shorter, sometimes merely a bluntish angle. *Underleaves* imbricate, (sub)quadrate. 0.35–0.4 mm wide, 4x stem width, apex truncate, plane, bases rather broad and slightly decurrent, insertion line shallowly curved. *Androecia* terminating elongated branches, bracts in 5–8 series. *Gynoecia* with 2–3 series of bracts, inner bracts obliquely spreading, sharply keeled and boat-shaped over 2/3 of length, lobe asymmetrically oblong, up to 1.3 mm long, lobule about as long as the lobe but narrower, both lobe and lobule with acute-acuminate apex and entire margins; inner bracteole as long as the bracts, oblong, tapering to a short bifid apex, incision very narrow, the two segments overlapping. *Perianths* immersed, pyriform with retuse apex, up to 0.8 mm long, somewhat inflated, with 4 long, sharp keels which are narrowly winged (1–2 cells wide) and irregularly notched to subentire above; beak conspicuous, 7–10 cells long. *Sporophyte* not observed.

Distribution (Fig. 20). Amazonia, Guianas; in lowland areas only. Although occurring throughout the vast Amazonian basin, *Schiffneriolejeunea amazonica* is only known from a few collections. The species seems to be exclusively epiphytic and grows on small trees and saplings in rather dry woodlands, scrub (caatinga) and savannas of inner Amazonia. In the Guianas the species seems to have a somewhat different ecology and has only been found in the crowns of mature rain forest trees.

Specimens examined. SURINAME. NICKERIE: Kabalebo Dam Project area, *Bekker 1631c* (U).

FRENCH GUIANA. Saül, *Montfoort & Ek 13* (U).

PERU. LORETO: Laguna Quistococha near Iquitos, *Hegewald 6357* (U, hb. Hegewald).

BRAZIL. AMAZONAS: Manaus-Caracarai Road km 45, *Prance et al. 11372* (INPA, LAF, NY, U). **RONDONIA:** near first rapids on Rio Pacaás Novos, *Reese 13562* (INPA, LAF, NY, U).

BOLIVIA. The type specimen.

Schiffneriolejeunea amazonica is distinguished from *S. polycarpa* by the characters mentioned in the key. By its sharply keeled female bracts, with lobe and lobule of equal length, and the sharply 4–keeled perianth *S. amazonica* closely resembles *S. occulta* (Steph.) Gradst. from West Africa. The latter species, however, has shorter lobules with only one tooth, broader leaves and female bracts, and obtuse bract apices (acute-acuminate in *S. amazonica*). The two species constitute an Afro-American species pair and occupy a rather isolated position within the genus *Schiffneriolejeunea* (Gradstein, 1985a).

2. Schiffneriolejeunea polycarpa (Nees) Gradstein, J. Hattori Bot. Lab. **38:** 335. 1974; *Jungermannia polycarpa* Nees *in* Martius, Fl. Bras. **1 (1):** 350. 1833; *Phragmicoma polycarpa* (Nees) Nees, Syn. Hep. 295. 1845; *Pty-*

chocoleus polycarpus (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 405. 1877; Evans, Bull. Torrey Bot. Club **35:** 162, Pl. 7. 1908; *Marchesinia polycarpa* (Nees) Kuntze, Revis. Gen. Pl. 2: 837. 1891; *Lejeunea polycarpa* (Nees) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 116. 1884; *Acrolejeunea polycarpa* (Nees) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893. Type. Brazil. Minas Gerais: *Martius s.n.* (holotype, STR; isotypes, B, BR,M, S,W) Fig 19.

Phragmicoma juliformis Nees var. ß, Syn. Hep. 298. 1845, nom. inval. Material. Brazil. Serra dos Orgãos, *Martius s.n.* (STR).

Lejeunea dominghensis Taylor, London J. Bot. **5:** 389. 1846; *Ptychocoleus dominghensis* (Taylor) Stephani, Spec. Hep. **5:** 33. 1912 ("*domingensis*"); *Acrolejeunea dominghensis* (Taylor) Bonner, Index Hep. 2: 17. 1963 ("*domingensis*"); *Acro-Lejeunea linguaefolia* sensu Spruce 1884, non Taylor 1846. Type. Dominican Republic. *Persoon s.n.,* 1813 (holotype, FH-TAYL; isotypes, BM, S, W).

Phragmicoma polycarpa Nees var. *liebmanniana* Gottsche, Mex. Leverm. 173. 1863. Type. Mexico. *Liebmann s.n.* (BM, C, W).

Phragmicoma caldana Aongstrøm, Öfvers, Föfh. Kongl. Svenska Vetensk.-Akad. **33:** 83. 1876. Type. Brazil. Caldas: *Windgren s.n.* (holotype. S).

Ptychocoleus multiflorus Stephani, Spec. Hep. **5:** 36. 1912; *Acrolejeunea multiflora* Stephani *in* Massalongo, Rev. Bryol. **38:** 10. 1911, nom. inval. Type. Brazil. São Paulo: along river Tieté near Salto de Ytù, *Mazzucchelli s.n.* (holotype, G).

Autoicous or dioicous. *Plants* up to 4 cm long × 1.5 mm wide, green to brownish green when alive, dull olive to dark or reddish brown when dry, creeping in mats. *Branching* irregularly pinnate, *Lejeunea*-type or *Frullania*-type, the *Frullania*-type branches always long and vegetative. *Stems* 0.12–0.2 mm in diam., in cross section composed of 15–22 epidermal cells surrounding 30–40 medullary cells, epidermis asymmetric, dorsal epidermal cells larger and often thinner-walled than ventral epidermal cells, medullary cells similar in size to the ventral epidermal cells, all cell walls thickened, walls of the epidermis usually brown (especially ventrally), inner walls colorless ; ventral merophyte 5–8 cell rows wide. *Leaves* imbricate, when dry suberect and convoluted, when moist widely spreading and convex, sometimes slightly squarrose, dorsal lobe ovate-suborbicular, 0.7–1.3 × 0.5–1.0 mm, apex rounded or obtuse, plane or narrowly recurved, ventral margin plane or slightly incurved, forming a wide angle of ca. 130–160° with the keel; leaf cells in mid-leaf ca. 20–30 × 14–18 μm, trigones small or large, intermediate thickenings frequent; oil bodies (Schuster, 1992) coarsely segmented, mostly 5–8(–9) in median leaf cells, ca. 3–3.5 × 6–7.5 μm, colorless. *Lobules* occasionally reduced, when well-developed 1/3–1/2 × lobe length, ovate to ovate-triangular, up to 0.5(–0.6) × 0.35(–0.45) mm, keel arched, apex oblique, with 1–2 teeth, first tooth 1–2 cells long, second tooth smaller or lacking. *Underleaves* contiguous to imbricate, flat or gibbose, transversely obovate-obdeltoid, 0.3–0.45 mm long × 0.5–0.8 mm wide, ca. 4× stem width, apex truncate or rounded, plane or slightly recurved, bases cuneate-decurrent, insertion line curved. *Androecia* terminal or intercalary on elongated branches, bracts in 5–15(–25) series, bracteoles usually recurved-subsquarrose. *Gynoecia* with 2–3 series of bracts, inner bracts obliquely spreading and squarrose distally, bluntly keeled over 1/2–2/3 of length, lobe ovate-oblong, up to 1.5 mm long, apex acute-acuminate, lobule ovate-lanceolate, ca. 3/4 × lobe length, apex acute-acuminate; inner bracteole shorter than the bracts, ovate-oblong, up to 1.3 mm long, apex short bifid to rounded entire, when bifid the two segments acute-acuminate, not overlapping. *Perianths* immersed or emergent to 1/3, up to 1.5 mm long, obovate with rounded apex, inflated, near apex with 4–5 short, broadly rounded, smooth keels: 2 lateral, 1–2 ventral and 1 dorsal; beak short, 2–3 cells long. *Sporophyte* as in the genus.

Distribution (Fig. 20). Tropical America, tropical Africa, Sri Lanka, southern India, at rather low elevations (up to 1600 m in Colombia and Venezuela). In tropical America, Schiffneriolejeunea polycarpa has a very disjunct distribution. It is rather common species in northern and southeastern portions of the neotropics (Mexico, Greater Antilles, SE Brazil) but in the humid, equatorial neotropics the species is lacking or very rare. *Schiffneriolejeunea polycarpa* is a xero-tolerant epiphyte and grows on bark and rotten wood in disturbed rain forest, in rather dry woodlands and scrub, on roadside trees and in plantations. Its preference for dryer areas may be

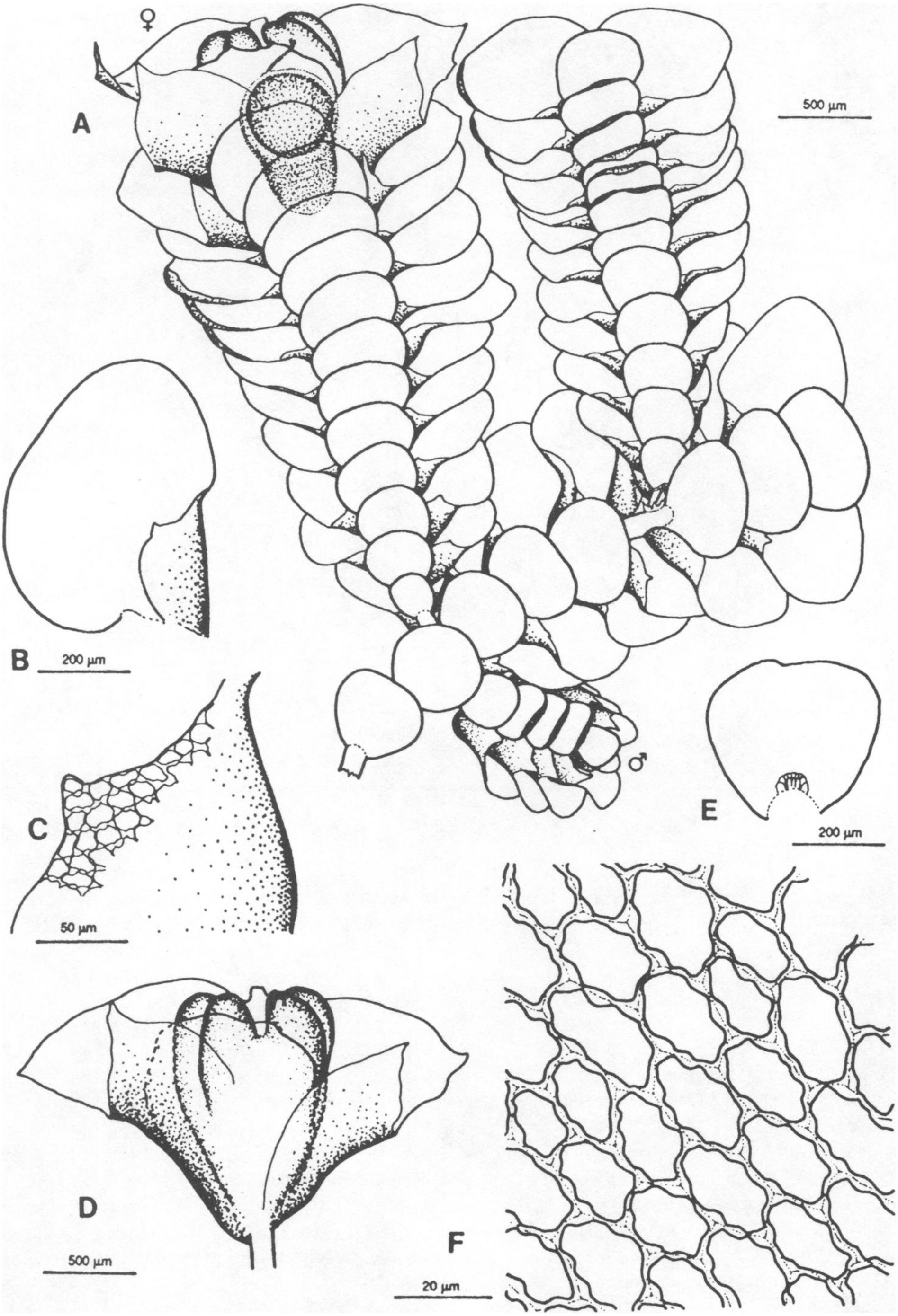

FIG. 19. *Schiffneriolejeunea polycarpa*. **A.** Habit, with androecial and gynoecial branch. **B.** Leaf. **C.** Lobule apex. **D.** Gynoecium. **E.** Underleaf. **F.** Leaf cells. From Brazil, *Vital 2591*.

FIG. 20. Distribution of *Schiffneriolejeunea amazonica* (stars) and neotropical distribution of *S. polycarpa* (dots).

reason why the species is almost lacking in equatorial areas.

Selected specimens examined. MEXICO. **CHIAPAS:** near Pueblo Nuevo NE of Tuxtla-Gutiérrez, *Sharp et al. 4015* (TENN); Agua Azul falls, *Gradstein 8251, 8254, 8257* (U). **OAXACA:** between Tuxtepec and Chiltepec, *Clayton B483* (F). **TAMAULIPAS:** above Gomez Farias, *Iwatsuki & Sharp 4639* (TENN). **VERACRUZ:** Catemaco, *Eggers & Frahm MX161* (U), *Sharp 15 p.p.* (TENN); Huatusco, *Hale & Söderström 19447* (US). Iicaltepec, *Liebmann 415* (C, W).

BELIZE. *Hunt s.n.*, 1910 (BM).

HONDURAS. **ATLÁNTIDA:** Lancetilla valley near Tela, *Standley 54384, 55255* (JE).

COSTA RICA. **LIMÓN:** along road Limón-Cahuita, *Sipman 12298b* (U).

CUBA. **ORIENTE:** Gran Piedra, *Samek et al. s.n.*, 1968 (PRC, U), *Pócs & Reyes 9097, 9111* (EGR, HAC); Sierra Maestra, Pico Turquino, *Pócs 9085/f* (HAC); Alto de Villalón, *Pócs & Caluff 9163/AB* (EGR, HAC, U).

JAMAICA. Vinegar Hill, *Evans 596* (B, BM, CINC, F, PC); Hardware Gap, *Griffin 21766* (FLAS, U); Castleton Gardens, *Griffin 21755* (FLAS, U).

DOMINICAN REPUBLIC. Without loc., *Duss s.n.* (BM), *Eggers s.n.* (BM); La Vega, Piedra Blanca near Jarabacoa, *Steere s.n.* (NY).

PUERTO RICO. Luquillo Mts., foot of Mt. El Toro (west side), *Gradstein s.n.* (U).

WINDWARD ISLANDS. DOMINICA: Without loc., *Elliott 1600* (BM). **MARTINIQUE:** Without loc., *Perrottet s.n.* (BM).

COLOMBIA. **CASANARE:** Sácama, *Aguirre & Gradstein 3106* (COL, U). **META:** Villavicencio, *Rangel 1967* (COL, U).

VENEZUELA. **DISTR. FEDERAL:** Caracas, *Moritz s.n.* (BM). **MERIDA:** Tovar, Laguna de Mariño, *Griffin & López PV-772* (NY).

TRINIDAD. Without loc., *Crüger s.n.* (BM).

GUYANA. Kanuku Mts., Maipama, *Jansen-Jacobs 1236* (U).

SURINAME. Rust en Werk, *Wullschlägel s.n.* (C).

BRAZIL. BAHIA: ex hb. Hampe (BM); Cravolandia, *Vital 6529, 6533* (SP, U); Serra da Agua de Rega, *Irwin et al. 31088, 31126* (NY, U). ESPÍRITO SANTO: Jacaraipé, *Schäfer-Verwimp 11570* (hb. Schäfer-Verwimp, U). GOIAS: Chapada dos Veadeiros, *Irwin et al. 33228* (NY, U). MINAS GERAIS: Caldas, *Lindberg s.n.* (S); road Capelinha-Malacacheta 9 km, *Vital 6513* (SP, U). RIO DE JANEIRO: Mt. Corcovado, *Lindman B15* (B, M, S), *Mosén 246* (F, S, W); Serra d'Estrella, *Beyrich 21* (S); Mun. Itatiaia, *Vital 8833* (SP, U). RIO GRANDE DO SUL: Canoas near Porto Alegre, *Lindman B74* (BM, S, UPP). SANTA CATARINA: Blumenau, *Ule s.n.* (BM); Sao Francisco, *Ule 10* (BM). SÃO PAULO: near São Bernardo, *Schiffner 2365* (W); Itapecirica, *Schiffner 1738* (W); along Rio Branco near Santos, *Schiffner 1933* (UPP, W); Itapetininga, *Schiffner 2188* (UPP, W); along road Cotia-Ibiuna, *Vital 2591* (SP, U); Reserva Biológica de Mogi Guaçu, *Vital 2667* (SP, U); near Brotas, *Vital 2701* (SP, U); Mun. Cananéia, *Vital 6746, 7039* (SP, U).

PARAGUAY. CORDILLERA: SE of Caacupé, *Geissler 14154* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

When fertile, *Schiffneriolejeunea polycarpa* is readily recognized by its gynoecium without innovations, sharply acute-acuminate female bracts, and a perianth with broadly rounded keels in the upper 1/4: two lateral keels, one ventral keel and sometimes a dorsal keel. A grove extending downwards from the apex usually splits the ventral keel into two, making the total number of keels four or five according to whether the confluent ventral keels are counted as one or two. Evans (1908) recorded the occasional occurrence of a sixth keel. The inner female bracteole in *S. polycarpa* is normally short bifid but may occasionally become rounded-entire (e.g., in the type of *Ptychocoleus multiflorus* Steph.). Entire female bracteoles have also been observed in African and Asiatic populations, which seem to exhibit this character more often than the neotropical populations. Transitions between bifid and entire bracteoles do occur (e.g., Brazil, *Vital 2591)* but are rare. One might, therefore, treat the plants with entire female bracteoles as a separate variety.

When gynoecia are lacking, *Schiffneriolejeunea polycarpa* may be confused with *Mastigolejeunea*. *Schiffneriolejeunea polycarpa* is normally readily recognized from the latter by its glossy brown to reddish brown color, *Mastigolejeunea* being green to darkish brown to black. *Mastigolejeunea*, furthermore, has somewhat longer, ovate-oblong leaves, which are flattened suberect when dry and often falcate when moist.

4. Mastigolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; *Lejeunea* subgen. *Mastigolejeunea* sect. *Trigonolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 100. 1884. Lectotype (Evans, 1907a). *Mastigolejeunea auriculata* (Wilson) Schiffner. Genus named for its flagelliform branches.

Plants up to 5 cm long × 1.5–2(–2.5) cm wide, somewhat glossy deep green to dark green when alive, usually becoming blackish or dark brown on age, creeping or ascending. *Branching Lejeunea*-type, short curved flagelliform branches frequently present. *Stems* rigid, with a partial hyalodermis, dorsal epidermal cells larger and somewhat thinner-walled than medulla and ventral epidermal cells (a full hyalodermis present in *M. recondita* from Asia), all cells walls thickened, usually with brownish pigmentation in the epidermis only, medulla colorless; ventral merophyte 5–10 cell rows wide. *Leaves* imbricate, when dry suberect-appressed to the stem and flattened with the apex visible in dorsal view, when moist widely spreading and often somewhat falcate, weakly to strongly convex and sometimes subsquarose, lobe ovate to oblong, apex rounded to obtuse (acute in some palaeotropical species), margins entire, dorsal base auriculate; leaf cells elongate, trigones usually coarse, cordate, intermediate thickenings scarce to frequent, one per wall, oil bodies segmented, ca. 3–8 per cell, ocelli lacking. *Lobules* 1/4–1/2× lobe length, never reduced, inflated along the keel, free margin usually plane, occasionally inflexed, mostly with only one tooth, a few species with several teeth; hyaline papilla positioned on the inner side of the lobule near the proximal base of the first tooth. *Underleaves* imbricate, often somewhat squarrose, obdeltoid with truncate apex and entire margins, gibbose, bases cuneate, slightly auriculate, insertion line straight or shallowly curved; underleaf base at the rhizoid disc bistratose. *Androecia* on short or long shoots with

5–25 series of bracts, bracts smaller than leaves, lobules enlarged, hypostatic (epistatic in some palaeotropical species), underleaves present throughout; antheridia (1–)2 per bract. *Gynoecia* with 1–2 lejeuneoid subfloral innovations, bracts in 1(–3) series, as large as or slightly larger than leaves, with rounded to acute apex and entire margins, lobules 1/3–3/4x lobe length, keel normally without wing (a small wing in *Mastigolejeunea calcarata* from Australasia), bracteoles undivided or emarginate, margins entire. *Perianths* flattened or inflated, with 3 rather sharp keels or with up to 10 plicae by the development of accessory folds, keels smooth. *Sporophyte*: seta not articulate; elaters 72 per capsule; otherwise as in the tribe. *Vegetative reproduction* by regeneration from leaf cells on dorsal leaf surfaces.

Distribution. The genus *Mastigolejeunea* is pantropical and contains about fifteen species, three of which occur in the neotropics. The center of diversity is Southeast Asia with nine species (Gradstein, 1991). The neotropical species occur in lowland and submontane regions, up to about 1500 m in the Andes. They usually grow on bark in primary or disturbed rain forest, in scrub or in plantations, and are xerotolerant.

Mastigolejeunea is closely related to *Thysananthus* from which it differs by the enlarged epidermal cells and the untoothed female involucre. The genus is also related to *Schiffneriolejeunea*; for affinities with the latter see under *S. polycarpa*.

Mastigolejeunea furthermore resembles *Frullanoides*. Both have a blackish color and a similar leaf areolation and may therefore be confused. Habitually, the two genera can easily be separated, however, by the position of the leaves in the dry state. In *Mastigolejeunea* they are rather flatly appressed against the stem when dry, with the apical portion plane and clearly visible in dorsal view. In *Frullanoides* the leaves are distinctly wrapped around the stem when dry. *Frullanoides* is furthermore recognized by its thin-walled epidermis ("hyalodermis"), lobule with many teeth, winged female bracts, epistatic male bracts, homogeneous oil bodies, rounded underleaf apices (usually truncate in *Mastigolejeunea*), etc.

All species of *Frullanoides*, moreover, have pluriplicate perianths whereas *Mastigolejeunea* perianths are mostly trigonous and more rarely pluriplicate. The only neotropical species of *Mastigolejeunea* with a pluriplicate perianth is *M. plicatiflora*. *Mastigolejeunea nigra* from eastern Africa and *M. undulata* and *M. recondita* from eastern Malesian are palaeotropical species with pluriplicate perianths. Except for *M. recondita* (which has a full hyalodermis and lacks blackish pigmentation), the pluriplicate species of *Mastigolejeunea* are essentially similar to the trigonous ones. Moreover, perianths with subsidiary folds may sometimes occur in species which normally produce triplicate perianths (see Thiers & Gradstein, 1989). Schuster (1963) and Gradstein (1975) have created a separate section to accomodate the species with pluriplicate perianths (*M.* section *Nigrae* Schust. = *M.* sect. *Brachiolejeuneoides* (Verdoorn) Gradst.), but I now believe that, with the exception of *M. recondita*, there isn't a good reason to classify the pluriplicate species in a separate section. This matter should be further considered in the framework of a world-wide revision of the genus *Mastigolejeunea*.

Key to the Species of *Mastigolejeunea*

1. Lobule of stem leaves with 2–3 distinct teeth; androecia usually on short, specialized male branches, the male bracts small throughout the spike, 1/2x leaf length or less; Amazonia, Guianas, rare. . . 2. *M. innovans.*
1. Lobule of stem leaves with only one distinct tooth; androecia terminal or intercalary on elongated, unspecialized branches, the male bracts more than 1/2x leaf length, at base of spike larger than at apex; throughout tropical America.
    2. Perianth with a sharp ventral keel, subsidiary folds lacking; leaves ovate-oblong, 1.2–1.5(1.7)x longer than wide, concave with upcurved ventral margins; underleaves usually concave and somewhat squarrose; autoicous or dioicous; widespread but lacking in Amazonia. . . . . . 1. *M. auriculata.*
    2. Perianth with a swollen, rounded ventral keel and with subsidiary folds; leaves oblong, 1.5–2x longer than wide, rather flat with plane ventral margins; underleaves flat; dioicous; rain forest areas of northern S America (Amazonia, Guianas, etc.). . . . . 3. *M. plicatiflora.*

1. Mastigolejeunea auriculata (Wilson) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3)**: 129. 1893; Schuster, Hep. Anth. N. America IV: 729, Figs. 646, 647. 1980; *Jungermannia auriculata* Wilson *in* Drummond, Musci Amer. Exsicc. (Southern States) nr. 170. 1841; *Lejeunea auriculata* (Wilson) Sullivant *in* Gray, Manual Bot. (ed. 2) 699. 1856; *Ptychocoleus auriculatus* (Wilson) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 405. 1877; *Marchesinia auriculata* (Wilson) Kuntze, Revis. Gen. Pl. 2: 837. 1891; *Phragmicoma versicolor* Lehmann & Lindenberg, Syn. Hep. 297. 1845, nom. superfl. Type. "On Trees, New Orleans and Louisiana," *Drummond, Musci Americani (Southern States) 170* (holotype, BM; isotypes, MANCH, PC). Fig.21.

The authority of the basionym is sometimes cited as "Wilson & Hooker" but Sayre (1971) has pointed out that Wilson was the actual author of the new bryophyte species published in Drummond's exsiccatae.

Phragmicoma teretiuscula Lindenberg & Gottsche, Syn. Hep. 745. 1847; *Marchesinia teretiuscula* (Lindenberg & Gottsche) Kuntze, Revis. Gen. Pl. 2: 837. 1891; *Mastigolejeunea teretiuscula* (Lindenberg & Gottsche) Stephani, Spec. Hep. **4:** 756, 766. 1912. Type. Mexico. "fructifera...ad Colipa, Mirador et Zacuapam," *Liebmann s.n.*, with gynoecia (syntypes, W-hb. Lindenberg 6000, 6002, 6004; isosyntypes, C, PC).

A sterile specimen from the East Indies, ex hb. Wight (W, not studied) was also cited in the protologue. Whether that specimen belongs to *M. auriculata* remains to be investigated.

Phragmicoma humilis Gottsche, Syn. Hep. 299. 1845; *Ptychocoleus humilis* (Gottsche) Trevisan, Mem. Reale Ist. Lomb. Mat. Nat. ser. 3, **4:** 405. 1877; *Lejeunea humilis* (Gottsche) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 101. 1884; *Mastigolejeunea humilis* (Gottsche) Schiffner in Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; Mizutani, J. Hattori Bot. Lab. **61:** 281-283, Fig. 1. 1986. Type. Indonesia. Java. *Junghuhn s.n.* (isotypes, G, W).

Phragmicoma salvadorica Aongstrøm, Öfvers, Förh. Kongl. Svenska Vetensk.- Akad. **33:** 83. 1876. Type. San Salvador, *Hjalmarsson s.n.* (holotype. S).

Phragmicoma carinata Mitten, Phil. Trans. Roy. Soc. London **168:** 398. 1879; *Mastigolejeunea carinata* (Mitten) Stephani, Spec. Hep. **4:** 759. 1912; VandenBerghen, Bull. Jard. Bot. Bruxelles **19:** 378, Fig. 33. 1949. Type. Africa. Rodriguez I., *Balfour s.n.* (holotype, NY).

Mastigolejeunea boliviensis Stephani, Spec. Hep. **4:** 764. 1912. Type. Bolivia. "Andes or.," Quebrada de Cuñucú, ca. 700 m, *Herzog 5863* (holotype, G), *syn. nov.*

Mastigolejeunea crispula Stephani, Spec. Hep. **4:** 1912. Type. Nigeria. Alt Calabar, *Moenkemeyer N16* (G).

Mastigolejeunea cruegeri Stephani, Spec. Hep. **4:** 764. 1912. Type. Trinidad. *Crüger s.n.* (holotype, G), *syn. nov.*

Mastigolejeunea cubensis Gottsche ex Stephani, Spec. Hep. **4:** 765. 1912. Type. Cuba. *Wright s.n.* (syntype, G; isosyntype, NY), *syn. nov.*

Mastigolejeunea pittieri Stephani, Spec. Hep. **4:** 766. 1912. Type. Costa Rica. Boruca, *Pittier & Durand 6070* (holotype, G), *syn. nov.*

Mastigolejeunea subvirens Stephani, Spec. Hep. **4:** 763. 1912; *Lejeunea auriculata* (Wilson) Sullivant var. *virens* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 102. 1884; *Mastigolejeunea auriculata* (Wilson) Schiffner var. *virens* (Spruce) Schiffner, Hedwigia **33:** 185. 1894. Type. Peru. San Martín: Mt. Guayrapurina, *Spruce L502* (lectotype, G, here designated; isolectotype, MANCH). Brazil. Pará: Rio Guaniá, *Spruce L502* (paralectotype, MANCH), *syn. nov.*

Mastigolejeunea innovans (Spruce) Stephani var. *parciflora* Herzog, Rev. Bryol. Lichénol. **20:** 132, 133. 1951 (var. "*latistipula*" Herzog in sched.). Type. Honduras. Atlantida: Lancetilla valley, near Tela, *Standley 55342 p.p.* (holotype, JE), *syn. nov.*

Autoicous or dioicous. *Plants* up to 5 cm long x 1.5–2(–2.5) mm wide, deep green to dull brown to blackish. *Stems* 0.15–0.25 mm in diam., in cross section composed of 15–30 epidermal cells surrounding 30–70 medullary cells, dorsal epidermal cells 1.5–3x larger than other stem cells; ventral merophyte 5–10 cell rows wide. *Leaves* when moist weakly to strongly convex, sometimes crisped, dorsal lobe oblong-ovate, 0.8–1.4 x 0.6–0.9 mm, 1.2–1.5(-1.7)x longer than wide, apex rounded or obtuse, plane, ventral margin often tilted vertically and upcurved to become hollow, sometimes plane, forming a wide angle or straight line with the keel; leaf cells in mid-leaf 25–40 x 15–25 μm, trigones usually coarse, intermediate thickenings usually scarce; oil bodies finely segmented, 2–4 per cell, large, 4–10 x 3–4 μm, ellipsoid to globose. *Lobules* plane or inflated, ca. 1/4–1/2x lobe length, subquadrate to ovate-rectangular, 0.3-0.5 x 0.2–0.3 mm, free margin plane or incurved, angled near the short (1–2 cells long) apical tooth, apex truncate or oblique, when oblique short or long continuing into the ventral leaf margin. *Underleaves* densely imbricate, usually concave and somewhat squarrose, broadly obdeltoid, 0.5–0.6 mm long x 0.55–0.8 mm wide, 3–4x stem width, apex plane or recurved, bases slightly auriculate. *Androecia* terminal or intercalary on non-specialized, elongated branches, bracts and bracteoles in 4–15 series, at base of spike about as large as leaves, becoming smaller towards spike apex (2/3x leaf

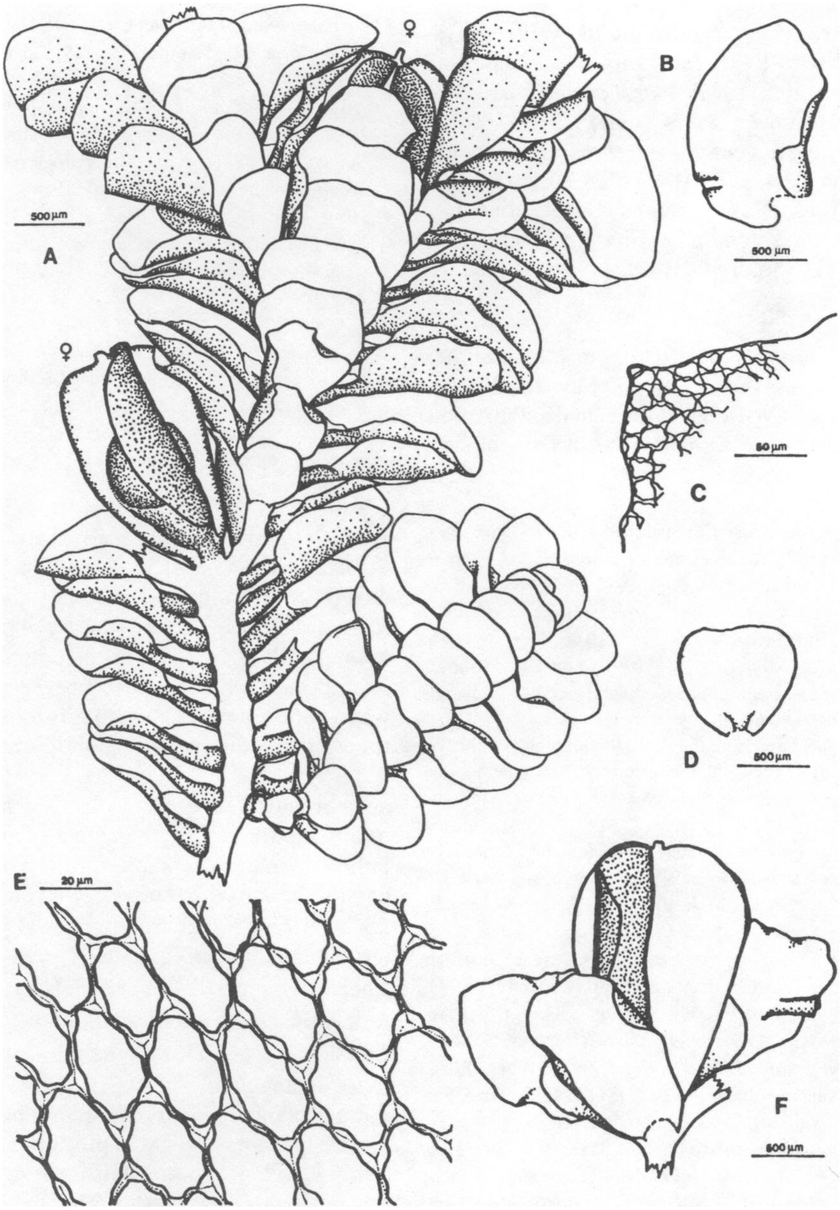

FIG. 21. *Mastigolejeunea auriculata.* **A.** Habit, with gynoecia and fertile innovation; note lejeuneoid leaf sequence of the innovation (first leafy appendage is lateral leaf). **B.** Leaf. **C.** Lobule apex. **D.** Underleaf. **E.** Leaf cells. **F.** Gynoecium. From Brazil, *Lisboa et al. 2535.*

size), lobules 2/3× lobe length, rather loosely imbricate. *Gynoecia* with 1(–2) subfloral innovations, innovations usually repeatedly fertile and gynoecia often in seriate arrangement, bracts in one series, erect or obliquely spreading to subsquarrose, lobe ovate-oblong, 1–1.5 mm long × 0.5–0.8 mm wide, apex obtuse to acute, lobule 1/2–3/4× lobe length, apex variable, obtuse to

FIG. 22. Neotropical distribution of *Mastigolejeunea auriculata* (triangles) and distribution of *M. plicatiflora* (dots).

broadly rounded to truncate; bracteole almost as long as the bracts, flat or squarrose, often gibbose, obovate-oblong, apex rounded to shallowly emarginate. *Perianths* immersed or emergent to 1/3, up to 1.5 mm long, obovate to cylindrical, flattened, sharply 3-keeled with one narrow, high ventral keel, keels smooth or irregularly and bluntly toothed-winged; beak short, 2–3 cells long. *Sporophyte* as in the genus.

Terpenoids: the sesquiterpene alloaromadendrene has been detected as the major component of this species (Gradstein et al., 1985: as *Mastigolejeunea humilis*, coll. *Gradstein 3836*).

Distribution (Fig. 22). *Mastigolejeunea auriculata* is a common pantropical species and has been described under many different names. In Africa the species has been known as *M. carinata* (Mitt.) Steph. and in Southeast Asia as *M. humilis* (Gott.) Schiffn. Its neotropical range is from sea level to about 1500 m and somewhat discontinuous. The species occurs throughout the coastal plain of southeastern United States, Central America and the greater Antilles, but lacks in the lesser Antilles. In South America *Mastigolejeunea auriculata* occurs in the northernmost regions bordering the Caribbean, along the Andes, in central and southern Brazil and in Paraguay. The species is almost entirely lacking, however, in the rain forest regions of the Amazon and Orinoco basins, where is it is replaced by *M. plicatiflora*.

Mastigolejeunea auriculata prefers rather open, sunny habitats and is largely lacking in shaded rain forest habitats. It grows on bark in the canopy, in gaps and at the edges of evergreen forests, in dry scrubby vegetations and coastal bushes, and in plantations and gardens, or on rock. In the Antilles it has frequently been found on limestone and coral rock.

Selected specimens examined. MEXICO. CHIAPAS: Lacandon forest reserve along Río Lacantun, near Chajul Biological Station, *Gradstein 7941, 8098, 8161* (U); Palenque, *Gradstein 8234* (U). SAN LUIS POTOSÍ: Gamaspo, *Pringle s.n., Underwood & Cook, Hep. Amer. 99* (BM, MANCH, US, NY). VERACRUZ: S of Catemaco, *Hale & Söderström 19798, 19854, 19837* (US). YUCATÁN: Chichen Ruins 120 km E of Merida, *Underwood 106* (NY), *Eggers & Frahm MX21,3* (U).

GUATEMALA. ALTA VERAPAZ: near Secanquim, *Maxon & Hay 3205* (US).

BELIZE. Wild Cane Cay and Punta Gorda, *Robertson s.n.* (NY, U).

HONDURAS. ATLÁNTIDA: La Fragua, *Standley 55751* (NY).

NICARAGUA. El Recreo 15 W of Rama, *Danin 2-G* (MO, U).

COSTA RICA. Type of *Mastigolejeunea pittieri.*

PANAMA. DARIÉN: trail El Real to Pirre, *Salazar & Gradstein 9216* (PMA, U). PANAMÁ: Summit Garden, *Salazar & Gradstein 9497* (PMA, U).

UNITED STATES. FLORIDA. DADE: Summit Garden, *Salazar & Gradstein 9497* (PMA, U).: Everglades, numerous colls. (NY). HIGHLANDS: Highlands Hammock State Park, *Griffin 987* (FLAS, NY, U), *Thiers 3149, 3150* (NY). JEFFERSON: Wacissa Springs, *Schornherst 304* (NY, U). SEMINOLE: Sanford, *Rapp s.n., Verdoorn, Hep. Sel. Crit. 334* (BM, MANCH, NY, U). **GEORGIA.** Thomasville, *Brown s.n.* (BM, NY). **MISSISSIPPI.** N of Gulfport, *Schuster M-320* (NY). **LOUISIANA.** Bayou Alexandre, *Langlois s.n., Underwood & Cook, Hep. Amer. 133* (BM, MANCH, NY).

BAHAMA ARCHIPELAGO. NEW PROVIDENCE: Coppice, *Britton many colls.* (NY); LONG ISLAND: Galloway Landing, *Correll 48165* (NY).

CUBA. HABANA: Loma de la Candela, *Léon 19391/B* (HAC); Sierra del Rosario, *Pócs & Reyes 9042* (EGR, U); I. de Pines, *Borhidi 5937, 5952* (EGR, U). ORIENTE: Finca Guadelupe Tiguabos, *Hioram 13787* (HAC); Holguin, N of Silla de Gibara, *Pócs & Borhidi 9036, 9037* (EGR, U); Sierra de la Gran Piedra, *Pócs & Caluff 9164* (HAC); Meseta de Santa Maria de Loreto, *Pócs & Reyes 9194* (HAC, U, NY); Guantánamo, Loma Lagunato, *Reyes 9193* (EGR, HAC, U). VILLA CLARA: Sierra de Escambray, Pico Potrerillo, *Pócs & Borhidi 9010* (EGR, U).

JAMAICA. BATH: near Sulphur River, *Evans 326* (BM, US). ST. MARY: Castleton Gardens, *Griffin s.n.* (FLAS, U). ST. ELISABETH: W of Maggotty, *Buck 5862* (NY). Westmoreland Hills, *Britton 494, 495* (NY).

CAYMAN ISLANDS. LITTE CAYMAN: *Proctor 35176* (NY).

HAITI. Bayeux, *Nash 161, 168* (NY); Massif de la Hotte, *Buck 9928* (NY).

DOMINICAN REPUBLIC. Parque Nacional del Este, *Zanoni & Mejia 17076* (NY), *Buck 5116* (NY).

PUERTO RICO. Mayaguez, Heller 4462 (NY, US), *Britton & Marble 712* (NY); Loiza, *Britton et al. 5743* (NY); Dorado, *Britton et al. 6716* (US); Mona I., *Britton et al. 1680, 1681, 1690, 1693* (NY); Reserva Forestal Cambalache, *Buck 16160* (NY).

VIRGIN ISLANDS. ST. JOHN. Bethania, *Britton & Marble 243, 362* (NY); Cinnamon Bay, *Gradstein 6410, Bryoph. Neotr. Exsicc. 245* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL). **ST. THOMAS.** Bordeaux, *Reese 14229* (NY). TORTOLA: Guana I., *Proctor 46571* (NY).

COLOMBIA. RISARALDA: St. Rosa de Cabal, *van Reenen et al. 1859* (COL, U); Cartago, *van Reenen & Griffin 1930, 1937* (COL, U); Mun. San Antonio de Chami, Geguades, *Gradstein 8644* (COL, U). TOLIMA: Venadillo, *van Reenen 2440* (COL, U).

VENEZUELA. MIRANDA: Parque Nacional Guatopo, *Nee 17754* (NY). SUCRE: Río Sabacual-Guaraunos, *Griffin & Bermudez s.n.* (FLAS, U).

TRINIDAD. Saddle Road, *Britton et al. 176* (NY).

GUYANA. Moraballi Creek, near Bartica, *Richards 428* (BM); Kanuku Mts., Maipama, *Jansen-Jacobs et al. 1175, 1192* (U).

SURINAME. Paramaribo, Palmgarden, *Gradstein 4620* (U), Cultuurtuin, *Bekker 1005, 1006* (U). NICKERIE: Kabalebo Dam project area, *Bekker 1253* (U).

FRENCH GUIANA. Tampoc, Sout Koumakou Soula, *Cremers 4721* (CAY, U); Saül, *Gradstein 6086* (U).

PERU. HUANUCO: Tingo María, *Hegewald 7903* (U). JUNÍN: Villa Amoretti, *Kunkel 373* (S); road La Merced-Oxapampa km 3, *Hegewald 8529* (U). LORETO: Pucallpa, *Hegewald 8243* (U). SAN MARTÍN: Tarapoto, *Spruce L179* (MANCH, US), cataractas de Ahashiyacu, *Gradstein 1826* (B, U); road Yurimaguas-Tarapoto km 95, *Frahm et al. 1684* (B, U), km 112, *Frahm et al. 1790* (B, U).

BRAZIL. DISTRICT FEDERAL: Sobradinho, *Irwin et al. 33237, 33240* (NY, U); Reserva de Aguas Emendadas, *Vital 6576* (SP, U). GOIAS: Formoso, *Vital 8518* (SP, U);. MATO GROSSO: Miranda, *Vital 2334, 2353* (SP, U); 15 km E of Bela Vista, *Vital 6445* (SP, U); Aripuaña, *Lleras & Lima P18282* (NY, U). MINAS GERAIS: Paracatu, *Vital 2635* (SP, U); Parque Florestal do Rio Doce, *Vital 8883* (SP, U). PARÁ: Obidos, *Spruce L58* (MANCH); Rio Guaniá, *Spruce s.n.* (MANCH); Monte Alegre, *Swallen 3395* (NY). RONDÔNIA: Serra dos Parecis, 27 km from Alta Floresta, Lisboa et *al. 2635, 2648* (MG, U); road Pimenta Bueno–Roulim de Moura, near Jaboti, *Lisboa et al. 2949, 2954, 2962* (MG, U); vicinity first rapids of Rio Pacaás Novos, *Reese 13561, 13593, 13655* (NY, U). SÃO PAULO: near Taipas, *Schiffner s.n.* (UPS).

BOLIVIA. BENI: vicinity Guayaramerín, *Reese 12826, 13037, 13132* (NY, U); Ballivian, Serranía del Pilón Lagas, *Gradstein 7128, 7218, 7265* (LPB, U). LA PAZ: Yolosa, *Gradstein 7070* (U); road Caranavi-San Borja km 30-40, *Gradstein 7076* U). SANTA CRUZ: Prov. Ichilo, 15 km S of Buena Vista, *Gradstein 7730* (U).

PARAGUAY. ALTO PARANA: 35 km N of Hernandarías, *Geissler 14511, 14517* (G); 80 km N of Hernandarías, *Geissler 14664* (G). AMAMBAY: Parque Nacional Cerro Corá, *Geissler 14752, 14772, 14818* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald

(1993). Material recorded from the Galapagos Islands by Clark (1953) belongs to *Dicranolejeunea axillaris*.

New World populations of *Mastigolejeunea auriculata* usually have rather strongly convex leaves, which are tilted vertically and have upcurved, sometimes undulated ventral margins. The underleaves are densely imbricate, hollow and often squarrose. Populations with rather plane leaves do occur but are less common; these plants approach *M. plicatiflora*. Differences between the two species are discussed under the latter.

Lobules of *Mastigolejeunea auriculata* are ca. 1/4–1/2× lobe length and almost flat to fully inflated. Inflated lobules typically have oblique, inflexed apical margins which continue rather longly into the ventral margin of the lobe. In plane lobules the apical margin is normally truncate, plane and ends rather abruptly at the keel. The apical tooth is always small, 1(–2) cells long and straight. Sometimes the margin is emarginate at the proximal side of the tooth and the suggestion is given of second tooth. A discrete second tooth has not been observed in *M. auriculata*, however. Spruce described a variety *virens* from South America with bidentate lobules, but the type material of this variety has lobules with only one discrete tooth. Lobules with more than one tooth are characteristic of *M. innovans*.

Innovations are normally single but in material from Mato Grosso paired innovations were frequently observed. Innovations are usually repeatedly fertile, giving rise to perianths in seriate arrangement. Strongly innovating specimens were sometimes erroneously named *Mastigolejeunea innovans*.

2. **Mastigolejeunea innovans** (Spruce) Stephani, Spec. Hep. **4:** 765. 1912; *Lejeunea innovans* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 103. 1884. Type. Brazil. Amazonas: Rio Uaupés, Panuré, "ad arborum truncos," *Spruce L42* (holotype, MANCH; isotype, BM).

Autoicous. *Plants* 2–4 cm long × 2–2.5 mm wide, dull olive-green to blackish-brown. *Stems* 0.2 mm in diam., in cross section composed of ca, 25 epidermal cells surrounding 60–70 medullary cells, dorsal epidermal cells 1.5–2x larger than other stem cells; ventral merophyte 8 cell rows wide. *Leaves* when moist strongly convex, dorsal lobe oblong-ovate, 1.1–1.4 × 0.7–0.9 mm, 1.5–1.8× longer than wide, apex rounded or obtuse, plane, ventral margin tilted vertically and upcurved to become hollow, forming a wide angle with the keel; leaf cells in mid-leaf 25–30 × 16–20 μm, trigones usually coarse, intermediate thickenings scarce; oil bodies not observed. *Lobules* inflated along the keel, 1/3–2/5× lobe length, ovate-rectangular, 0.3–0.4 × 0.2–0.25 mm, free margin plane, near apex waving and with 2–3 blunt, triangular teeth tipped by a single cell, the teeth becoming progressively smaller away from the apex, on branch lobules sometimes with only one tooth (type specimen!), apex truncate to oblique, short or continuing into the ventral leaf margin. *Underleaves* obdeltoid, 0.5–0.6 mm long × 0.6–0.8 mm wide, 3–42× stem width, apex plane, bases slightly auriculate. *Androecia* usually occupying small, specialized branches with 5–15 series of bracts and bracteoles, rarely terminating an ordinary vegetative branch, bracts small throughout the spike, 1/2× leaf length or less, lobules 2/3× lobe length, densely imbricate. *Gynoecia* with one subfloral innovation, innovations usually repeatedly fertile and gynoecia often in seriate arrangement, sometimes crowded, bracts in one series, obliquely spreading to subsquarrose, lobe oblong, ca. 1.5 mm long × 0.8 mm wide, apex rounded, lobule 1/2× lobe length, apex broadly rounded and often retuse-short bifid; bracteole almost as long as the bracts, flat, gibbose, oblong, apex truncate to shallowly emarginate. *Perianths* immersed or slightly emergent, up to 1.5 mm long, oblong, flattened, sharply 3-keeled with one narrow, high ventral keel, keels smooth or irregularly and bluntly toothed-winged above; beak short, 2–3 cells long. *Sporophyte* not observed.

Illustration. Stephani, Icones Hepaticarum Jard. Bot. Genève, Zug 1985: nr. 7403.

Distribution. Brazil (inner Amazonia), French Guiana, at elevations up to 200 m. *Mastigolejeunea innovans* is a rare species of non-flooded, virgin lowland rain forest of northern South America; probably it is a canopy epiphyte. In French Guiana (Saül) it was found on branches in the outer canopy of a *Couratari gloriosa* tree, at 30–40 m above the ground.

Specimens examined. FRENCH GUIANA. St. Jean du Maroni, *Gouverneur Rey 40 p.p.* (PC); Saül, *Montfoort & Ek 970, 971* (U).

BRAZIL. AMAZONAS: Distrito Agropecuário, Reserva 1501 ("km 41") of the WWF/INPA Project, *Boom et al. 8602* (INPA, NY).

Conservation. *Mastigolejeunea innovans* is a rare South American species of Lejeuneaceae and may be considered threatened in view of its restricted occurrence in undisturbed rain forest. There is as yet no reason to classify the species as "endangered" because it occurs in areas where deforestation is not alarming. Moreover, it may be undercollected because of its growth in the canopy of the high forest. The species was classified as rare ("at risk") by Gradstein (1992c).

Mastigolejeunea innovans is a misunderstood species. The repeatedly innovating stems, which according to Spruce would be the diagnostic feature of the species, are by no means discriminative and are also common in *M. auriculata*. *Mastigolejeunea innovans* is excellently characterized, however, by its stem leaves which have lobules with 2–3 teeth (branch leaves may have lobules with only a single tooth!) and by the small, specialized male branches.

3. **Mastigolejeunea plicatiflora** (Spruce) Stephani, Spec. Hep. **4:** 766. 1912; *Lejeunea plicatiflora* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 104. 1884. Type. Venezuela. Amazonas: San Carlos del Río Negro, "ad arbores," *Spruce, Hepaticae Amazonicae et Andinae 1543* (lectotype, MANCH 15909, here designated; isolectotypes, BM, G, W).

Dioicous. *Plants* up to 3 cm long × 2 mm wide, usually brown, not black, creeping in mats. *Stems* 0.15–0.2 mm in diam., in cross section composed of 15–22 epidermal cells surrounding 30–40 medullary cells; ventral merophyte 5–6 cell rows wide. *Leaves* when moist weakly convex, dorsal lobe oblong, 1–1.3 × 0.5–0.7 mm, 1.7–2× longer than wide, apex rounded, plane, ventral margin usually plane, rarely slightly upcurved, forming a wide angle with the keel; leaf cells as in *M. auriculata*; oil bodies not observed. *Lobules* ca. 1/5–1/3× lobe length, ovate-subrectangular, free margin plane, angled near the short (1–2 cells long) apical tooth, apex truncate or oblique, not or short continuing into the ventral leaf margin. *Underleaves* plane, broadly obdeltoid, ca. 0.5 mm long × 0.55–0.7 mm wide, 3–4× stem width, apex plane or recurved, bases slightly auriculate. *Androecia* as in *Mastigolejeunea auriculata*. *Gynoecia* with one subfloral innovation, innovations often repeatedly fertile with gynoecia in seriate arrangement, bracts in one series, erect, lobe narrow oblong, 1.3–1.7 mm long × 0.5–0.7 mm wide, apex rounded, lobule 1/2–3/4× lobe length, on average 3× longer than wide, apex rounded; bracteole about as long as the bracts, oblong, apex truncate. *Perianths* immersed or emergent to 1/3, up to 1.5 mm long, obovate to cylindrical, inflated, with a swollen, rounded, high ventral keel which tends to split into 2–3 folds, the ventral and dorsal surface of the perianth in addition often with 1–3 small subsidiary keels above, keels smooth; beak short, 2–3 cells long. *Sporophyte* as in the genus.

Illustration. Stephani, Icones Hepaticarum Jard. Bot. Genève, Zug 1985: nr. 7405.

Distribution (Fig. 22). Brazil, Venezuela, Colombia, Guianas (inland regions); from sea level up to 700 m. *Mastigolejeunea plicatiflora* is a common species of the evergreen lowland rain forests of the Amazon and Orinoco basins and the inland regions of the Guianas; it has also been found in the lowland rain forests of Bahia and northern Colombia. It apparently replaces *M. auriculata* which is virtually lacking in these rain forest areas.

Mastigolejeunea plicatiflora grows on bark in the canopy and understory of periodically inundated rain forest or upland forest (igapó, terra firme, caatinga, campina forest). The species seems to be largely restricted to virgin forest and lacks in deforested areas.

Specimens examined. COLOMBIA. MAGDALENA: Santa Marta, near Bonda, *Baker s.n.* (G, NY).

VENEZUELA. AMAZONAS: San Carlos del Río Negro, *Spruce L406* (MANCH); Cerro Neblina, Río Mawarinuma, *Buck 11069* (NY); Atabapo, base of Cerro Duda, *Thiers 5011* (NY). APURÉ: Reserva Forestal San Camilo, *Steyermark et al. 101744* (NY, VEN). BARINAS: Reserva Forestal Caparo, *Steyermark et al. 102081* (NY, VEN). BOLÍVAR: Río Caura, *Steyermark & Gibson 95792, 95793* (US).

GUYANA. UPPER MAZARUNI: Waramadan, *Gradstein 5680* (U).

SURINAME. NICKERIE: Kabalebo Dam project area, *Bekker 1068, 1557, 1579* (U)

FRENCH GUIANA. Saül, *Montfoort 1018, 1019, 1020, 1021, 1023* (U), *Gradstein 6082, 6134* (U).

BRAZIL. ACRE: near Sena Madureira, *Nelson 484, 559, 584* (NY). AMAZONAS: Maués, *Nelson 26* (FLAS, U); Manaus, in igapó, *Prance et al. 11729* (NY, U), *Griffin et* *al. 800, 802* (FLAS, U); road Manaus-Itacoatiara km 26, Ducke forest reserve, *Griffin et al. 111, 336, 350, 358* (FLAS, U); road Manaus-Caracai km 60, campina forest, *Griffin et al. 997* (FLAS, U); id. km 130, Rio Lages, *Griffin et al. 431, 455* (FLAS, U); along Rio Negro between Manaus and São Gabriel, *Schuster 7 colls.* (NY); Rio Uatumã, *Buck 2163* (NY). Bahia: Mun. Itanagra, *Boom & Mori 972* (NY). Pará: Obidos, Spruce s.n. (G); Serra do Cachimbo, *Reese 16310, 16459, 16678* (NY); Mun. Conçeiao do Araguaia, *Plowman et al. 8543* (NY). Roraima: Rio Sumuru, 214 km N of Boa Vista along Manaus-Venezuela highway, *Buck et al. 2038* (NY, U).

Mastigolejeunea plicatiflora has often been confused with *M. auriculata*. The two species are indeed rather similar morphologically although their habitats and ranges are quite distinct (see Fig. 22). Morphological differences include the rather flat underleaves and leaves with plane margins of *M. plicatiflora*, the more elongated leaves of the latter (1.5–2× longer than wide), and its perianth which has a swollen ventral keel with subsidiary folds. Furthermore, *M. plicatiflora* seems to be always dioicous, has rather small lobules (usually not more than 1/4× leaf length) and, characteristically, is brownish in color, not black. Except for the perianth, the morphological differences between the two species are not very sharp and some overlap has been found.

5. **Thysananthus** Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **8:** 24. 1844; *Lejeunea* subgen. *Thysanolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 105. 1884; *Lejeunea* subgen. *Mastigolejeunea* sect. *Thysanolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 100. 1884; *Thysanolejeunea* (Spruce) Stephani, Hedwigia **28:** 263. 1889, nom. inval.? Type. *Thysananthus comosus* Lindenberg ex Lehmann. Genus named for its brush-like shoots.

Plants rather dull olive green to brown or black, ascending or pendent, not dendroid. *Branching Lejeunea*-type, short curved flagelliform branches present. *Stems* rigid, epidermal cells as large as medulla cells, all cell walls strongly thickened and brown; ventral merophyte four or more cell rows wide. *Leaves* when dry suberect-convoluted (plane in the Asiatic subgen. *Sandeanthus*), when moist widely spreading and convex, often somewhat falcate, lobe ovate to oblong, apex rounded or acute-apiculate, margins toothed or entire, dorsal base auriculate; leaf cells elongate, with cordate trigones and intermediate thickenings (cells isodiametrical with almost evenly thickened walls in subgen. *Sandeanthus*), trigones usually coarse and often coalesced, oil bodies coarsely segmented, *Calypogeia*-type, ca. 3–10 per cell, ocelli lacking; vitta present or absent. *Lobules* usually small, 1/4× lobe length or less, never reduced, inflated along the keel, with 1–2 teeth; hyaline papilla positioned on the inner side of the lobule near the proximal base of the first tooth. *Underleaves* ± spathulate to subquadrate, often somewhat squarrose and concave due to upcurved margins, gibbose in the lower half, apex rounded to emarginate, margins toothed or entire, bases cuneate, usually slightly auriculate, insertion line straight; underleaf base at the rhizoid disc bistratose. *Androecia* on short or long shoots with 3–25 series of bracts, bracts usually smaller than leaves, lobules enlarged, hypostatic or epistatic, underleaves present throughout; antheridia two per bract. *Gynoecia* with 1–2 lejeuneoid subfloral innovations, bracts in 1(–3) series, as large as or slightly larger than leaves, margins toothed (rarely entire), lobules well-developed, keel unwinged or occasionally with a small wing; bracteoles undivided or short bifid, margins toothed, rarely entire. *Perianths* flattened, with 3 sharp keels, keels toothed, rarely entire. *Sporophyte*: seta not articulate; elaters 72 per capsule; otherwise as in the tribe. *Vegetative reproduction* by regeneration from leaf cells.

Distribution. The genus *Thysananthus* is pantropical and contains about ten species in two subgenera: subgen. *Thysananthus*, which is distributed throughout the tropics, and subgen. *Sandeanthus* B. Thiers & Gradst., which is restricted to the Indo-Pacific area. Southeast Asia is the center of diversity of *Thysananthus*, with nine species occurring in the area (Gradstein, 1991).

Fulford (1941) recognized four species of *Thysananthus* in tropical America (*T. amazonicus*, *T. comosus*, *T. evansii*, *T. pterobryoides*) but in this treatment only neotropical species, *T. amazonicus*, is accepted. *Thysananthus evansii* and *T. pterobryoides* are now placed in the genus *Fulfordianthus* and *T. comosus* is excluded from the neotropics (see below).

In the Mitten herbarium (NY) there is a neotropical specimen ("Andes Bogotensis, *Weir*") of *Thysananthus spathulistipus*, an Old World species which is widely distributed in Southeast Asia and eastern Africa. Presumably the specimen has been mislabelled; it was identified as *T. amazonicus* by Fulford (1941).

Thysananthus is most closely related to *Mastigolejeunea*, from which it differs mainly by the lack of enlarged epidermis cells and the dentate female involucres. *Fulfordianthus*, which was recently segregated from *Thysananthus* (Gradstein, 1992), is only remotely allied to the latter. Differences are discussed under the genus *Fulfordianthus*.

1. **Thysananthus amazonicus** (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; *Lejeunea amazonica* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 106. 1884. Type (Fulford, 1941). Brazil. Pará: *Spruce s.n., Hepaticae Amazonicae et Andinae* (lectotype MANCH; isolectotypes, G, MANCH, NY). Fig. 23.

Paroicous and autoicous. *Plants* up to 6 cm long × 2–3.5 mm wide, dark green to dull brown to blackish, ascending to pendent, forming small festoons, irregularly and usually sparsely branched (± regularly pinnate in coll. San Carlos, *Spruce s.n.*). *Stems* 0.15–0.2 mm in diam., in cross section composed of ca. 30 epidermal cells surrounding 50–60 medullary cells; ventral merophyte 8 cell rows wide. *Leaves* (sub)imbricate, when moist usually somewhat falcate, dorsal lobe asymmetrically oblong, 1–1.5 × 0.5–0.8 mm, 1.5–2.2x longer than wide, apex apiculate, rarely obtuse, plane or somewhat curved downwards, margins entire, towards apex often with a few obscure, bluntish projections but never toothed, ventral margin upcurved in the lower half, becoming plane above, forming a wide angle or straight line with the keel; cells in mid-leaf 20–40 × 10–20 μm, towards the base strongly elongated; oil bodies ca. 3 per cell in midleaf, at leaf base up to 6 per cell, coarsely segmented, narrow ellipsoid to subglobose, 6–12 × 2–4 μm, smaller towards leaf apex. *Lobules* oblong-rectangular, 0.2–0.4 × 0.15–0.2 mm, up to 1/4 (–1/3)x lobe length, free margin plane or incurved, apex truncate, usually with (1–)2 short teeth, the teeth rarely reduced. *Underleaves* imbricate, subsquarrose, broadly obdeltoid to spathulate, 0.5–0.9 mm long × 0.45–0.8 mm wide, 3–4x stem width, apex emarginate-lunulate, plane, entire or with a few obscure, bluntish teeth. *Androecia* just below the gynoecium or terminal-intercalary on small lateral branches, bracts and bracteoles in 2–6 series, bracts variable in size, when below the mature gynoecium much larger than on male branches, lobules swollen, hypostatic or epistatic; antheridia 1–2 per bract. *Gynoecia* with only one innovation, innovations usually repeatedly fertile and gynoecia often in seriate arrangement, bracts in 1(–2) series, erect or obliquely spreading to subsquarrose, lobe oblong, ca. 1.5 × 0.6–0.8 mm, apex acute-apiculate, margin with a few teeth near apex or subentire, lobule broadly ovate to oblong, 1/2–2/3x lobe length, apex emarginate, margins irregularly toothed above; bracteoles gradually arising from the underleaves, inner bracteole usually almost as long as the bracts, (broadly to) narrowly oblong, 1–1.5 × 0.5–0.7 mm apex emarginate to short bifid, toothed. *Perianths* exserted to 1/3(1/2), narrow oblong-cylindrical, ca. 1.5 mm long, flattened and with truncate apex, sharply 3-keeled with a narrow, high ventral keel, keels irregularly and bluntly toothed-winged in the upper half to subentire; beak short, 3 cells long. *Sporophyte* as in the genus.

Terpenoids: cadinane-type sesquiterpenes and diterpene acetates are main components; the chemical constitution of the species varies considerably (Gradstein et al., 1985).

Distribution (Fig. 24). Guianas, Amazonian part of Brazil, Colombia, Venezuela, Trinidad; disjunct on eastern Cuba; from sea level to about 1000 m. *Thysananthus amazonicus* is an epiphyte of rather mesic lowland and submontane evergreen forest and scrub and is locally very common in the Guianas and along the upstream portions of the Rio Negro. It is usually pendent from branches and twigs, in the canopy and in rather open situations in the undergrowth on treelets, lianas, and saplings; occasionally it is found on trunks. The species is particularly abundant in rather open and dry evergreen forests on white sand, where it may form large festoons on branches and twigs.

Specimens examined. CUBA. HOLGUIN: Cuchillas de Moa, La Breña, *Reyes 9173/S* (HAC). **ORIENTE:** Guantanamo, La Melba, *Bisse & Lippold 11201b, 11457b* (JE), *Bisse & Rojas 3251a* (JE), *Pócs & Reyes 9170/BF* (HAC).

COLOMBIA. AMAZONAS: Río Caqueta, 12 km N of Isla

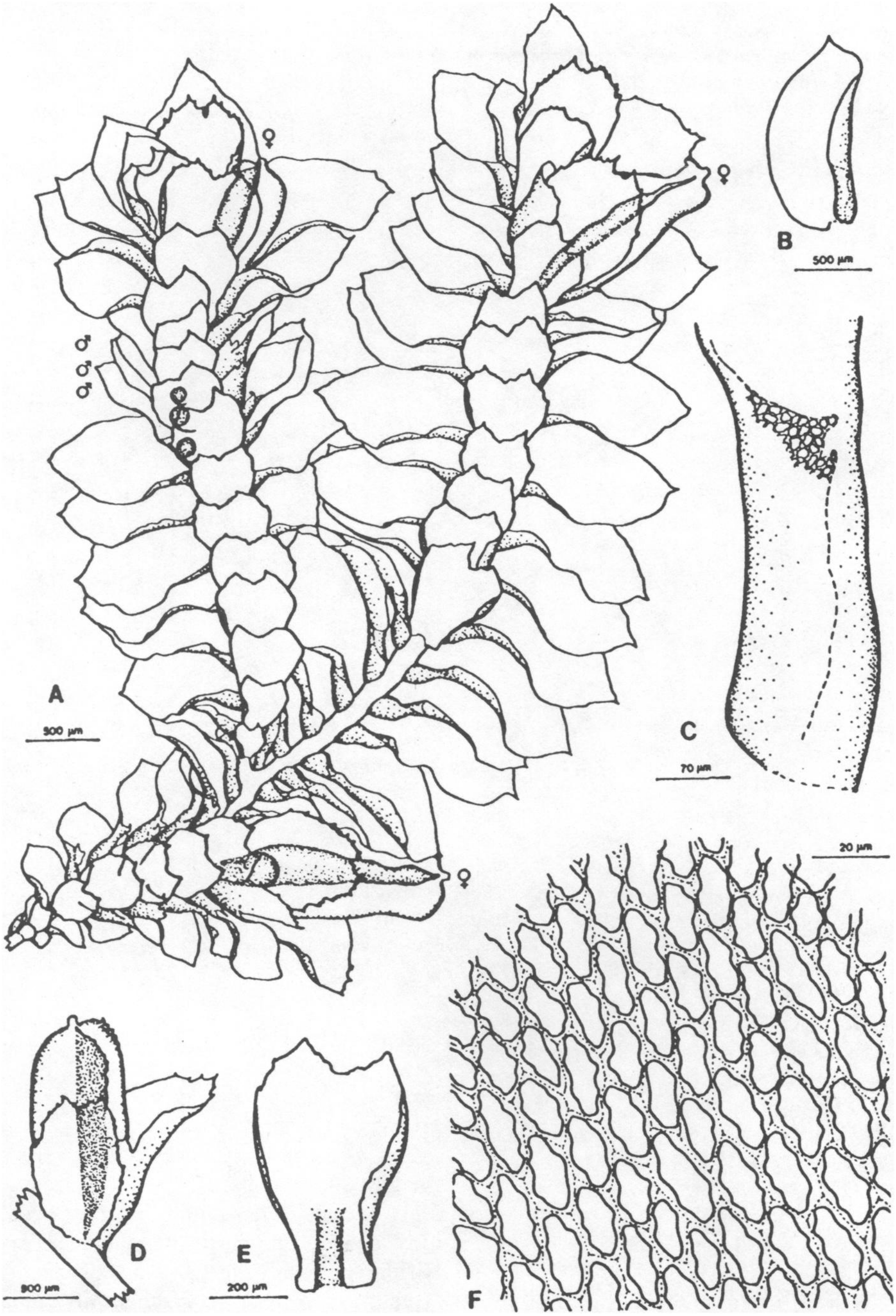

FIG. 23. *Thysananthus amazonicus*. **A.** Habit of paroicous plant with gynoecia and androecia. **B.** Leaf. **C.** Lobule. **D.** Gynoecium. **E.** Underleaf. **F.** Leaf cells. From Brazil, *Prance et al. 22208*.

Mariname, *Mohr & Sosa 20* (COL, U).

VENEZUELA. **AMAZONAS:** Casiquiari, *Spruce L41c* (MANCH); San Carlos del Río Negro, *Spruce s.n.* (MANCH); Cerro Neblina, along Río Mawarinuma, *Buck seven colls.* (NY), *Halling 4174* (NY). **BOLÍVAR:** Cerro Guaiquinima, *Sipman 26654, 26678* (B, U).

TRINIDAD. East of Sangre Grande, *Britton 2876* (NY); without loc., *Fendler s.n.* (NY).

GUYANA. Dakara Cr., near Timehri, *Gradstein* 4709 (U); Moraballi Creek, near Bartica, *Richards 188, 510* (BM);

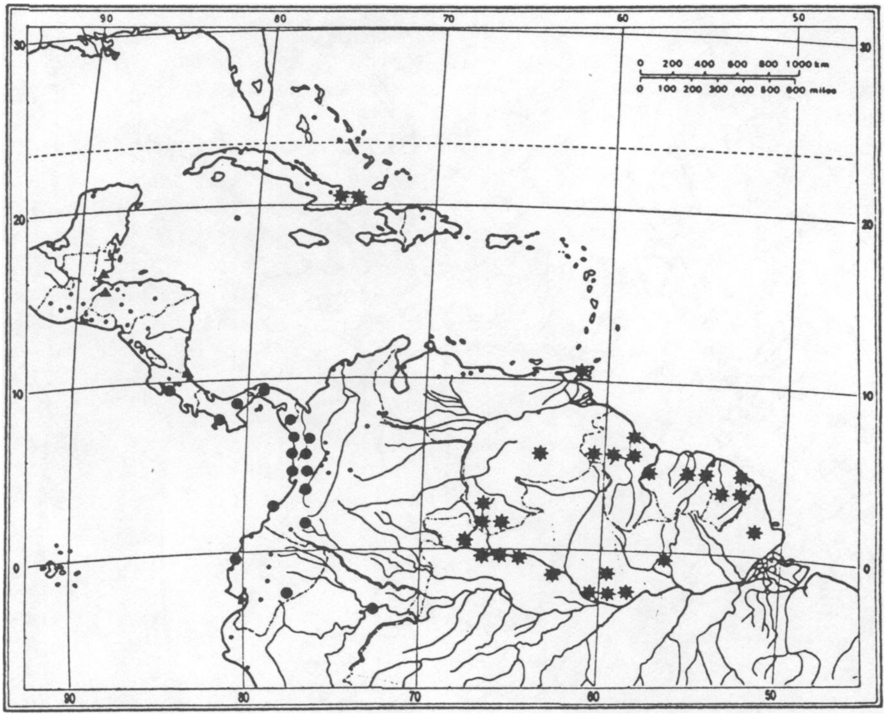

FIG. 24. Distribution of *Fulfordianthus evansii* (triangles), *F. pterobryoides* (dots) and *Thysananthus amazonicus* (stars).

Mabura Hill, *Cornelissen & ter Steege 111, 681, 743, 762, 860, 861, 911* (U); Upper Mazaruni District, Jawalla, *Gradstein 4857, 4835* (U), Roraima, *Gradstein 4993, 5151* (U), Waramadan, *Gradstein 5693, Bryoph. Neotrop. Exsicc. 150* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, USJ, XAL).

SURINAME. Para Cr., *Suringar 124* (G); Jodensavanne, *Lindeman 3937C* (U); Kabalebo Dam project area, *Bekker 15 colls.* (U), *Florschütz-de Waard & Zielman 5187A, 5189A, 5529A* (U).

FRENCH GUIANA. Trail St. Laurent-Apatou km 65, *Cornelissen & ter Steege C0270* (U); road Cayenne-Cacao at bridge over Rio Comté, *Gradstein 6658* (U); Montsinery, *Gradstein 5793* (U); Montagnes de Kaw, *Cornelissen & ter Steege C0265, C0311* (U); Bas Oyapock, Haute Crique Armontabo, *Cremers 7141* (CAY, U); Saül, *Montfoort 1164-1169* (U), *Aptroot 15381, 15447* (U), *Gradstein 6131* (U).

BRAZIL. AMAPÁ: Mun. Mazagão SW of Rio Preto, *Mori & Cardoso 17481* (NY). AMAZONAS: Rio Madeira, *Ule 585* (G); Manaus, *Ule 571* (G); Mun. Castanha, Rio Januca, *Schäfer-Verwimp 7271* (JE); road Manaus-Caracarai km 61, *Prance et al. 18714* (NY, U), km 130, *Berg et al. P19514* (NY, U), ibid., *Griffin et al. 718* (FLAS, U); along Rio Negro between Manaus and São Gabriel, *Schuster 10 colls.* (NY); Rio Negro, Umirisál, *Spruce s.n.* (MANCH), Javita, *Spruce s.n.* (MANCH), São Gabriel, *Spruce s.n.* (MANCH); Rio Uaupés, Panuré, *Spruce s.n.* (MANCH); Rio Uatumã, *Buck 2786, 2934, 3161* (NY). PARÁ: Tanau, *Spruce s.n.* (MANCH); Rio Trombetas, vic. Cachoeira Porteira, *Prance et al. 22208, 22268* (NY, U).

Uses. Along the Río Caqueta, Colombia, *Thysananthus amazonicus* is called "lama" and is used as a painkiller against snake and scorpion poisoning (Mohr & Sosa, in sched.).

Thysananthus amazonicus is a very distinct species and can hardly be confused with any other species in the region where it occurs. It is most closely related to the Asiatic *T. comosus*. Differences with the latter are discussed under "Excluded Species." *Thysananthus amazonicus* is vegetatively somewhat similar to weakly branched, entire-leaved phases of *Bryopteris filicina* (previously described as *Bryopteris flaccida*). *Bryopteris filicina* differs, however, by its larger size, the dendroid and usually regularly pinnate habit, the rounded and more strongly dentate underleaf apex, the *Frullania*-type branches, and the very different gynoecium. The emarginate underleaf apices, characteristic of *T. amazonicus*, are also present in *Fulfordianthus pterobryoides* but that species is readily recognized by its toothed leaves, pinnate branching, erect, dendroid growth and very different leaf areolation.

Thysananthus amazonicus varies somewhat in size, color, leaf length, and degree of dentation of the female involucre. The leaf lobule may have one or two teeth and sometimes there are no teeth at all, e.g. in the lectotype specimen. The leaf lobule is usually 1/4 or less the length of the leaf but in some Cuban specimens the lobules may be slightly larger, up to 1/3× leaf length.

Excluded Species

Thysananthus lehmannianus (Nees) Stephani = *Spruceanthus semirepandus* (Nees) Verdoorn (Geissler & Gradstein, in press)

Thysananthus dissopterus (Spruce) Stephani, Hedwigia **29:** 4. 1890; *Lejeunea dissoptera* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 108. 1884. Type. "Guiana," ex hb. Hooker, paralectotype of *Thysananthus comosus* Lindenberg (holotype, MANCH; isotypes, BM, G)

= *Thysananthus comosus* Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **8:** 25. 1844. Type (Spruce 1884). Malaysia. Pulo Penang, *Wallich s.n.* (lectotype, W; isolectotype, BM)

Thysananthus comosus is the type species of the genus *Thysananthus* and is widely distributed in Southeast Asia. The species was described by Lindenberg based on two specimens, one from Asia ("Pulo Penang") and one from South America ("Guiana"). Spruce (1884) considered the two specimens different and named the South American plant *Lejeunea dissoptera* (= *T. dissopterus*). Fulford (1941), however, treated *T. dissopterus* as a synonym of *T. comosus*. I have studied the type collections kept in Vienna (W) and London (BM) and have found that the two specimens are identical except for the fact that the material from Pulo Penang is male whereas the plants from Guiana are female.

Although closely related to *Thysananthus comosus*, *T. amazonicus* is readily distinguished from the latter by the longer leaves (more than 1.5× longer than wide), the emarginate underleaves (rounded-subtruncate in *T. comosus*), and the bluntly toothed perianth keels (strongly ciliate-laciniate in *T. comosus*). Moreover, *T. amazonicus* is monoicous whereas *T. comosus* is dioicous. *Thysananthus comosus* seems much more similar to entire-leaved forms of the Asiatic *T. convolutus* Lindenberg (= *T. gottschei* Jack & Steph.) and the differences between these two taxa are obscure and in need of study.

Besides the syntype collection from Guiana there is another neotropical specimen of *Thysananthus comosus* in the Mitten Herbarium: Brazil, "Janiai," *Spruce s.n.* (NY). This specimen is very poor and consists of only a single stem. The two neotropical specimens of *T. comosus* are old and very poorly labelled collections and in view of the Asiatic distribution of the species there is reason to doubt their neotropical origin. The Guianas have been rather well collected in recent times and there has been little habitat disturbance in the area. If *T. comosus* indeed occurs there it should have been rediscovered. The locality of the Brazilian specimen ("Janiai") is obscure and there is no duplicate in the Spruce herbarium. Fulford (1941) cited "Tanau" as locality of this material but the *Thysananthus* specimen from "Tanau" in the Spruce herbarium (MANCH) belongs to *T. amazonicus*.

I therefore believe that the neotropical specimens of *Thysananthus comosus* are mislabelled and of Asiatic origin. There are many other examples of such mislabelled bryophyte specimens in the Hooker and Mitten herbarium, for example the Pacific records of *Bryopteris filicina* and *Symbiezidium transversale*. Pending the discovery of genuine New World material, I propose that *T. comosus* is excluded from the neotropical flora.

6. **Fulfordianthus** Gradstein, Bryologist **75:** 44. 1992. Type. *Lejeunea pterobryoides* Spruce (= *Fulfordianthus pterobryoides* (Spruce) Gradstein). Genus named after Margaret H. Fulford, well-known American hepaticologist.

Thysanopsis Schuster, J. Hattori Bot. Lab. **72:** 219. 1992, nom. inval. (without latin descr., no type indicated).

Plants dendroid, differentiated into a creeping, stoloniform primary stem which gives rise to several erect, leafy secondary stems, the secondary stems 1–10 cm long × 1.5–4 mm wide, regularly spatiated and densely pinnately, sometimes irregularly branched (forked in female parts), dull dark-green with glossy light-green growing points, becoming brownish on age. *Branches* thecal, *Lejeunea*-type, flagelliform branches lacking. *Stems* rigid, 0.2–0.5 mm in diam., differentiated into a dark brown, thick-walled cortex (4–5 cells across) surrounding a colorless, thin-walled medulla, cortical cells as large as or smaller than the medullary cells, epidermal layer consisting of ca. 60–120 rows of cells; ventral merophyte numerous cells wide (more than 10). *Leaves* widely spreading and plane or loosely deflexed when dry, convex when moist, leaf lobes ovate to oblong, apex with or without a sharp point, margins plane, crenulate to sharply dentate; leaf cells mostly isodiametrical and small, ca. 10–15 μm long, at leaf base narrowly elongated, 20–40 μm long, forming an obscure, short vitta, all cells (also those of stems) evenly thickened, trigones lacking, oil bodies lacking. *Lobules* small, up to 1/5× leaf length, never reduced, ovate, at apex with a long (5–10 cells), curved tooth. *Underleaves* obcuneate, 3–4× stem width, apex deeply emarginate, margins toothed, bases subauriculate, line of insertion straight. Asexual reproduction lacking. Dioicous. *Androecia* in terminal or intercalary spikes on branches, bracts in 3–25 series, somewhat smaller than leaves, lobules strongly swollen and almost as long as lobes, hypostatic; antheridia two per bract. *Gynoecia* terminating lateral *Lejeunea*-type branches or innovations, with paired, repeatedly fertile pycnolejeuneoid innovations forming dichasia, bracts in one series, suberect, toothed, deeply divided into a lobe and a long lobule ca. 2/3× lobe length, keel without wing; bracteole as long as bracts, oblong, sharply keeled-folded over its entire length, apex truncate, margins toothed. *Perianths* large, cylindrical, 2–3 cm long, sharply 3-keeled, keels entire or slightly toothed towards apex, inner surface of perianth mamillose near apex. *Sporophyte*: seta not articulate; elaters 72 per capsule; otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution (Fig. 24). *Fulfordianthus* is a neotropical genus with two species in Central America and northwestern South America, at elevations ranging from sea level to 1500 m. The genus is largely restricted to the Chocó geographical province, an area which includes the very wet Pacific coast of northern South America and adjacent Central America and which is known for his its high level of endemism among vascular plants (Gentry, 1982). A few records of *Fulfordianthus* come from western Amazonia.

The species of *Fulfordianthus* grow in the understory of virgin rain forest on bark and occasionally on rock.

Fulfordianthus has traditionally been associated with *Thysananthus* but has recently been segregated from the latter because of its dendroid growth, regularly pinnate branching, the strongly differentiated subepidermis of the stem, the small isodiametric leaf cells with evenly thickened walls, lacking any trace of trigones, the lack of oil bodies, and the pycnolejeuneoid innovations (Gradstein, 1992). Thiers (1985) recorded the occasional presence of lejeuneoid innovations but I have observed pycnolejeuneoid innovations only. The lack of oil bodies is the most striking feature of this genus and is unique among Lejeuneaceae.

The genus closest to *Fulfordianthus* is *Dendrolejeunea* (Spruce) Lacout., a monotypic genus which is widely distributed in tropical Asia (Gradstein, 1992). The only neotropical genus which may be confused with *Fulfordianthus* is *Bryopteris*, which has the same growth habit. *Bryopteris* has many different morphological features, however, and is wholly unrelated to *Fulfordianthus*. Differences are discussed under *F. pterobryoides*.

The lack of oil bodies and trigones in *Fulfordianthus* and the dendroid habit are unusual features within the family Lejeuneaceae and make this genus a highly specialized taxon. Morphological specialization is also found in many other endemic hepatic genera of tropical America and is suggestive of a relatively recent, Tertiary (or late Cretaceous) origin of these taxa (Schuster, 1990). Most of the endemic neotropical hepatics are found in the Antilles, the northern Andes and in the Guayana Highland and adjacent Amazonian lowlands. *Fulfordianthus* constitutes the first example of a highly apomorphic endemic from the Chocó.

Schuster (1992) has recently published a very different description of the ramification system in *Fulfordianthus* (as *Thysanopsis* nom. inval.). According to this author, the main axis produces several to many *Frullania*-type (!) branches prior to ending in a gynoecium; *Lejeunea*-type branches would be restricted to rather undeveloped microphyllous branches. No mention is made of the dendroid growth habit.

Key to the Species of *Fulfordianthus*

1. Plants 2–10 cm long, usually regularly and densely pinnate; leaf margins dentate, teeth 1–5 cells long; Peru to Costa Rica, from sea level to 1500 m. 1. *F. pterobryoides.*

1. Plants smaller, 1–2 cm long, dichotomous or irregularly branched; leaf margins crenulate to denticulate, teeth up to 1 cell long. Along the Caribbean coast of Central America, at sea level . . . . 2. *F. evansii.*

1. Fulfordianthus pterobryoides (Spruce) Gradstein, Bryologist **95:** 44. 1992; *Lejeunea pterobryoides* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 109. 1884; *Thysananthus pterobryoides* (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; Fulford, Bull. Torrey Bot. Club **68:** 35, Figs. 13–27. 1941; *Thysanopsis pterobryoides* (Spruce) Schuster, J. Hattori Bot. Lab. **72:** 22. 1992, nom. inval. Type. Ecuador. Río Pastasa, on twigs of shrubs, *Spruce s.n.* (holotype, MANCH; isotypes, BM, G). Fig. 25.

Bryopteris wallisii Stephani, Hedwigia **24:** 89. 1885. Type. Ecuador. Manabi: Utria, along the Pacific coast, *Wallis s.n.* (holotype, G)

Plants with feather-like, more or less regularly and often densely pinnate to bipinnate secondary stems, 2–8 cm long x 1.5–2 mm wide, all vegetative branches thecal, *Lejeunea*-type. *Stems* with over 100 epidermal rows of cells. *Leaves*: dorsal lobe ovate-oblong, 1–1.3 x 0.5–0.7 mm, ca. 1.8x longer than wide, apex broadly rounded and plane, with or without a sharp point, margins usually sharply dentate above the middle, teeth variable in size, 1–5 cells long, sometimes weakly developed only, strongest on branch leaves, ventral margin plane or narrowly incurved, curved or straight; leaf cells rounded-quadrate to subrectangular, in mid-leaf ca. 10–15 x 10 μm, towards the base strongly elongated, 20–40 x 10–15 μm, the cell walls uniformily thickened, oil bodies lacking. Lobules 0.1–0.2 mm long, with a long (5–8 cells), curved tooth. *Underleaves* loosely imbricate, subsquarrose, 0.5–0.6 mm long x 0.6–0.7 mm wide, margins slightly toothed above the middle. *Androecia* as in the genus. *Gynoecia* on short lateral *Lejeunea*-type branches and on (paired) innovations, bract lobes narrowly oblong, ca. 1.5 x 0.5 mm, lobule oblong to lanceolate, ca. 2/3x lobe length, apex of lobe and lobule acute, the margins sharply toothed above; bracteole as long as the bracts, narrowly oblong, margins (and sometimes the fold) toothed above. *Perianths* as in the genus, with a short, 3 cells long beak. *Sporophyte* as in the genus, elaters with a very dark brown spiral.

Distribution (Fig. 24). Costa Rica, Panama, western Colombia, Ecuador, northern Peru; in Central America only found above 500 m, in South America from sea level to 1500 m. *Fulfordianthus pterobryoides* is an example of a Chocó element, with a range extending along the Pacific coastal regions of northern South America northwards into Central America. The species is not entirely restricted to this region, however, and has also been found on the Amazonian side of the Andes in Putumayo and Loreto. It grows on the base and lower portions of small tree trunks, treelets and lianas in primary and secondary lowland and submontane rain forests; occasionally the species occurs on rock.

Specimens examined. COSTA RICA. Candelaria near San José, *Lehmann 1038* (BM, G, PC, US).

PANAMA. CHIRIQUÍ: Fortuna, *Spörle & Aranda 1.39* (NY, PMA, U). COCLE: El Cope, cloud forest, *Salazar et al. 1491, 1503* (NY, PMA). DARIÉN: Cerro Pirre, *Salazar & Gradstein several colls.* (PMA, U). PANAMÁ: Cerro Jefe, *Salazar & Chung 5226* (PMA, U); Canazas Mts., above Torti Arriba, *Folsom et al. 6705* (MO, U). Coiba I., *Seemann s.n.* (NY).

COLOMBIA. Without loc., *Wallis s.n.* (BM, NY). CAUCA: Isla Gorgona, *Rudas & Aguirre 187* (COL, U). CHOCÓ: Mecana, *Gentry & Juncosa 40994A, 40996A* (MO, U); Quibdo, Río Neguá, *Mägdefrau 1501* (U); Mun. Nuqui, El Amargal, 5 km SW of Arusi, *Gradstein 8809, 8829, 8836* (COL, U); road Quibdo-Istmina, near Certegui, *Gradstein 8781, 8782* (COL, U); road St. Cecilia-Tado km 40, *Gradstein 8754* (COL, U); road Tutunendo-El Carmen at point 20, *Gradstein 8919, 8939* (COL, U). PUTUMAYO: 40 km NW of Puerto Asís, *King & Guevara C1083* (COL, U, US). VALLE: Cordoba, *Killip 11776, 11801* (NY); road Buenaventura-Cali 28 km, *Bischler 329* (COL, U). Sarare, Santa Librada, *Bischler 2004* (COL, U).

ECUADOR. Types of *Lejeunea pterobryoides* and *Bryopteris wallisii.*

PERU. LORETO: Río Macusari, *McDaniel & Marcos*

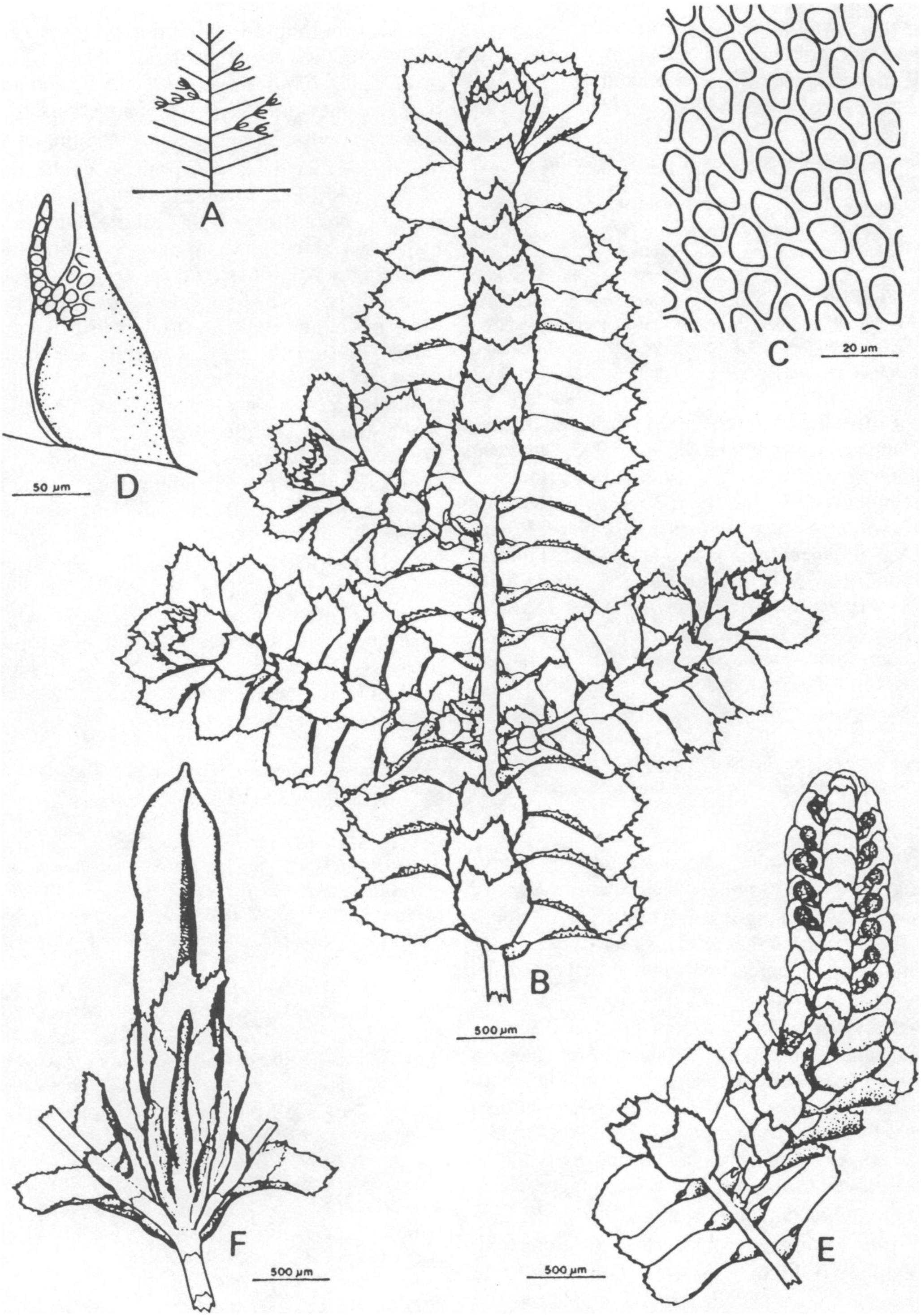

FIG. 25. *Fulfordianthus pterobryoides*. **A.** Dendroid growth form, schematic. **B.** Habit; note collared, *Lejeunea*-type branches and emarginate underleaves. **C.** Leaf cells. **D.** Lobule. **E.** Androecial branch. **F.** Gynoecium. From Colombia, *Gentry & Juncoso 40994A, 40996A*.

11038 (NY); Maynas, between Río Napo and Río Amazonas, *Timme & Maddox 4830* (NY).

Fulfordianthus pterobryoides is a very beautiful and distinct species. It is readily recognized by its large size, erect, feather-like habit, deeply emarginate underleaves and its sharply toothed leaves. It is habitually somewhat similar to *Bryopteris*, but the latter differs essentially by its *Frullania*-type rather than *Lejeunea*-type branching, its strongly convoluted leaves (when dry), its elongated leaf cells with cordate trigones and numerous small intermediate thickenings, the rounded underleaf apex and its subsessile gynoecia without innovations. Moreover, in *Bryopteris* the cells of the epidermis are larger and thinner-walled than those of the inner cortical layers; in *F. pterobryoides* the epidermis is not enlarged.

The species varies somewhat in size and some populations may be only weakly pinnate. Forms with weakly toothed leaves (e.g. Putumayo, *King & Guevara C1083*) approach *F. evansii*, which, however, differs by its much smaller size and different branching.

A peculiar feature of *Fulfordianthus pterobryoides* is that the *Lejeunea*-type branches may sometimes arise at some distance from the ventral leaf base, up to half-way between two adjacent leaves. Such an "intermediate" position of *Lejeunea*-type branches is unusual. Further branch anomalies are seen in the innovations which sometimes (in one of a pair of innovations) produce the first leaf and underleaf at nearly equal levels. In this case the position of the underleaf relative to the leaf should be determined from subsequent leaf cycles towards the apex of the innovation (Barbara Thiers, pers. comm.).

2. **Fulfordianthus evansii** (Fulford) Gradstein, Bryologist **95:** 46. 1992; *Thysananthus evansii* Fulford, Bull. Torrey Bot. Club **68:** 34. 1941; *Thysanopsis evansii* (Fulford) Schuster, J. Hattori Bot. Lab. **72:** 220. 1992, nom. inval. Type. Belize. Punta Gorda, *unknown collector* (holotype, CINC).

Plants: secondary stems up to 2 cm long × 1.5–2 mm wide, irregularly branched or, when female, dichotomous by repeatedly fertile innovations. *Stems* with ca. 60–90 epidermal rows of cells. *Leaves*: dorsal lobe oblong, ca. 1 × 0.5–0.6 mm, 1.8–2 × longer than wide, apex broadly rounded, plane, with or without a short point, margins crenulate-denticulate above the middle by protruding cells and cell tips, ventral margin narrowly upcurved, ± straight; leaf cells quadrate-hexagonal to subrectangular, in mid-leaf ca. 10–15 × 10 μm, towards the base strongly elongated, 20–40 × 10–15 μm, the cell walls uniformily thickened, oil bodies lacking. *Lobules* 0.1–0.2 mm long, with a long (up to 10 cells), curved tooth. *Underleaves* loosely imbricate, squarrose, 0.5–0.6 mm long × 0.6–0.7 mm wide, margins slightly toothed above the middle. *Androecia* as in the genus. *Gynoecia* terminating main stem or innovations, bract lobes oblong, 1–1.2 × 0.5–0.7 mm, lobule ovate-oblong, ca. 2/3× lobe length, apex of lobe and lobule acute, the margins irregularly toothed above; bracteole 1.5–1.8 mm long, margins irregularly toothed above. *Perianths* as in the genus, beak 3–10 cells long. *Sporophyte* not observed.

Illustration. Fulford, Bull. Torrey Bot. Club **68:** 34, Figs. 1–12. 1941.

Distribution (Fig. 24). Guatemala, Belize, northern Costa Rica, at sea level. *Fulfordianthus evansii* is a rare taxon of undisturbed lowland rain forest along the Caribbean coast of Central America.

Specimens examined. GUATEMALA. East Coast, *Watson 116 p.p.* (NY).

BELIZE. Type of *Fulfordianthus evansii.*

COSTA RICA. LIMÓN: Tortuguero, *Steere CR31* (NY, U), *Eggers CR12,1* (JE, U).

Conservation. In view of its exclusive occurrence in undisturbed lowland rain forest of Central America, an area where deforestation proceeds at an alarming speed, the rare *Fulfordianthus evansii* may be considered threatened with extinction. Moreover, two of the three localities known of the species are old records. The only recent collections are from Tortuguero National park, Costa Rica. The species has been classified as an endangered taxon (Gradstein, 1992c). Its continued existence in Central America needs confirmation.

Fulfordianthus evansii is recognized by its small stature and lack of feather-like fronds characteristic of *F. pterobryoides*. The secondary stems are rather short and are either irregularly branched or, when female, forked by the repeatedly fertile, paired innovations. The leaves of *F. evansii* are elliptical, about as broad at apex as at the base, and the margins are crenulate-denticulate by projecting cell tips or whole cells. Contrary to *F. pterobryoides*, the teeth in *F. evansii* are never more than one cell long.

The differences in the leaves of *Fulfordianthus evansii* and *F. pterobryoides* are somewhat gradual and forms of *F. pterobryoides* with weakly toothed, elliptical leaves occur. Their larger size and more regularly pinnate branching separate these forms from *F. evansii*. The two species, moreover, have different altitudinal ranges. *Fulfordianthus evansii* is exclusively known from coastal forests, at sea level, whereas all Central American collections of *F. pterobryoides* are from elevations above 400 m.

7. **Bryopteris** (Nees) Lindenberg, Syn. Hep. 284. 1845; *Frullania* subgen. *Bryopteris* Nees, Naturgesch. Eur. Leberm. **3:** 211. 1838; *Lejeunea* subgen. *Bryolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 111. 1884, nom. illeg. Type (Evans, 1907a). *Bryopteris filicina* (Swartz) Nees. Genus named for its fern-like habit.

Plants dendroid, differentiated into a creeping, stoloniform primary stem which gives rise to several erect, leafy secondary stems, the secondary stems up to 25 cm long × 2–4 mm wide, irregularly to regularly pinnately or dichotomously branched, dull dark-green with glossy light-green growing points, becoming brownish with age. *Branches Frullania*-type when vegetative, rarely thecal, *Lejeunea*-type; sexual branches always thecal, *Lejeunea*-type; flagelliform branches lacking. *Stems* rigid, dark brown, up to 0.5 mm in diam., differentiated into a dark brown, thickwalled epidermis, a dark brown, very thickwalled subepidermis (2–4 cells across), and an almost colorless to pale brown, much thinner-walled medulla, epidermis cells in 50–80 rows, about 2× larger than subepidermis cells, medulla cells larger than subepidermis cells, gradually becoming larger towards stem centre; ventral merophyte more than ten cells wide. *Leaves* usually strongly erect-convoluted when dry (sometimes spreading), obliquely to widely spreading and often falcate when moist, lobes of the primary stem leaves small, ovate-orbicular, with entire margins and ± rounded apex, those of the secondary stems asymmetrically ovate to narrowly oblong, apex sharply pointed, dorsal base auriculate, length of insertion line about 1/2× merophyte length, ventral base short decurrent, margins toothed in upper half or entire; leaf cells elongated, strongly so towards base and sometimes forming an obscure vitta, with cordate trigones and 0–3 intermediate thickenings on the longer cell walls; oil bodies small, homogeneous, *Massula*-type, numerous per cell; ocelli lacking. *Lobules* produced both on primary and secondary stem leaves, small, up to 1/4× leaf length, never reduced, inflated-ovate, entire or with several large teeth; hyaline papilla long cylindrical, marginal or on inner lobule surface. *Underleaves* of primary stems small, distant, with entire apex, those of the secondary stems much larger, imbricate or distant, subquadrate-obdeltate to rectangular-spathulate, concave with upcurved to recurved margins, sometimes squarrose, apex rounded to truncate, sharply toothed, margins entire or toothed in upper half, bases short decurrent, line of insertion straight or curved. Dioicous or monoicous. *Androecia* on short-specialized (rarely elongated) branches of the *Lejeunea*-type, bracts and bracteoles in 4–12 series, much smaller than leaves and underleaves, lobules strongly swollen and almost as large as lobes, hypostatic; bracteoles becoming smaller towards apex of spike; antheridia two per bract. *Gynoecia* on short-specialized (rarely elongated) *Lejeunea*-type branches, innovations lacking, bracts and bracteoles in 3–4 series, suberect and appressed, their margins irregularly toothed to lacerate, bracts deeply divided into lobe and lobule, lobule ovate, lobule oblong-lanceolate, keel without wing; bracteole as long as bracts, narrowly oblong, sharply keeled-folded over its entire length, apex bifid. *Perianths* oblong to cylindrical, slightly to distinctly exserted, sharply 3-keeled over entire length, keels smooth; beak 2–4 cells long. *Sporophyte* (Stotler & Crandall-Stotler, 1974): seta not articulate, consisting of 30–100 cells in transverse section; elaters 72(?) per capsule; sporeling *Frullania*-type; otherwise as in the tribe. *Vegetative reproduction* by means of caducous branchlets (cladia) of the *Lejeunea*-type and regenerants from leaf cells.

Distribution. The genus *Bryopteris* occurs in tropical America and on the East African islands and is one of the most common genera of Ptychanthoideae in the neotropics. Stotler and Crandall-Stotler (1974) recognized six species in the neotropics, two of which are accepted in this treatment. The species grow on bark or rock in moist primary and disturbed rain forests at rather low elevations and may form large festoons on branches of trees and shrubs. They are usually indicative of frequent occurrence of clouds or mist at the sites where they occur.

Bryopteris is readily recognized by its erect or pendent growth and ± feather-like or dichotomous branching, its large size, *Frullania*-type branches, its toothed underleaves, the elongated leaf cells with well-defined cordate trigones, and its gametoecia which are produced on short-specialized branches. The insertion line of the leaves is j-shaped as usual in Ptychanthoideae and extends over about half the length of the merophyte. Leaves and underleaves of the primary stoloniform stems are much smaller than those of the secondary stems and always have entire margins and a rounded leaf apex. According to Stotler and Crandall-Stotler (1974) lobules are lacking in primary stem leaves, but those that I observed did produce ordinary lobules. Primary stem leaves and underleaves may also be found at the base of secondary stems and occasionally on branches. A specimen of *B. filicina* from Costa Rica (*Steere CR-88*) had a few unusually long branches with both primary stem and secondary stem leaves. The variation observed demonstrates the strong morphological plasticity of *Bryopteris*.

Unusual features of *Bryopteris* are the rather thick seta and the *Frullania*-type sporeling (Stotler & Crandall-Stotler, 1974). Stotler and Crandall-Stotler (1974) also suggested that *Bryopteris* produces "*Bryopteris*-type" instead of *Lejeunea*-type branches, but I have been unable to distinguish between the two branch types (see also Thiers, 1985). Another ususual character is the very long, linear shape of the hyaline papillae (Fig. 27).

Within the New World *Bryopteris* may only be confused with *Fulfordianthus*, which has a similar growth habit. The latter, however, has *Lejeunea*-type instead of *Frullania*-type branches, evenly thickened cell walls without trigones, and gynoecia on elongated shoots with two innovations.

Bryopteris is most closely related, and habitually very similar to the Old World genus *Ptychanthus*. Both genera share a similar growth habit, branching, leaf morphology and areolation. However, in *Ptychanthus* the epidermis cells are not or scarcely larger than the subepidermis cells in cross section (epidermis cells much larger in *Bryopteris*), the trigones of the leaf cells are somewhat irregular in shape and are often elongated along the walls (well-defined cordate and not elongated in *Bryopteris*), the oil bodies are segmented rather than homogeneous, the gametoecia are produced on normal, elongated *Frullania*-type branches, the gynoecia have single, repeatedly fertile innovations, and the perianths are pluriplicate. Sterile herbarium material is best separated by the very different epidermis (cross section). According to Stotler and Crandall-Stotler (1974), *Frullania*-type branches of Bryopteris and *Ptychanthus* have somewhat different basal leaf appendages but I have been unable to confirm their observations. Half-leaves of *Frullania*-type branches in *Ptychanthus* are different from those of *Bryopteris filicina* but are similar to those found in *B. diffusa* (see below).

Key to the Species of *Bryopteris*

1. Branching dichotomous; lobule with several large teeth; leaf margins entire; underleaves 3–4x as wide as the stem; throughout tropical America, uncommon. . . . . 1. *B. diffusa*.
1. Branching regularly or irregularly pinnate; lobule without teeth; leaf margins sharply toothed near apex (rarely entire); underleaves 1.5–2x stem width; throughout tropical America, very common. . . . 2. *B. filicina*.

1. Bryopteris diffusa (Swartz) Nees, Syn. Hep. 286. 1845; *Jungermannia diffusa* Swartz, Nova Gen. Spec. Pl. Prodr. 144. 1788; *Lejeunea diffusa* (Swartz) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 115. 1884. Type. Jamaica and Haiti/Dominican Republic ("Hispaniola"), *Swartz s.n.* (holotype, S; isotypes, C, S, STR). Fig. 26.

Bryopteris diffusa (Swartz) Nees var. *subserrata* Gottsche, Mex. Leverm. 169. 1863. Type (Stotler, in sched.). Mexico. Veracruz: Mirador, *Liebmann 275a* (C).

Dioicous. *Plants* up to 20 cm long, laxly dichotomous with very long branches. *Branches* and stems as in the genus. *Leaves* oblong or ovate-oblong, about 1.5–2 x 1–1.3 mm, obliquely spreading, on older stem portions sometimes falcate, apex sharply apiculate, rarely obtuse, margins entire, rarely with a few small, bluntish teeth

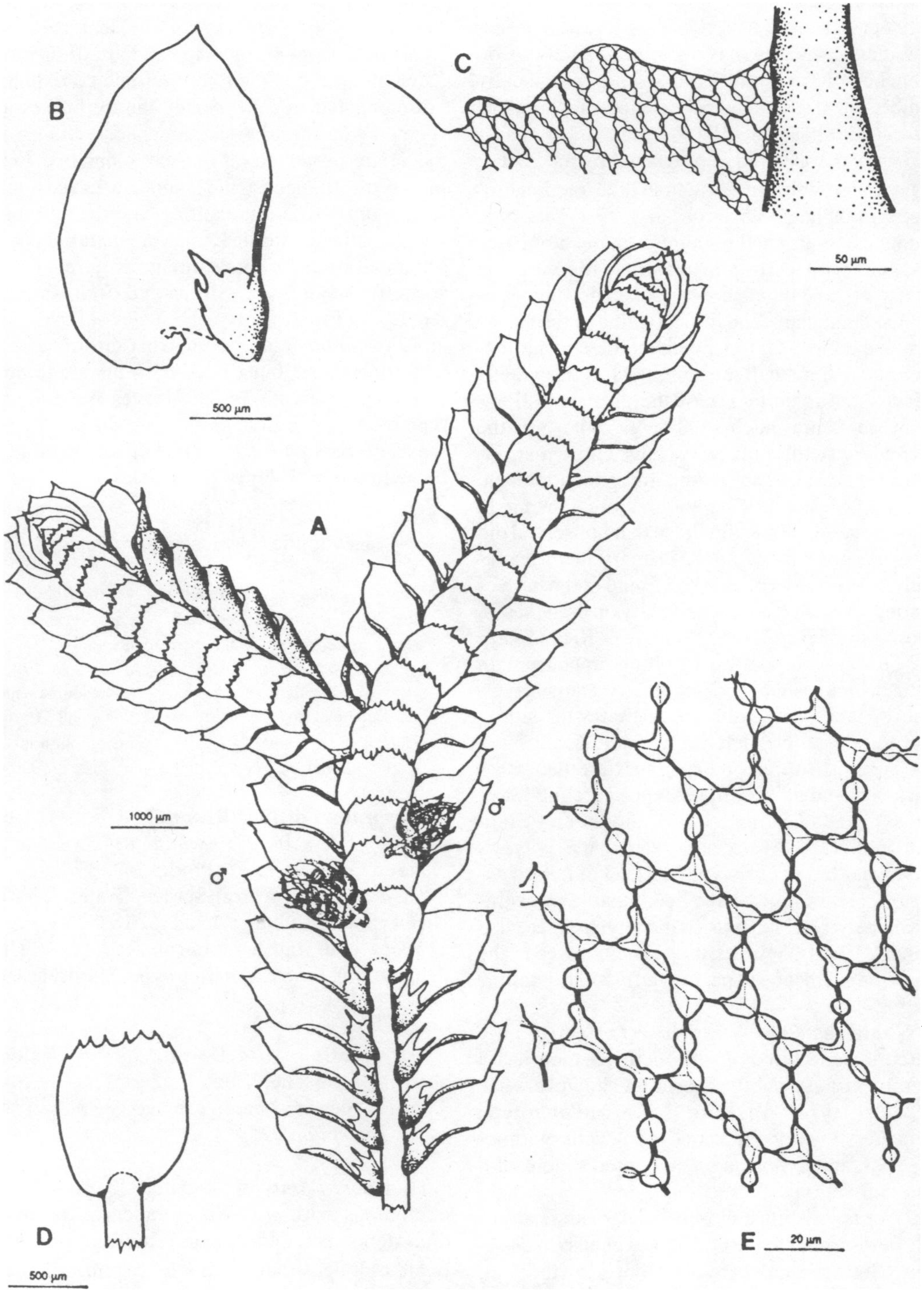

FIG. 26. *Bryopteris diffusa*. A. Habit of male plant, with two specialized androecial branches. B. Leaf. C. Lobule apex. D. Underleaf. E. Leaf cells. From Brazil, *Irwin et al. 32534*.

near apex, dorsal base strongly auriculate, ventral margin plane or slightly incurved near the keel; median leaf cells 35–50 x 15–25 µm, trigones and intermediate thickenings as in the genus, rather small; oil bodies (P. Geissler, in sched.) c. 10 per cell, homogeneous. *Lobules* up to 1/4x leaf length, ovate, inflated, free margin inflexed in lower half, plane in upper half and with 3(–4) long, unequal teeth, first and third usually smaller than second tooth, averaging 3–8 cells long, uniseriate to triangular from 2–4 cells wide base, sometimes one of these teeth reduced or enlarged and equalling the second tooth in size, second tooth very large, triangular to lanceolate, 6–20 cells long and 3–8 cells wide, its margins entire or with 1–2 short accessory teeth; occasionally a small fourth tooth present; hyaline papilla on the inner surface near the proximal base of the first tooth. *Underleaves* obdeltate-subquadrate, about 3.5x stem width, 0.7–1.1 x 0.9–1.2 mm, apex rounded to truncate, sharply toothed, margins plane or narrowly recurved, entire, bases rather abruptly narrowed and folded, distinctly decurrent, insertion line arched; rhizoids arising from rather large, swollen area at underleaf base, normally rudimentary or lacking. *Androecia*: male bracts with obtuse to apiculate apices. *Female bracts* with weakly dentate lobe margins and more strongly dentate to lacerate lobules. *Perianths* rare.

Terpenoids: striatene, various acetates and a small quantity of pinguisane-type sesquiterpenes (Gradstein et al., 1985).

Distribution. Scattered throughout tropical America, at elevations from about 100 to 1500 m. *Bryopteris diffusa* has a somewhat disjunct, submontane range and is apparently lacking in the Lesser Antilles and in most of the Andes. The species occurs in virgin and disturbed evergreen forests and woodlands and grows on tree trunks, branches and twigs. On twigs the species usually forms long, pendent festoons.

Selected specimens examined. MEXICO. CHIAPAS: W of Tuxtla- Gutiérrez, *Hale & Söderström 19911* (US). VERACRUZ: Zacuapan, *Purpus 5538* (NY, US); Orizaba, *Smith 12* (NY).

NICARAGUA. GRANADA: Volcán Mombacho, *Baker 8522* (NY).

COSTA RICA. CARTAGO: near Pejivalle, *Standley & Valerio 46866* (US). GUANACASTE: El Arenal, *Standley & Valerio 45255* (US). LIMÓN: near Cairo, *Standley & Valerio 48761* (US). SAN JOSÉ: Santiago, *Maxon 92* (NY). Turrialba, *Maxon 197* (NY).

CUBA. ORIENTE: Guantanamo, La Prenda, *Hioram & Maurel 2571, 2593, 6073* (NY); Mountains N of Guantanamo, *León 3917* (NY).

JAMAICA. Cockpit country, *Welch 20961* (NY).

HAITI. Massif de la Hotte, 41 km S of Roseau, *Buck 9058, 9077* (NY).

DOMINICAN REPUBLIC. MONTE CRISTY: Sabaneta, *Valeur 521* (NY); MACORIS: Consuelo, *Taylor 246* (NY). PACIFICADOR: Pimentel, *Abbott 718* (US).

BARBADOS. *Baron de Schach s.n.* (NY).

VENEZUELA. BARINAS: NW of Barinitas, *Nee & Whalen 17086* (NY). BOLÍVAR: Altiplanicie de Nuria, *Steyermark 88503, 88528* (NY, VEN, US); near Matacuchillo E. of Santa Elena airport, *Steyermark & Dunsterville 112291* (MO, U, VEN). CARABORO: Guaremales, *Pittier 8839* (NY). FALCÓN: Península de Paraguaná, *Griffin et al. PV-1662* (FLAS, NY, U); Parque Nacional Quebrada de la Cueva El Toro, *Liesner et al. 7900B* (MO, U). LARA: S of Sanare, *Steyermark & Espinoza 108798* (US). MIRANDA: near Aricagua, *Steyermark & Carreño 106963* (NY, US, VEN); Parque Nacional Guatopo, *Nee 17938, 17941* (NY). YARACUY: between Salon and Temería, *Steyermark et al. 100363A* (US). ZULIA: E of Churuguarita, *Bunting 9510* (NY).

TRINIDAD. Saddle road, *Britton et al. 175* (NY, US); Southern Watershed Reserve, *Britton et al. 1115* (NY, US).

GUYANA. Upper Mazaruni, Kamarang, *Robinson 85-20* (NY, U, US).

FRENCH GUIANA. Haute Oyapock, Wayampi de Trois Sauts, *Cremers 4811* (CAY, U).

PERU. AMAZONAS: Bagua, between Aramango and Montenegro, *López et al. 4238* (US). SAN MARTÍN: Tarapoto, *Spruce s.n.* (MANCH, NY).

BRAZIL. BAHÍA: Serra do Tombador, *Irwin et al. 32534* (NY, U); Mun. Porto Seguro, *Thomas et al. 6033* (NY); Mun. Itanagra, *Boom & Mori 952* (NY). MINAS GERAIS: Caldas, *Regnell 43* (S); Sierra d'Estrella, *Beyrich s.n.* (NY, W). PARÁ: Rio Curua, *Strudwick & Sobel 4117* (MG, NY); Serra dos Carajas, *Daly et al. 1828* (MG, NY). PARANÁ: Serra do Mar, *Dusén 3835* (NY). RIO DE JANEIRO : Corcovado, *Mosén 257* (NY, S). RIO GRANDEDO SUL: Santo Angelo, *Lindman B-180* (S). SANTACATARINA: Taragua, *Carl 30* (S). SÃO PAULO: Rio Grande, *Schiffner s.n., Crypt. Exsicc. Mus. Nat. Vindob. 4270* (NY, U, US, W); road São Paulo-Curitiba km 277, *Frahm 1699, Bryoph. Neotrop. Exsicc. (ed. Gradstein) 33* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, XAL); Buri, *Vital 2613* (SP, U).

BOLIVIA. LA PAZ: near Coroico, *Buchtien s.n.* (NY); Mapiri, *Williams 2206* (NY); Inquisivi, near Choquetanga, *Lewis 89-1014* (LPB, U). SANTA CRUZ: Parque Nacional Amboró, *Nee 36012* (NY).

PARAGUAY. ALTO PARANA: 35 N of Hernandarías, *Geissler 14568* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Bryopteris diffusa is a very distinct taxon and due to its laxly dichotomous habit and large size can hardly be confused with any other species. From *B. filicina* it differs in many respects (see Key), particularly its entire leaf margins, large lobule teeth, broad underleaves with arched insertions, and larger leaf cells with relatively small trigones. A further difference is seen in the half-leaves of the *Frullania*-type branches of the two. In *B. diffusa* the half-leaf is inserted across the dorsal base of the branch and entirely covers the lower dorsal surface of the branch, which therefore is visible only after removal of the half-leaf. In *B. filicina*, however, the half-leaf is inserted on the lateral, adaxial surface of the branch and is positioned in front rather than on top of the branch, which as a consequence can be observed in dorsal view without removal of the half-leaf. A half-leaf similar to the one found in *B. diffusa* is also present in *Ptychanthus*.

The striking differences between *Bryopteris filicina* and *B. diffusa* would seem to warrant their placement in separate sections or subgenera were it not that the differences are bridged by the two other species known in *Bryopteris*: *B. gaudichaudii* Gott. (Madagascar and Réunion) and the fossil *B. succinea* Grolle (Micenic amber of the Dominican Republic). *Bryopteris gaudichaudii* is superficially similar to *B. diffusa* by its forked branching and large underleaves with deeply arched insertions. Yet, the lobules of *B. gaudichaudii* are untoothed as in *B. filicina* and the leaves are somewhat toothed. *Bryopteris succinea*, known only from a single shoot fragment with androecia, has leaves similar as in *B. filicina* but the underleaf insertions are arched like those of *B. diffusa*. Unfortunately, the branching habit remains unknown in *B. succinea*. The distributions and relationships of the four species are clearly suggestive of an old, possibly Gondwanan origin of the genus (see Stotler & Crandall-Stotler, 1974; Grolle, 1984).

Bryopteris diffusa shows considerable variation in the size of the lobule teeth. Usually the median tooth is much larger than the others but sometimes they are about equal in size and occasionally the first tooth is the largest. This variation can be observed on leaves of single stems. Branch leaves often have smaller teeth than stem leaves. In other respects the species is rather stable. The leaf apex is almost always apiculate (rarely obtuse) and the margins of the lobes are entire except for an occasional bluntish tooth near apex. The depth of the underleaf insertion varies somewhat and rather deeply arched underleaf insertions were observed in collections from Venezuela. The underleaf bases, moreover, were unusually longly decurrent in these specimens.

Gynoecia are common throughout the range of the species but perianths are rare and were mostly observed in collections from South America. Their restricted occurrence apparently correlates with the uneven distribution of the male plants, which were rather common in the collections from South America but were virtually lacking in materials from the West Indies and Central America.

2. **Bryopteris filicina** (Swartz) Nees, Syn. Hep. 284. 1845; *Jungermannia filicina* Swartz, Nova Gen. Spec. Pl. Prodr. 145. 1788; *Bryopteris filicina* (Swartz) Nees var. *hookeriana* Gottsche et al., Syn. Hep. 285. 1845; *Lejeunea filicina* (Swartz) Nees & Montagne *in* d'Orbigny, Voy. Amér. Mér. 7, Bot.(2): 64. 1839. Type. Jamaica, *Swartz s.n.* (holotype, S). Fig. 27.

Jungermannia trinitensis Lehmann & Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **5:** 12. 1833; *Bryopteris trinitensis* (Lehmann & Lindenberg) Lehmann & Lindenberg, Syn. Hep. 285. 1845. Type (Stotler & Crandall-Stotler 1974). Trinidad. *Beyrich s.n.* (lectotype, S; lacking in hb. Lindenberg), *syn. nov.*

Bryopteris filicina (Swartz) Nees var. *arguta* Gottsche et al., Syn. Hep. 285. 1845. Type. Brazil. Minas Gerais: *Martius s.n.* (lectotype, STR, here designated).

Bryopteris tenuicaulis Taylor, Syn. Hep. 285. 1844; *Lejeunea tenuicaulis* (Taylor) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 113. 1884. Type. Ecuador. Esmeraldas: *Jameson s.n.* (holotype, FH).

Bryopteris fruticulosa Taylor, London J. Bot. **5:** 382. 1846; *Lejeunea fruticulosa* (Taylor) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 112. 1884. Type. Dominican Republic. Ex hb. Hooker (holotype, FH; isotype, NY), *syn. nov.*

Bryopteris liebmanniana Lindenberg & Gottsche, Syn. Hep. 738. 1847. Type. Mexico. Donagues, *Liebmann 149* (holotype, W; isotypes, C, U), *syn. nov.*
Stotler and Crandall-Stotler (1974) designated the specimen in C as the lectotype; however, the material in the Lindenberg herbarium (W) may be considered the holotype.

Bryopteris trinitensis (Lehmann & Lindenberg) Lehmann & Lindenberg var. *intermedia* Gottsche et al., Syn. Hep. 738.

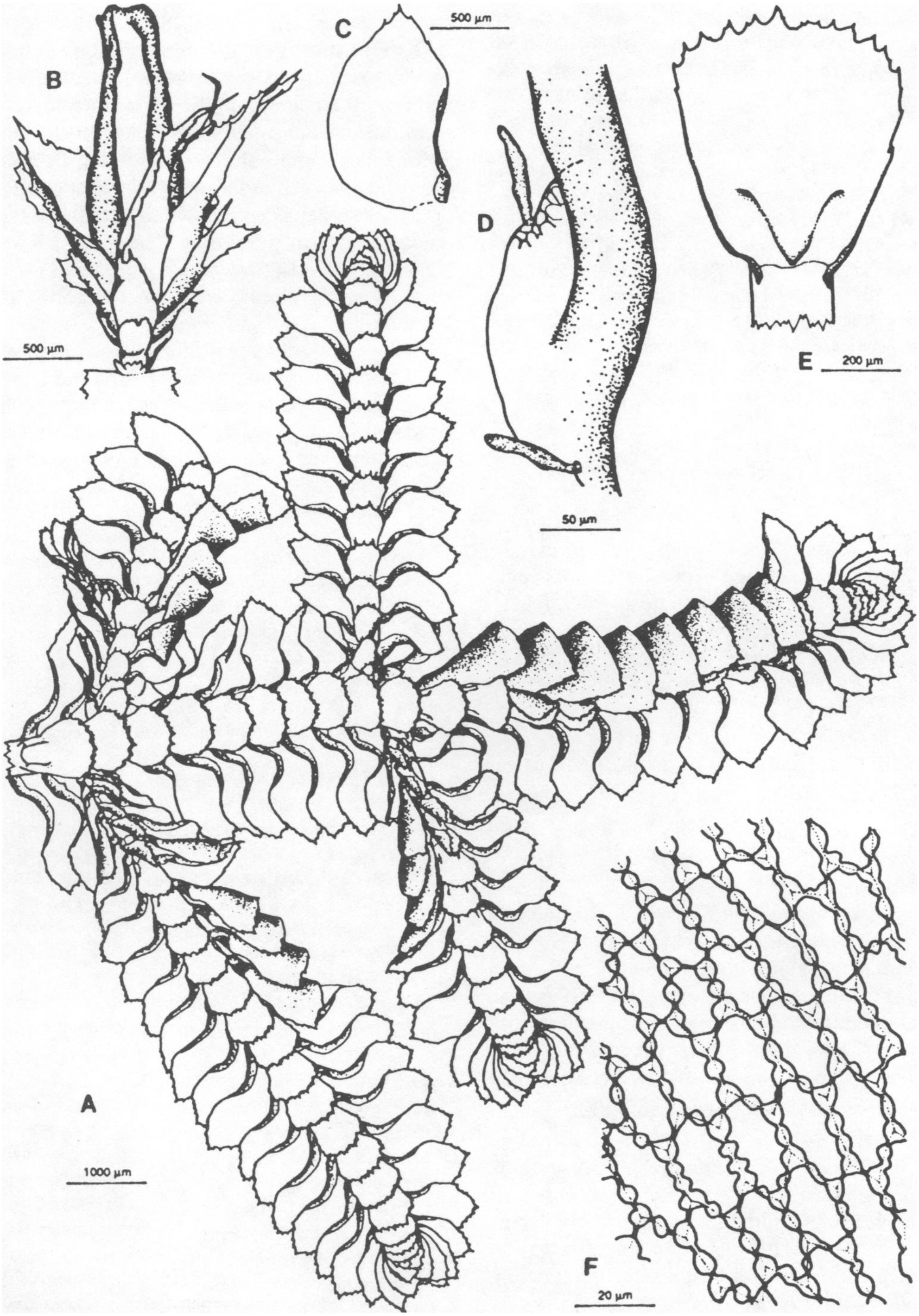

FIG. 27. *Bryopteris filicina.* **A.** Habit. **B.** Gynoecial branch. **C.** Leaf. **D.** Lobule, showing linear hyaline papillae at base and apex. **E.** Underleaf. **F.** Leaf cells. A, C–D, F from Dominican Republic, *Buck 4333*. B from Brazil, *Vitt 20764*. E from Colombia, *Aguirre et al. 3120*.

1847. Type (Stotler & Crandall-Stotler, 1974). Venezuela. Merida, *Moritz 98b* (lectotype, W; isolectotype, S).

Bryopteris galapagana Gottsche, Ann. Sci. Nat. IV, **8:** 341. 1857; *Jungermannia filicina* Swartz var. *tenuis* Wilson & Hooker, Trans. Linn. Soc. London **20:** 165. 1847, *nom. nud.* Type. Ecuador. Galapagos Is.: Floreana ("Charles"), *Andersson s.n.* (lectotype, S; isolectotype, S).

Bryopteris flaccida Lindenberg & Hampe, Linnaea **24:** 640. 1851. Type. Costa Rica, *Oersted 4* (holotype, BM; isotypes, C, NY, S; lacking in the Lindenberg herbarium), *syn. nov.*

Lejeunea longispica Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 114. 1884; *Bryopteris longispica* (Spruce) Steph., Spec. Hep. **5:** 6. 1912. Type. Peru. San Martín: Mt. Guayrapurina, *Spruce s.n.* (holotype, MANCH).

Bryopteris brevis Stephani, Spec. Hep. **5:** 3. 1912. Type. Bolivia. Santa Cruz: Cerro Amboró, *Herzog s.n., hb. Levier 5842* (holotype, G).

Bryopteris fruticulosa subspec. *monoica* Stotler, Bryophyt. Biblioth. **3:** 108. Type. Peru. Muna, *Bryan 998* (holotype, NY), *syn. nov.*

Dioicous or autoicous. *Plants* up to 25 cm long, usually feather-like, the secondary stems regularly and often densely pinnate to bi- or even tri-pinnate, sometimes branching more sparsely and irregularly pinnate (in very long plants). *Branches* as in the genus, tiny secondary or tertiary flagelliform branches of the *Bryopteris*-type sometimes present. *Stems* as in the genus. *Leaves* ovate-oblong to narrowly oblong, often falcate, 1.3–2.2 × 0.9–1.3 mm, sharply and irregularly toothed in the upper half to ± entire, ventral margin plane or incurved; median leaf cells 20–35(–40) × 10–15 µm; oil bodies ca. 15–25 per cell, homogeneous. *Lobules* small, up to 1/5× leaf length, ovate, free margin gently curved towards the ventral margin, ± inflexed or plane, with a shallow indentation in the upper half, otherwise entire; hyaline papilla projecting upwards from the inner side of the free margin proximal to the indentation. *Underleaves* slightly broader than long to distinctly elongated and up to 2× longer than wide, 0.8–1.7 × 0.8–1 mm, 1.5–2× stem width, apex rounded to truncate, sharply toothed, margins plane or narrowly recurved, entire or toothed above the middle, bases narrowly decurrent or subauriculate, insertion line straight or narrowly curved; rhizoids sparse, often lacking. *Reproductive structures* as in the genus.

Terpenoids: bazzanene, bicyclogermacrene and norpinguisone-methylether have been recored as main constituents; the chemical constitution of the species seems to be considerably variable (Gradstein et al., 1981, 1985).

Distribution. Very common throughout tropical America, from sea level up to 2500 m. In addition, there are a number of doubtful records from the palaeotropics (Mauritius, Nepal, Java, Solomons Is., and Tahiti; see Stotler & Crandall-Stotler, 1974). All of these are based on old, 18th or 19th century specimens and may have been mislabelled or misidentified. The specimen from Nepal, described as *Bryopteris nepalensis* Steph., belongs to *Ptychanthus striatus* according to Mizutani (1976).

The species grows in virgin and disturbed very humid rain forests and woodlands on tree trunks, branches and occasionally on moist rocks. It is a good indicator of mist. Most records are from submontane and lower montane elevations but in wet coastal areas the species may approach sea level.

Selected specimens examined. MEXICO. CHIAPAS: Lagunas de Montebello, *Frahm s.n.* (NY, U); Lacandon forest reserve, near Chajul Biological Station, *Gradstein 7959, 8010, 8076, 8154* (U). GUERRERO: Mun. General Heliodoro Castillo, *Thomas & Contreras 3769* (NY). OAXACA: El Faro, *Conzatti 3822* (NY); Sierra Juarez, *Robinson s.n.* (S, US). VERACRUZ: Mun. Hidalgotitlán, *Thomas & Grimes 3546* (NY); Mirador, *Purpus 383, 431* (NY, S, US).

GUATEMALA. ALTA VERAPAZ: Cubilquitz, *Türckheim 4938* (G, NY); near Coban, *Türckheim 5406, 5833* (G, NY). QUEZALTENANGO: Volcán de Zunil, *Standley 65311, 65430* (NY).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley 54122, 56764* (NY, US). CORTEZ: N of Lake Yojoa, *Morton 7640c* (US). Guaimaca, *Weaver 4* (NY).

BELIZE. Maya Mts., *Robertson s.n.* (NY); near border with Guatemala, *Schipp 878* (NY).

EL SALVADOR. *Calderon 1768a* (US).

NICARAGUA. BLUEFIELDS: near Cerro San Isidro, *Proctor 27093* (NY, U). GRANADA: Volcán Mombacho, *Baker 2369, 2506* (NY).

COSTA RICA. CARTAGO: Alto de la Estrella, *Standley 39284* (US). GUANACASTE: Monteverde, *James 33* (US). HEREDIA: Yerba Buena, *Standley & Valerio 49965* (US). LIMÓN: near Tortuguero, *Steere 76, 87, 88, 89* (NY). PUNTARENAS: San Vito de Java, *Moore s.n.* (F, NY). SAN JOSÉ: near Cartago, *Griffin & Morales 147* (FLAS, NY), *Maxon 86* (NY); Parque Nac. Chirripó, *Chaverri et al. 1875* (U); Santa Maria de Dota, *Kappelle 2033* (U).

PANAMA. BOCAS DEL TORO: *Mendoza 1610* (PMA, NY). CHIRIQUÍ: near David, *Hélion s.n.* (NY); N of Audubon Cabin, *Croat 13616A* (MO, U). COCLÉ: El Valle de Anton, *Brako 8435* (NY); road Llano Grande-Coclesito km 7, *Antonio 1385, 1401* (MO, U). DARIÉN: SW of Boca de Cupe, *Allen 8689* (MO, NY, U); Cerro Pirre, *Salazar & Gradstein 9211, 9244* (PMA, U); Cerro Sapo, *Hammel 1247, 7296* (MO, U). PANAMÁ: Cerro Campana, *Stimson 5395, 5417* (US), *Salazar & Gradstein s.n.* (PMA, U). VERAGUAS: Cerro Tute W of Santa Fé, *Knapp & Sytsma 2477* (MO, U). Peninsula Azuero, Cerro Canajague, *Troll s.n., Hepaticae Sel. et Crit. (ed. Verdoorn) 47* (NY, U).

CUBA. ORIENTE: Sierra Maestra, Loma del Gato, *Léon et al. 10251* (NY); Baracoa, El Yunque Mt., *Underwood & Earle 667* (NY); *Ekman 3942, 3943* (S).

JAMAICA. Cockpit country, Troy, *Evans 666* (NY), *Underwood 2883* (NY); Hollymount, Mt. Diabolo, *Maxon 2205* (NY, US), *Maxon & Killip 450* (S, US); Cinchona, John Crow Peak, *Britton & Marble 214a* (NY, US).

HAITI. SUD: Cotà, *Ekman 156* (S).

DOMINICAN REPUBLIC. LA VEGA: La Sal on road to Casabito, *Buck 7983* (NY), *Zanoni et al. 20290* (NY). PEDERNALES: Las Abejas, N of Cabo Rojo, *Zanoni & Mejía 16689* (NY), *Buck 4333* (NY, U), *Reese 14942* (NY, U). PUERTO PLATA: Pico El Murazo, *Buck 4935* (NY), *Reese 15454* (NY).

PUERTO RICO. Maricao, *Steere 5545* (MICH, NY, U), *Britton 2491* (NY), *Pagán 5587* (MICH, U).

WINDWARD ISLANDS. GUADELOUPE. Without loc., *Herminier s.n.* (S, W). **DOMINICA.** Morne Diablotin, *Elliott 641, 690* (BM).

COLOMBIA. CASANARE: Sácama, *Aguirre et al. 2957, 3120* (COL, U). CAUCA: Tambito, *Bischler 280* (COL, PC, U). CUNDINAMARCA: Laguna Pedro-Palo, *Bischler 3035* (COL, PC, U), *VanderHammen et al. 2356* (COL, U). HUILA: San Agustín, *Bischler 611* (COL, PC, U), *Cleef 1730* (COL, U); Mun. La Plata, Merenberg, *Aguirre & Gradstein 6383* (COL, U). META: Villavicencio, *Linares & Gradstein 1544* (COL, U); La Macarena, *Schultes 11141* (COL, NY). RISARALDA: St. Rosa de Cabal, *van Reenen et al. 1829* (COL, U); Mun. San Antonio de Chami, Geguades, *Gradstein 8651* (COL, U). SANTA MARTA: near S. Sebastian, *Winkler C-12* (U). VALLE: La Cumbre, *Killip 11282* (NY); road Cali-Buenaventura km 72, *Bischler 316* (COL, PC, U).

VENEZUELA. ARAGUA: road La Victoria-Colonia Tovar, N of Pie de Cerro, *Luteyn et al. 8284* (NY); near Colonia Tovar, *Liesner & Medina 13494* (MO, U). DISTRICT FEDERAL: El Avila, *Nee & Whalen 16849* (NY); Libertador, NE of Colonia Tovar, *Steyermark et al. 127791* (MO, U, VEN). LARA: N of Urachiche, *Steyermark et al. 111726* (NY, US, VEN); Parque nacional Yacambu, *Steyermark et al. 103507* (MO, U, VEN). MÉRIDA: E of Santo Domingo, *Nee & Whalen 16949* (NY). PORTUGUESA: E of Chabusquén, *Steyermark et al. 126693, 126730* (MO, U, VEN). SUCRE: Rio Grande, *Bermudez A42* (MO, U). TACHIRA: above Bailadores, *Griffin 2186* (FLAS, NY, U); SE of Delicias, *Steyermark 118378* (MO, U). TRUJILLO: near Boconó, *Steyermark & Rabe 97397* (NY, US, VEN).

TRINIDAD. Mount Tocuche, *Britton et al. 1490* (NY, US).

GUYANA. Kanuku Mts., Mt. Iramaikpang, *Smith 3600, 3672* (NY, U, US), near Moco Moco village, *Maas & Westra 3857* (U), Cool Wind Mt., *Jansen-Jacobs et al. 381, 383A* (U).

SURINAME. Brownsberg, *Maas et al. 2317* (U), *Bekker 1024, 1061* (U), *Gradstein 4673, 4677* (U); Tafelberg, *Maguire 24643M* (NY, U); Lely Mts., *Lindeman et al. 355, 808* (NY, U).

FRENCH GUIANA. Mts. de Kaw, Camp Caiman, *Cremers 5800* (CAY, U); région Paul Isnard, *Feuillet 416* (CAU, U); Mts. Atachi Bacca, *de Granville 832* (CAY, U); Saül, *Cremers 4059, 5883* (CAY, U), *Gradstein 6132, 6216* (U), *Mori 18101, 18853* (NY); Tumac Humac Mts., *de Granville 1293a* (U).

ECUADOR. AZUAY: Gualaquiza, *Allioni 6505* (G). ESMERALDAS: E of San Mateo, *Steere & Balslev 7 colls.* (NY). GUAYAS: W of Bucay, *Lojtnant & Molau 15613* (AAU, NY). LOS RIOS: Hacienda Clementina, *Harling 2118* (S); Rio Palenque Forest reserve, *Gradstein et al. 6935* (U). NAPO: Anangu, *Churchill & Sastre 13852* (NY). PASTAZA: W of Puyo, Thiers 4749, 4770 (NY). PICHINCHA: near San Miguel de los Bancos, *Buck 10323, 10528* (NY); W of Chiriboga, *Brako 4947c* (NY). SANTIAGO-ZAMORA: *Mendéz 2230, 2263* (S). TUNGURAHUA: road Banos-Puyo, near Río Pastaza bridge, *Thiers 4805* (NY). GALÁPAGOS ISLANDS: Floreana, *Gradstein H182, Bryoph. Neotrop. Exsicc. 33* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, XAL); Isabela, Cerro Azul, *Gradstein & Sipman 391* (COLO, U), Alcedo, *VanderWerff 1443, 2018* (U); Pinta, *Gradstein et al. H511* (NY, U); Santa Cruz, *Weber B-13514* (COLO, NY), *Gradstein & Weber H38, H103* (COLO, NY, U); San Cristobal, *Gradstein & Lanier H299* (U).

PERU. CUZCO: Macchu Picchu, *Cook & Gilbert 842* (US), Herrera 3297 (US). HUANUCO: Sinchono, *Aguilar 889* (US); Tingo Maria, *Hegewald 8333* (NY, U). JUNÍN: road San Ramon-Tarma, *Hegewald 8534* (NY, U).

BRAZIL. AMAZONAS: Rio Negro, Serro Curicuriari, *Schuster 540, 567, 647, 712* (NY), *Buck 2473, 2495* (NY). GOIAS: N of Formosa, *Irwin et al. 15559* (NY, US). MATO GROSSO: Mun. Cuiabá, *Thomas et al. 4494* (NY); Veu de Noiva, *Prance et al. 19400* (NY). PARÁ: Rio Maicuru, *Strudwick & Sobel 3771* (MG, NY, U). RIO DE JANEIRO: S face of Mt. Itatiaia, *Eiten 6409* (NY); Serra dos Orgãos, *Frahm 1710* (U). RIO GRANDE DO SUL: Cambará do Sul, *Wasum et al. 2305* (NY), Nova Prata, *Wasum et al. 2908* (NY). RORAIMA: Serra Tepequem, *Prance et al. 4469* (INPA, NY, U). SANTA CATARINA: Curitybanos, Reitz & Klein 15012 (US). SÃO PAULO: near Iguape, *Schiffner s.n., Crypt. Exsicc. Mus. Hist. Nat. Vind. 4271* (NY, U, W); Itú, *Hoehne 671* (JE, NY); Barro do Turvo, *Vital 2805* (SP, U).

BOLIVIA. BENI: Ballívian, Serranía del Pilón Lajas, *Gradstein 7150, 7162, 7206, 7304* (LPB, U). COCHABAMBA: road Cochabamba–Villa Tunari, *Gradstein 7512* (LPB, U). LA PAZ: near Coroico, *Buchtien 22, 196*

(JE, S, US); road Caranavi–San Borja 30–40 km, *Gradstein 7080* (LPB, U). SANTA CRUZ: Parque Nacional Amboró, *Nee 35010, 36015* (NY). TARIJA: Acre, SW of La Marmora, *Lewis 84-2282* (LPB, U).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Bryopteris filicina is one of the most common and conspicuous liverworts of neotropical upland rain forests and because of its large size has more often been collected than any other species of Lejeuneaceae. The material cited above is only a small fraction of the enormous amount of material available in the various herbaria and includes, in particular, recent specimens. Older collections have been cited *in extenso* in Stotler and Crandall-Stotler (1974). Because of its wide distribution *B. filicina* shows considerable morphological variation. It has been described in the past under many different names, some of which were accepted by Stotler and Crandall-Stotler (1974) as discrete taxa. I have found the variation in this species to be continuous and have been unable to recognize more than one taxon.

The species has sometimes been confused with *Bryopteris diffusa*, which differs in many respects, however. Relationships among these two species and with the African *B. gaudichaudii* and the fossil *B. succinea* are briefly discussed under *B. diffusa*. Old World records of *B. filicina* usually represent *Ptychanthus striatus*, which has a similar growth habit. For differences between the two genera see above.

Branching in *Bryopteris filicina* is regularly pinnate in rather short or young plants growing away from the substrate in a straight manner, but pendent, more elongated stems and plants growing in deep shade usually have a more laxly and more irregularly pinnate to bipinnate (to tri-pinnate) habit. The secondary and tertiary branches of these plants are rather small and stand at almost right angles with the main branches. Tiny, flagelliform branchlets of the *Lejeunea*-type are often produced in these plants. Sometimes they are easily detached, e.g. in coll. *Gradstein 8651* from Colombia, and function as means of vegetative reproduction. They may also develop on more densely and regularly pinnate forms, however. The laxly branched plants have been described as *B. trinitensis* and *B. tenuicaulis* but in my interpretation they are mostly somewhat etiolated shade forms. Leaves in these forms are often rather short ovate and plane and somewhat distant.

Leaves in *Bryopteris filicina* may be toothed all along the upper half of the dorsal and ventral leaf margins but more often there are only few teeth and some populations have mostly entire leaves. The latter were described as *B. flaccida*. The teeth are always sharp but vary considerably in size and on a single stem leaves with many or with few teeth may be found. Occasionally, small primary shoot-type leaves and underleaves with entire margins are produced on elongated branches, resembling stolons! Spreading of the leaves may be oblique or wide and in the latter case they may become strongly falcate. The ventral leaf margin is usually distinctly upcurved but in weaker populations with small, spatiated leaves described as *B. tenuicaulis* margins are plane.

Underleaves of *Bryopteris filicina* vary considerably in length and in some populations they are very short and broader than long whereas in others (e.g. Colombia, *Bischler 6110*) they are elongated rectangular and twice as long as wide. Size of ther male barcteoles also varies considerably and in some populations they are very tiny and become reduced towards the apex of the spike. The specialized male spikes of *Bryopteris* are unusual for members of the subfamily Ptychanthoideae and are a feature reminiscent of the Lejeuneoideae. Female shoots, finally, are normally short–specialized as usual in the genus. I have seen a collection from Brazil (*Burchell 2515*), however, in which the female branches were distinctly elongated and had several series of vegetative leaves preceding the involucre.

ACROLEJEUNINAE Gradstein *subtrib. nov.*

Ptychantheae subtribe Acrolejeuninae Gradstein. Type. *Acrolejeunea* (Spruce) Schiffner.

Guttae olei homogeneae.

Plants creeping, ascending or pendent, never dendroid. Stem epidermis cells usually colorless and larger than medullary cells (not larger and sometimes brown in *Spruceanthus* and *Marchesinia*). Median leaf cells isodiametric or elongated, trigones simple-triangular to radiate, or cordate; oil bodies homogeneous. Innovations pycnolejeuneoid (lejeuneoid in *Spruceanthus*) or lacking. Perianth variable: with 1–2 sharp ventral keels, pluriplicate, or (*Marchesinia*) flat and without ventral keels.

Distribution. Pantropical. The subtribe Acrolejeuninae consists of eight genera, six of which occur in the neotropics: *Spruceanthus*, *Marchesinia*, *Lopholejeunea*, *Caudalejeunea*, *Acrolejeunea* and *Frullanoides*. Other members of this subtribe are *Cephalolejeunea* and *Trocholejeunea*, both in Asia.

The stem hyalodermis of most genera, the homogeneous oil bodies and the pycnolejeuneoid innovations are the characteristic features of this group. The subtribe is linked to the Ptychanthinae by the genus *Spruceanthus*.

8. **Spruceanthus** Verdoorn, Ann. Bryol. Beih. **4:** 159. 1934. Type. *Spruceanthus semirepandus* (Nees) Verdoorn. Genus named after Richard Spruce, well-known British hepaticologist and explorer of the Amazon basin.

For description see under the species.

Distribution. The genus *Spruceanthus* is mainly distributed in Southeast Asia and Australia, where six species occur (Gradstein, 1991). One species is known from the neotropics.

1. **Spruceanthus theobromae** (Spruce) Gradstein, Beih. Nova Hedwigia **80:** 26. 1985; *Lejeunea theobromae* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 99. 1884; *Ptychanthus theobromae* (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893. Type. Ecuador. Los Rios: "Río Ventana propre Guayaquil, in *Theobromae cortice*," *Spruce s.n.* (G, MANCH 17343, 17344, W). Fig. 28.

Autoicous or paroicous, usually fertile. *Plants* robust, 3–3.5 mm wide, brown green when dry, loosely ascending to pendent (?) from bark. *Branching Lejeunea*-type, fertile plants becoming dichotomous by forked innovations, recurved flagelliform branchlets present on lower portions of stem. *Stems* robust, in cross section ca. 12–13 cells across, composed of ca. 35 epidermal cells surrounding numerous (over 100) medullary cells, outer medullary cells differentiated into a 1–2 layered subepidermis, epidermal and subepidermal cells smaller and more strongly thickened than inner medullary cells, wall of epidermis and subepidermis brownish pigmented, inner walls colorless; ventral merophyte ca. 16 cells wide. *Leaves* widely spreading when dry, contiguous to subimbricate, dorsal lobe ± oblong, 1.8–2.2 × 1.2–1.4 mm, apex rounded to apiculate, plane, margins entire, dorsal margin plane, ventral margin plane or slightly upcurved, forming a straight line with the keel; leaf cells distinctly elongate, in mid-leaf 35–40 × 15–20 mμ, trigones very small, irregularly radiate, tending to become coalesced, intermediate thickenings inconspicuous, 0–several per wall, the cell walls mostly thin, towards leaf margin conspicuously thickened; oil bodies not observed (homogeneous, *Massula*-type in Asiatic species); ocelli lacking. *Lobules* very small, all reduced to a small fold, apical tooth one-celled; hyaline papilla not observed. *Underleaves* rather small, distant, transversally ovate to suborbicular, 2–2.5× stem width, ca. 0.6 × 0.5 mm, apex rounded, margins plane, the basal portions somewhat wrapped around the stem and concave in the corners, the bases and the insertion line straight. *Androecia* on short lateral branches or on main stem below the gynoecium, bracts smaller than leaves, in 3–7 series, lobule large, inflated, hypostatic, underleaves present throughout; antheridia not observed. *Gynoecia* with 1–2 lejeuneoid subfloral innovations, usually one pair of innovations below and repeatedly fertile single innovations above, the innovations often very short with perianths arranged in a series, bracts in one series, smaller than leaves, up to 1.5 mm long, lobe broadly lanceolate, acute, margins entire or with a few blunt teeth, lobule up to 1/2–2/3× lobe length, with 1–2 teeth near apex, keel short 0.1–0.2× lobe length, without wing, inner bract slightly different from outer bract, more flattened, narrower and with shorter keel; bracteole squarrose-canaliculate, narrow oblong, ca. 1.2 mm long, margins irregularly erose-dentate above, apex short bifid. *Perianths* long exserted, with 5–8 keels above: 2 lateral keels, 1–2 weak dorsal keels and 3–4 ventral keels (3 of them inserted on swollen main keel). *Sporophyte* (immature; seta non-articulate in Asiatic species): spores isodiametrical, with rosettes; elaters 72(?) per capsule, each with one spiral. *Vegetative reproduction* not observed.

Distribution. A rare species known only from coastal Ecuador where it has been collected three times in the Province Los Rios, between Quevedo and Guayaquil. The species has been found growing on bark of a tree along a rivulet in virgin

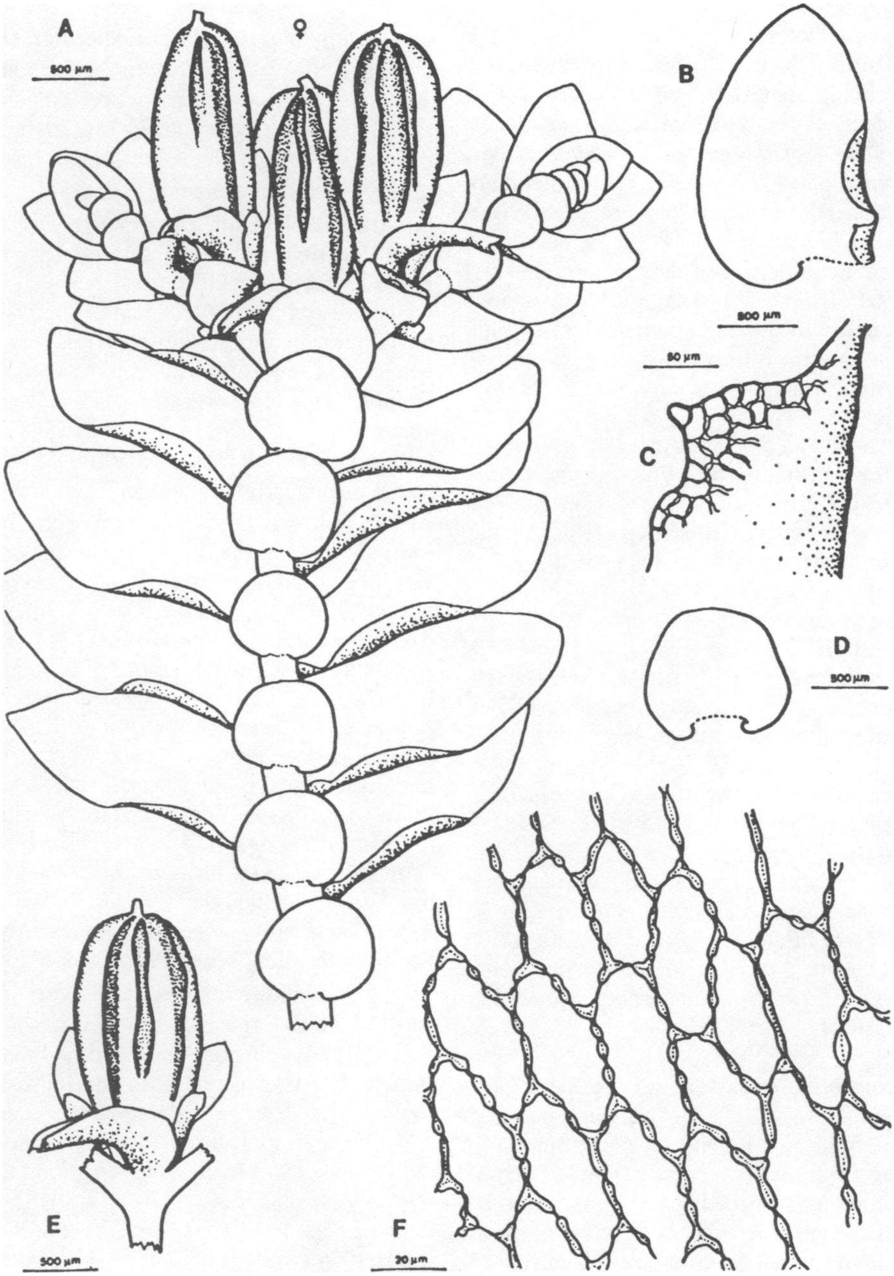

FIG. 28. *Spruceanthus theobromae*. **A.** Habit, with three gynoecia. **B.** Leaf. **C.** Lobule apex. **D.** Underleaf. **E.** Gynoecium. **F.** Leaf cells. From the type.

semi-deciduous rain forest at the foot of the Andes, and on cocoa trees, ca. 150–300 m.

Specimens examined. ECUADOR. Los Ríos: Hacienda Clementina, Samana, *Harling 2106b* (JE, U), Mumbe, *Harling 2120a* (JE).

Conservation. *Spruceanthus theobromae* has only been collected in the mid 19th century and in 1947. Since the 1960s most of the region where it occurs has been deforested, but the forest in the area of the Hacienda Clementina, where Harling collected the species in 1947, may still be intact (Prof. Gunnar Harling, pers. comm., Feb 1991). It is unknown whether *S. theobromae* continues to exists in the area; the species has been classified as "endangered" by Gradstein (1992c) and has been included in the IUCN World Red List. Its conservation is of considerable importance as the species is the only representative of *Spruceanthus* in the New World.

Spruceanthus theobromae is a very distinct species, easily recognized by relatively large size (3–3.5 mm wide), its dichotomous habit, and its numerous, 5–8-plicate perianths which are often arranged in a series. By its gynoecia *S. theobromae* somewhat resembles *Archilejeunea* subgen. *Dibrachiella* (*A. auberiana*, *A. parviflora*), but differs by it much larger size and pendent (?) growth, robust stems with a clearly differentiated epidermis and subepidermis, flagelliform branches at the stem bases, elongated leaf cells, and by the pluriplicate perianths. All of these are diagnostic characters of the genus *Spruceanthus*, except for the elongated leaf cells which are a unique feature of *S. theobromae*. All other species of *Spruceanthus* have isodiametric leaf cells.

Spruceanthus and *Archilejeunea* also differ by the occurence of homogeneneous oil bodies in the former and segmented oil bodies in the latter (Thiers & Gradstein, 1989). In *S. theobromae* oil bodies have not yet been observed, however.

9. Marchesinia S. Gray[1], Nat. Arr. Brit. Pl. **1:** 679. 1821 "*Marchesinius*," corr. Carrington 1870; Evans, Bull. Torrey Bot. Club **34:** 543. 1907; *Phragmicoma* Dumortier, Comment. Bot. 112. 1822, nom. illeg. *Lejeunea* subgen. *Homalolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 132. 1884; *Homalolejeunea* (Spruce) Lacouture, Rev. Bryol. **35:** 106. 1908, hom. illeg. Type. *Jungermannia mackaii* Hooker (= *Marchesinia mackaii* (Hooker) S. Gray). Genus named after J. G. Marchesini, Italian Professor of medicine and one of the sponsors of Micheli's Genera Plantarum.

Plants 2–10 cm long x (1–)2–4 mm wide, dull or glossy green to brown to black, ascending or pendent when fertile, largely growing free from the substrate and often forming mats, irregularly pinnate, female shoots forked by paired, repeatedly fertile innovations. *Branching* predominantly *Lejeunea*-type, occasionally *Frullania*-type, flagelliform branches lacking. *Stems* rigid, brown, in cross section with weakly enlarged epidermis, epidermal cells quadrate-rectangular, dorsal epidermal cells wider and somewhat higher than the medullary cells, ventral epidermal cells not larger than medullary cells, all cell walls thickened, epidermal walls brown, medulla colorless; ventral merophyte (4–)6–11 cell rows wide. *Leaves* plane or deflexed when dry, obliquely to widely spreading when moist, apex rounded to acuminate, rarely obtuse, plane or reflexed, margins entire or toothed; leaf cells isodiametric-hexagonal to slightly elongate, averaging 30 µm in diam., walls sometimes with darkish pigmentation, trigones usually triradiate, sometimes very small, intermediate thickenings usually frequent, one per wall, oil bodies homogeneous in neotropical species, ocelli and vitta lacking (the type species of the genus, *Marchesinia mackayi* from Europe, has segmented oil bodies; see Geissler, 1990). *Lobules* 1/6–1/3x lobe length, sometimes reduced, flat or slightly inflated, with 1–4 teeth; hyaline papilla positioned below the proximal base of the apical tooth on the inner surface of the lobule. *Underleaves* 3–8x stem width, apex rounded, margins entire or toothed, bases usually decurrent, insertion line deeply arched in neotropical species; underleaf base at the rhizoid disc bistratose, in cross section with up to eight (or more?) rhizoid disc initial cells. *Androecia* on elongated branches, terminal or intercalary, bracts smaller than leaves, becoming progressively smaller towards apex of spike, lobules large, hypostatic, bracteoles present throughout spike, smaller than underleaves; antheridia 2 per bract. *Gynoecia* with (1–)2 pycnolejeuneoid subfloral innovations, bracts in one series, suberect, about as large as leaves but narrower, often toothed, lobules reduced or well-developed, keel unwinged; bracteoles as long as bracts, undivided or bifid, often toothed. *Perianths* usually exserted and becoming brown when mature, obovate-oblong, strongly flattened with plane ventral and dorsal surface, the lateral margins entire, the apex

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[1] By S. Rob Gradstein and Patricia Geissler.

broadly truncate and distinctly beaked, cell walls thin-walled below, thickened towards apex. *Sporophyte:* seta not articulate, made up of (16–) 25 outer cell rows surrounding (4–)20 inner cell rows; elaters 72 per capsule (van Slageren, 1985), with two pale brown spirals; otherwise as in the tribe. *Vegetative reproduction* by caducous or fragmenting leaves in *Marchesinia brachiata. Chemistry:* eugenol-derivates, luteolin di-C-glycosides.

Distribution. The genus *Marchesinia* occurs in tropical America, tropical Africa and western Europe and contains five species, two of which occur in tropical America. The genus occurs throughout the humid portions of tropical America, from the lowlands to high montane elevations up to 3300 m. The species grow on bark and rock in primary and secondary rain forests, in scrub and in plantations.

In the neotropics *Marchesinia* may be recognized when sterile by its rigid, brown stems with irregular, *Lejeunea*-type branching, elongated leaves with isodiametric cells and radiate trigones, small, rather flat lobules with several teeth and large, strongly decurrent underleaves with deeply arched insertion line. The depth of the insertion almost equals the length of the underleaf (measured from the rhizoid disc to the apex).

The genus is most closely related to *Lopholejeunea.* The two genera share the occurrence of blackish pigmentation in cell walls; morphological differences include the different stem structure, the different gynoecium, etc. Chemically, the two genera are also quite different: eugenol-derivates are the chemical markers of *Marchesinia* whereas calamenanes characterize *Lopholejeunea.*

Sterile *Marchesinia* closely resembles *Symbiezidium* (Brachiolejeuneae), but the latter has strongly inflated, never reduced lobules with involuted free margin and without or with an obscure tooth; in *Marchesinia* lobules are rather flat and the free margin is usually plane (incurved in very small lobules) and has (1–)2–4 evenly spatiated teeth. When fertile, *Marchesinia* is immediately recognized by its flat, smooth perianth positioned on an elongated shoot and with (1–)2, usually fertile innovations; male spikes have bracts with large, hypostatic lobules and bracteoles throughout the spike. In neotropical *Symbiezidium* the perianth is somewhat inflated, ciliate-laciniate and positioned on a very short lateral branch, with one short, sterile innovation; the male spike has one or two bracteoles limited the base of the spike only. A flat perianth with two innovations is also found in the Andean genus *Lindigianthus*, but the latter has broadly recurved leaves (± plane in *Marchesinia*), fragile stems made up of thin-walled cells (thick-walled in *Marchesinia*) and epistatic male bracts. Habitually *Lindigianthus* is easily recognized in the field and in the herbarium by its glossy brown color.

Within Ptychanthoideae, *Marchesinia* is one of the few genera with a rather thick seta consisting of more than 20 longitudinal rows of cells. In material of *M. brachiata* from the Galapagos Islands (*vanderWerff 1439*, U) we found a seta of about 40–45 longitudinal cell rows: ca. 25 outer cells and 16–20 inner cells. A thick seta was also recorded by van Slageren and Berendsen (1985).

Key to the Species of *Marchesinia*

1. All underleaves sharply toothed, underleaf margin recurved; leaves rectangular with broad apex, with 4-12 teeth near apex and along the ventral margin. Andes (Colombia-Bolivia), 500–2500 m . . . 2. *M. robusta.*
1. Underleaves entire (sometimes toothed on female shoots), margin plane or recurved; leaves ovate-oblong, narrowed to apex, entire or with a few (up to 6) teeth near apex. Common throughout tropical America, lowland to 3300 m. . . . . 1. *M. brachiata.*

1. **Marchesinia brachiata** (Swartz) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; Evans, Bull. Torrey Bot. Club **34:** 546, Pl. 32. 1907; *Jungermannia brachiata* Swartz, Nova Gen. Spec. Pl. Prodr. 144. 1788; *Lejeunea brachiata* (Swartz) Nees, Syn. Hep. 313. 1845; *Symbiezidium brachiatum* (Swartz) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877. Type. Jamaica. *Swartz s.n.* (holotype, S; isotypes, BM, E, S). Fig. 29.

Lejeunea languida Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **5:** 59. 1836; *Symbiezidium languidum* (Nees & Montagne) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Marchesinia languida* (Nees & Montagne) Stephani, Spec. Hep. **5:** 149. 1912. Type. Peru. "Yungas," *d'Orbigny 194* (holotype, PC; isotypes, BM, G, JE, PC, S, STR, U, W).

Lejeunea bongardiana Lehmann & Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **7:** 18. 1838;

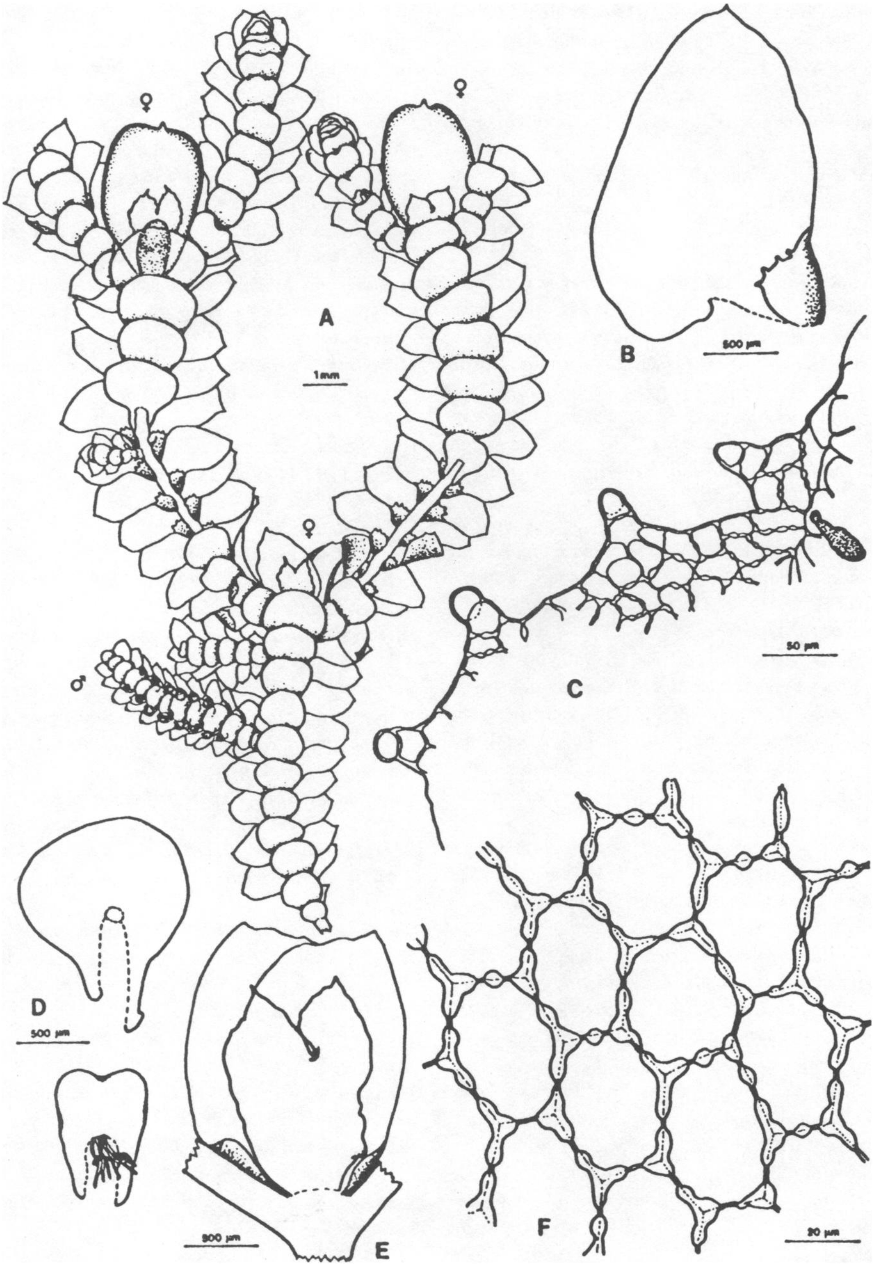

FIG. 29. *Marchesinia brachiata*. **A.** Habit, with three gynoecia and one androecial branch. **B.** Leaf. **C.** Lobule free margin. **D.** Underleaves. **E.** Gynoecial bracts and bracteole. **F.** Leaf cells. From Galapagos Is., *VanderWerff 1439*.

Phragmicoma bongardiana (Lehmann & Lindenberg) Lindenberg, Syn. Hep. 740. 1847; *Marchesinia bongardiana* (Lehmann & Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 405. 1877. Type. Brazil. Rio de Janeiro, *Bongard s.n.* (holotype, S; isotypes, G, PC, S, STR).

Phragmicoma guilleminiana Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **16:** 128. 1841; *Marchesinia guillemini-*

ana (Nees & Montagne) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 405. 1877; *Lejeunea guilleminiana* (Nees & Montagne) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 134. 1884. Type. Brazil. Rio de Janeiro, Mt. Corcovado, *Guillemin s.n.* (holotype, PC; isotypes, G, S, STR).

Phragmicoma guilleminiana ß *mexicana* Gottsche, Mex. Leverm. 171. 1863. Type. Mexico. Veracruz: Orizaba, *Müller s.n.* (lectotype NY, here designated; isotype, BM, G).

Phragmicoma guilleminiana Nees & Montagne var. *inermis* Gottsche ex Schiffner, Hedwigia **33:** 179. 1894. Type. Cuba. *Wright s.n.* (lectotype, FH, here designated; isolectotypes, BM, G, MANCH, NY). A form with entire female involucre.

Lejeunea guilleminiana (Nees & Montagne) Spruce var. *cardiantha* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 134. 1884. Type. Ecuador. Pallatanga, *Spruce s.n.* (holotype, MANCH 17571).

Lejeunea complicata Hampe *in* Gottsche, Lindenberg & Nees, Syn. Hep. 321. 1845; *Phragmicoma bongardiana* ß* *complicata* (Hampe) Gottsche, Lindenberg & Nees, Syn. Hep. 741. 1847. Type. Venezuela. Caracas, *Moritz s.n.* (holotype, BM; isotype, S)

Phragmicoma galapagona Ångström, Ofvers. Förh. Kongl. Svenska Vetensk.-Akad. 30, **5:** 114. 1873; *Brachiolejeunea galapagona* (Ångström) Stephani, Spec. Hep. **5:** 139. 1912; *Marchesinia galapagona* (Ångström) Stephani, Spec. Hep. **5:** 146. 1912. Type. Ecuador. Galapagos Is.: Floreana ("Charles"), 1852, *Andersson s.n. (holotype, S; isotypes, FG, G).*

Phragmicoma nigrescens Ångström, Ofvers. Förh. Kongl. Svenska Vetensk.-Akad. **30:** 115. 1873. Type. Ecuador. Galapagos Is.: Floreana ("Charles"), *Andersson s.n. (holotype, S; isotypes, FH, G, S, U).*

Lejeunea siliculosa Wilson ex Spruce, Trans. Proc. Bot. Soc. Edinburgh **15:** 134. 1884; *Marchesinia siliculosa* (Wilson ex Spruce) Stephani, Spec. Hep. **5:** 143, 153. 1912. Type. Colombia. *Purdie s.n.* (holotype, BM; isotype, NY), *syn. nov.*

Lejeunea palaeflora Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 136. 1884. Type. Ecuador. Chimborazo, *Spruce s.n.* (holotype, MANCH 17588; isotypes, FH, M, W, YU).

Lejeunea clavulata Spruce, Mem. Torrey Bot. Club **1:** 121. 1890; *Brachiolejeunea clavulata* (Spruce) Stephani, Spec. Hep. **5:** 129. 1912. Type. Bolivia. Mapiri, *Rusby 3072* (holotype, MANCH 17551).

Lejeunea guilleminiana (Nees & Montagne) Spruce var. *laxa* Stephani, Hedwigia **29:** 17. 1890. Type. Brazil. Rio de Janeiro, *Luschnath s.n.* (holotype, G; isotype, W).

Lopholejeunea saxatilis Gottsche ex Steph., Spec. Hep. **5:** 71. 1912; *Phragmicoma saxatilis* Gottsche ex Ångström, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. **33 (7):** 83. 1876, nom. inval. Type. Brazil. Minas Gerais: Caldas, *Lindberg s.n.* (holotype, S; isotype, PC), *syn. nov.*

Brachiolejeunea lacerostipula Stephani, Spec. Hep. **5:** 119. 1912. Type. Brazil. São Paulo: Apiahy, *Puiggari 140b* (holotype, G 20162).

Marchesinia cubensis Stephani, Spec. Hep. **5:** 148. 1912. Type. Cuba. *Wright 135* (holotype, G 21837; isotypes, FH, G), *syn. nov.*

Marchesinia saccata Stephani, Spec. Hep. **5:** 151. 1912; *Marchesinia brachiata* (Swartz) Schiffner var. *saccata* (Stephani) Herzog, Rev. Bryol. Lichénol. **20:** 137. 1951. Type. Costa Rica. Alajuela: Río Naranjo, *Tonduz 3091* (holotype, G 18818; isotype, G).

Marchesinia quadridens Stephani, Spec. Hep. **5:** 152. 1912. Type. Jamaica. *Maxwell s.n.* (holotype, G 21843), *syn. nov.*

Marchesinia denticulata Stephani, Spec. Hep. **5:** 153. 1912. Type. Panama. Chiriqui: *Hélion s.n.* (holotype, G 21838), *syn. nov.*

Ptychocoleus dentilobulus Stephani *in* Herzog, Biblioth. Bot. **17:** 250. 1916. Type. Bolivia. Florida de San Mateo, *Herzog 3663* (holotype, G 14614; isotypes, JE, L, M, MANCH, S, UPS, W).

Marchesinia longissima Stephani *in* Herzog, Biblioth. Bot. **87:** 252. 1916. Type. Bolivia. Cochabamba: Tablas, *Herzog 4532* (holotype, G; isotypes, B, M), *syn. nov.*

Dicranolejeunea oblongifolia Stephani *in* Herzog, Biblioth. Bot. **87:** 254. 1916. Type. Bolivia. Cochabamba: Tablas, *Herzog 4533* (holotype, G).

Marchesinia trapezoidea Herzog, Hedwigia **67:** 251. 1927. Type. Brazil. Rio de Janeiro: Mt. Corcovado, *Herzog. s.n.* (holotype, JE; isotype, B), *syn. nov.*

Marchesinia trollii Herzog *in* Verdoorn, Ann. Bryol. **5:** 137. 1932. Type. Panama. Peninsula Azuero, Cerro Canajagua, *Troll s.n., Verdoorn (ed.), Hep. Sel. Crit. 156* (holotype, JE; isotypes, B, BR, FH, G, JE, M, NY, S, U, US, YU), *syn. nov.*

Marchesinia minor Herzog, Rev. Bryol. Lichénol. **20:** 137. 1951. Type. Costa Rica. Guanacaste: Tilarán, *Standley 44393* (holotype, JE; isotype, US), *syn. nov.*

Marchesinia longirostris Herzog, Rev. Bryol. Lichénol. **20:** 138. 1951. Type. Costa Rica. Guanacaste: Tilarán, *Standley 44309* (holotype, JE; isotypes B, US), *syn. nov.*

Marchesinia longirostris Herzog var. *rivularis* Herzog, Rev. Bryol. Lichénol. **20:** 138. 1951. Type. Costa Rica. Cartago: Río Reventado, *Standley 49561* (holotype, JE; isotypes, B, US), *syn. nov.*

Marchesinia aquatica Herzog, Feddes Repert. Spec. Nov. Regni Veg. **57:** 174. 1955. Type. Colombia. Norte de Santander: near Chinácota, *Killip 20812* (holotype, JE; isotypes, B, JE), *syn. nov.*

Marchesinia cavistipula Herzog, Feddes Repert. Spec. Nov. Regni Veg. **57:** 202. 1955. Type. Bolivia. Tipuani, Hacienda Simaco, *Buchtien s.n.* (holotype, JE; isotype, B), *syn. nov.*

Dioicous or autoicous; *plants* variable in size, 2–10 cm long × 1.5–3 mm wide, deep green to olive green to blackish, when dry becoming dull brown or blackish. *Stems* in cross section composed of 15–32 epidermal cells surrounding numerous (up to 100) medullary cells; ventral merophyte 6–11 cell rows wide. *Leaves* imbricate to distant, plane or convex, not squarrose, dorsal lobe ovate to oblong, ca. 0.8–2.5 mm long × 0.8–1.8 mm wide, apex broadly rounded, mostly apiculate to short acuminate, margins plane or somewhat recurved, ventral margin almost straight, forming an angle of 90–150° with the keel, margins entire or with a few (up to 6) sharp teeth near apex, teeth variable in length, 1–10 cells long and up to 5 cells wide at base; median cells about 30–50 µm in largest diam.; oil bodies homogeneous, *Massula*-type but rather large, 7–15 per cell, bluntly ellipsoid to globose, 5–9 × 3–5 µm. *Lobules* obovate-obtrapezoid to oblong, 1/6–1/3× lobe length, sometimes reduced, keel normally arched, straight in reduced lobules, free margin straight or gently curved, sometimes sinuate, usually plane (incurved in very small lobules), with (1–)2–4 evenly spatiated teeth, teeth 1–2(–3) cells long, straight or inflexed, the first tooth longest. *Underleaves* imbricate or distant, plane to deeply concave with broadly recurved margins, broadly obovate-orbicular, 3–8× stem width, apex rounded or truncate, plane or recurved, margins entire, becoming toothed on female shoots especially towards the female involucre, bases decurrent, in weak etiolated forms variable and sometimes cuneate or auriculate. *Androecia* with up to 20 series of bracts. *Gynoecia* with two subfloral innovations, bract lobes as long as leaves but narrower, apex sharply acute-apiculate, margins toothed in the upper half or ± entire, lobules ovate-lanceolate, 1/3–1/2× lobe length or reduced to a small fold, entire, rarely with a few teeth; bracteole obovate-oblong to spathulate, 1–1.5 mm long × 0.7–1 mm wide, apex truncate to short bifid with sharply pointed lobes, margins irregularly toothed above to subentire. *Perianths* immersed to long exserted, ca. 2–4 mm long × 1.5–2 mm wide. *Sporophyte* as in the genus. *Vegetative reproduction* by means of caducous or fragmenting leaves.

Chemistry: dimethyl-eugenol and two luteolin di-C-glycosides are important chemical constituents of this species (Gradstein et al., 1985; Kruijt et al., 1986).

Distribution. Throughout the humid portions of tropical America, from sea level up to 3300 m; also in tropical Africa. *Marchesinia brachiata* grows on bark in the canopy and undergrowth of primary and secondary rain forests, usually in partial shade, in humid scrubby vegetations and in plantations. The species grows also on rock.

Fossil *Marchesinia brachiata* has been found in Miocenic amber of the Dominican Republic (see FOSSILS).

Selected specimens examined. MEXICO. CHIAPAS: El Suspiro, *Hale & Söderström 20152* (US); Puerto Vientes, *Robinson 9851* (US). **OAXACA:** Valle Nacional, *Robinson 10127* (US). **SAN LUIS POTOSÍ:** Jilitla, *Massey s.n.* (PC). **VERACRUZ:** Huatusco, *Liebman s.n.* (G); s.l., *Eggers & Frahm MX15,3* (U).

GUATEMALA. ALTA VERAPAZ: Finca Mocca, *Johnson 120* (YU).

EL SALVADOR. *Büttner 1889* (G).

COSTA RICA. ALAJUELA: Río Naranjo, *Tonduz 15575, 15683* (G). **HEREDIA:** Yerba Buena, *Standley & Valerio 50019* (YU). **PUNTARENAS:** Monteverde, 1962 *James s.n.* (US); Coto Brus, *Sipman 11936* (U). **SAN JOSÉ:** La Palma, *Werckle 1910* (FI, PC, YU), *Maxon 474* (NY, YU), *Standley 28050* (B).

PANAMA. PANAMÁ: Summit Garden, *Salazar & Gradstein 9496* (PMA); Barro Colorado Is., *Standley 40789* (YU).

CUBA. HABANA: Lomas de Camoa, *Léon 2700* (HAC, NY); laguna Ariguanabo, *Léon 5038, 9746* (HAC, NY, YU). **MATANZAS:** Madruga, *Britton et al. 661* (NY, YU). **ORIENTE:** Sierra Maestra, Loma del Gato, *Léon et al. 10593* (HAC), Pico Turquino, *Léon & Ekman 11283* (HAC), *Pócs 9085* (EGR, HAC, U); Sierra de la Gran Piedra, *Reyes 1424* (HAC), *Pócs & Reyes 9057* (EGR, HAC, U). **PINAR DEL RÍO:** S. Anafe, *Léon 7444* (YU). **VILLA CLARA:** Sierra de Escambray, Pico Potrerillo, *Pócs & Borhidi 9010* (EGR, HAC, G, U), Topes de Collantes, *Pócs & Borhidi 9004* (HAC).

JAMAICA. John Crow's Peak, *Underwood 690, 727, 741, 851* (NY, YU); Morce's Gap, *Maxon & Killip 1284 (US, YU); Mt. Helen*'s Gap, 1981, *Ammann s.n. (G); Troy, Evans 640, 683* (YU); St. James, *Hegewald 8203, 8204* (U).

HAITI. *Picarda s.n.* (G).

DOMINICAN REPUBLIC. Barahona, Polo, *Abbott 1856* (YU).

PUERTO RICO. Luquillo Mts., *Heller 1145* (NY, US, YU), El Yunque, *Evans 59* (NY, YU); Toro Negro, *Griffin 21758* (U).

LEEWARD ISLANDS. ST. MAARTEN. *Suringar 102* (G). **SABA.** *Suringar 98, 100* (G), *van Slageren H23-8* (G, U).

WINDWARD ISLANDS. MARTINIQUE. Mt. Peleé, Grande Rivière, *Duss 618, 636, 652* (G, NY). **ST. VINCENT.** Richmond Park, *unknown collector* (BM, MANCH).

TRINIDAD. *Fendler s.n.* (E, NY, YU).

COLOMBIA. BOYACÁ: road Chiquinquirá-Pauna, *vanderHammen et al. 1766* (COL, U); Chobugan, *Grubb & Guymer 8304* (BM). **CASANARE:** Sacama, *Aguirre et al. 2942, 3024* (COL, G, U). **CUNDINAMARCA:** laguna Pedro-Palo, *Bischler 3030* (COL, PC, U); San Antonio de Tena, Chicaque, *Linares & Gradstein 3514* (COL, U). **HUILA:** Hoya del Magdalena, *Bischler 622* (COL, PC, U). **META:** Villavicencio, *Gradstein 1520a* (G). **RISARALDA:** Santa Rosa de Cabal, Termales, *Aguirre et al. 6226, Bryoph. Neotrop. Exsicc. (ed. Gradstein) 143* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PAN, QCA, S, SP, USJ, XAL), El Limbo, *van Zanten & Gradstein 567* (U). **SANTANDER:** Charalá, *Castro et al. 157* (COL, U). **TOLIMA:** St. Isabel, *van Reenen 2203* (COL, U). **VALLE:** La Guarida, *Cuatrecasas 22142* (US).

VENEZUELA. FALCÓN: Paraguaná peninsula, *Griffin & Wingfield 1665* (U); Cerro Maracuica 38 km E of Coro, *Wingfield 13494* (U). **LARA:** Río Guyamure above Río Clara, *Griffin et al. 377* (FLAS, U). **MÉRIDA:** La Pedregosa, *Hertel 10180* (JE, M). **MONAGAS:** *Griffin & Bermúdez 12* (FLAS, U). **SUCRE:** *Griffin & Bermúdez 73, 93* (FLAS, U). **ZULIA:** *Griffin 57, 187, 349* (FLAS, U).

SURINAME. Brownsberg, *van Slageren H400* (U).

FRENCH GUIANA. Saül, *Montfoort & Ek 1015, 1016, 1017* (U); Haute Tampoc River, *Cremers 4792* (CAY, U).

ECUADOR. CARACHI: road Tulcán-Maldonado W of pass, *Gradstein & Mues 6826, 6827, 6841* (U). **CHIMBORAZO:** *Spruce s.n.* (G). **GUAYAS:** Ventanas, *Spruce 17659* (MANCH). **LOS RÍOS:** Río Palenque Forest Reserve, *Gradstein & Mues 6867* (U); *Harling 2112* (JE, S). **GALÁPOGOS ISLANDS:** Floreana, Cruz Farm, *Gradstein H184, Bryoph. Neotrop. Exsicc. 41* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PAN, QCA, S, SP, USJ, XAL). Isabela, volcán Alcedo, *van der Werff 1439, 1472* (U); Pinta, *Gradstein et al. H518* (U). San Cristobal, *Gradstein & Lanier H314* (U). Santa Cruz, *Balasz 13* (EGR, U), *van der Werff 1557, 1789* (U), *Gradstein & Weber H26* (COLO, U).

PERU. HUANUCO: Tingo María, *Hegewald 7879, 7911* (U). **JUNÍN:** Huacapistana, *Killip & Smith 24169* (JE). **SAN MARTÍN:** *Frahm, Geissler et al. 1561* (G). **PASCO:** Oxapampa, *Hegewald 8442* (U).

BRAZIL. BAHIA: *Vital 6543* (JE, U). **ESPIRITO SANTO:** Vargem Alta, *Schäfer-Verwimp 10378* (G). **MINAS GERAIS:** Santa Barbara, *Schäfer-Verwimp 11457* (G). **PARANA:** Curitiba, *Schäfer-Verwimp 8252* (G); Foz de Iguaçu, *Schäfer-Verwimp 9319* (G). **RORAIMA:** *Ule 651* (G). **PERNAMBUCO:** Res. Nat. Brejo dos Cavalos, *Pôrto 2089, 2713* (G, PC). **RIO DE JANEIRO:** Serra Itatiaia, *Dusén s.n.* (G), *Schäfer-Verwimp 9249* (G). **SANTA CATARINA:** *Yano 2250* (U). **SÃO PAULO:** Apiahy, *Puiggari 660, 681, 1405* (G); Rio Branco Santos, *Schiffner s.n.* (UPS, W); São Paulo, *Geissler 14412* (G); I. San Sebastian, *Schäfer-Verwimp 6749, 7329* (G).

BOLIVIA. BENI: Ballivían, Serranía del Pilón Lagas, *Gradstein 7249* (LPB, U). **COCHABAMBA:** Incacorral, *Gradstein 7539* (LPB, U); Tablas Monte, *Gradstein 7463, 7478* (LPB, U); road Cochabamba-Villa Tunari km 112, *Gradstein 7516* (LPB, U). **LA PAZ:** Coroico, *Schmidt 1951* (JE, S).

PARAGUAY. ALTO PARANA: Salto Monday, *Schäfer-Verwimp 9373* (G), *Geissler 14611* (G).

ARGENTINA. MISIONES: Parque Nacional Iguazú, *Schäfer-Verwimp 9341* (G).

Marchesinia brachiata is a polymorphic species (Evans, 1907) and has been described under many different names. The species probably carries more synonyms than any other neotropical species of Lejeuneaceae. The plants vary considerably in size, leaves may be imbricate or distant and entire or toothed, lobules may be well-developed or reduced and underleaf margins may be plane or broadly recurved. Phenotypes with somewhat distant leaves and underleaves are common in *M. brachiata*, particularly at lower elevations. The leaves and underleaves of these forms, for which the epithets "*bongardiana,*" "*languida,*" and "*palaeflora*" have been used, are rather flat, the leaf apex usually has a few coarse, irregular teeth, the lobules are small or reduced, and the underleaf bases may be straight or auriculate instead of decurrent. The plants are frequently sterile and reproduction takes place by means of caducous leaves or leaf fragments.

Oil bodies in *Marchesinia brachiata* are always of the *Massula* type. The report of *Bazzania*-type oil bodies in the species (Geissler & Gradstein, 1981) is erroneous and was based on a misidentified specimen of *Symbiezidium barbiflorum*.

2. **Marchesinia robusta** (Mitten) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; *Lejeunea robusta* Mitten, Hooker's J. Bot. Kew Gard. Misc. **3:** 359. 1851; Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 137. 1884; *Marchesinia quadridens* Stephani, Spec. Hep. **5:** 152. 1912, nom. inval. Type. Ecuador. Vicinity of Quito, *Jameson s.n.* (holotype, NY; isotypes, BM, G).

Dioicous; *plants* usually long and robust, 3–10 cm long × 2.5–4 mm wide, deep green to blackish, becoming brown or blackish when dry. *Stems* in cross section composed of ca. 18–25 epidermal cells surrounding numerous medullary cells; ventral merophyte 7–10 cell rows wide. *Leaves* loosely imbricate, widely spreading when moist, bent downwards when dry, dorsal lobe ovate-oblong to oblong, ca. 1.1–2.8 mm long x 1–1.25 mm wide, apex broadly rounded, sometimes apiculate, margins plane or somewhat recurved, ventral margin almost straight, forming a sharp angle with the keel, margins toothed near apex and along the ventral margin, the teeth regularly spatiated, on stems ca. 4–15 per leaf, fewer on branches, teeth 1–3(–4) cells long, the tooth at apex often longer; median cells about 20–35 µm in largest diam.; oil bodies homogeneous, *Massula*-type, 12–20 per cell, oblong-ovate, 4–7 µm long. *Lobules* obovate-obtriangular, never reduced, up to 1/4x lobe length, keel straight or arched, free margin ± straight, with 3–4 short, evenly spatiated teeth, teeth 1–2 cells long, often inflexed. *Underleaves* subimbricate, strongly concave and with recurved apex and lateral margins, broadly orbicular, 4–6x stem width, apex rounded, margins sharply toothed to near the base or in the upper half only, bases broadly decurrent, sometimes auriculate. *Androecia* with 8–12 series of bracts. *Gynoecia* with two subfloral innovations, bract lobes ca. 2 mm long x 1 mm wide, apex acute-apiculate, margins sharply toothed in the upper half or ± entire, lobules narrow ovate-lanceolate, up to 1/2x lobe length, with a few teeth; bracteole ± oblong, 1–1.5 mm long, apex short bifid with sharply pointed lobes, margins sharply and irregularly dentate-ciliate above. *Perianths* usually long exserted, ca. 3 mm long x 2 mm wide. *Sporophyte* as in the genus.

Illustration. Herzog, Feddes Repert. Spec. Nov. Regni Veg. **57:** 173, Fig. 10a–e. 1955.

Distribution. Tropical Andes (Colombia to Bolivia) and Costa Rica, uncommon; occurring at submontane and lower montane elevations, 650–2500 m alt. *Marchesinia robusta* grows on bark in the canopy and at the margins of primary and old-growth secondary rain forest, in partial shade. The species has also been recorded growing on rock (Spruce, 1884).

Selected specimens examined. COSTA RICA. PUNTARENAS: Coto Brus, *Sipman 11936* (U). **SAN JOSÉ:** La Palma, *Standley 28050* (B).

COLOMBIA. CASANARE: Sacama, *Aguirre et al. 2989* (COL, U). **HUILA:** Mun. La Plata, Finca Merenberg, *Aguirre & Gradstein 6388* (COL, U). **SANTANDER:** Elida, *Bischler 59* (COL, PC, U); Charta, *Killip 19192* (JE).

VENEZUELA. LARA: Río Clara, *Griffin et al. 433* (NY).

ECUADOR. PICHINCHA: along road Lloa-Rio Cristal, *Gradstein & Mues 6784* (G, U). **TUNGURAGUA:** Baños, *Spruce s.n.* (FH, G, M, MANCH, US, W, YU)

PERU. AYACUCHO: *Killip & Smith 22583* (B, FH, JE, S). **HUANUCO:** Tingo Maria, *Hegewald 7819, 8335* (U). **SAN MARTÍN:** above Rioja, *Frahm, Geissler et al. 485, 1548, 1769* (G).

BOLIVIA. BENI: Serranía del Pilón Lagas, *Gradstein 7149, 7225, 7230* (LPB, U). **COCHABAMBA:** road Cochabamba-Villa Tunari km 112, *Gradstein 7498* (LPB, U).

Marchesinia robusta resembles robust forms of *M. brachiata* but differs by its underleaves which are sharply toothed on vegetative as well as on sexual shoots. In *M. brachiata* underleaves are entire or they are somewhat toothed on female shoots, especially towards the involucre. Leaves of *M. robusta* usually have more teeth than those of *M. brachiata* and, moreover, the teeth are not restricted to the apical margin but extend along the ventral margin. In some populations of *M. robusta* (Ecuador, *Gradstein 6784*; Peru, *Hegewald 7819*) dentation of leaves and underleaves is rather weak, however, the underleaves being toothed only along their upper margin and leaves bearing only 2–4 small teeth near apex. Branch leaves and underleaves of these weakly toothed forms of *M. robusta* may even be subentire. The variation in the dentation of the few specimens of *M. robusta* examined suggests that the species is only weakly differentiated from *M. brachiata* and that intermediate forms may occur. Possibly the species deserves to be reduced to varietal rank under *M. brachiata*.

Although Spruce (1884) described *Marchesinia robusta* as being paroicous or autoicous, all specimens which we examined (including those collected by Spruce) were dioicous.

Excluded Species

Marchesinia lehmanniana (Nees) Kuntze (*Phragmicoma lehmanniana* Nees)
= *Spruceanthus semirepandus* (Nees) Verdoorn (Geissler and Gradstein, in press)

Marchesinia testudinea (Taylor) Kuntze (*Phragmicoma testudinea* Taylor)
= *Pycnolejeunea macroloba*

Marchesinia pseudocucullata Gottsche ex Stephani
= *Cyrtolejeunea holostipa* (Spruce) Evans

10. Lopholejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; *Lejeunea* subgen. *Lopholejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 119. 1884. Lectotype (Evans 1907). *Lopholejeunea sagraeana* (Montagne) Schiffner (= *Lopholejeunea subfusca* (Nees) Schiffner). Genus named for its laciniate perianths.

Heterolejeunea Schiffner, Hedwigia **80:** 87. 1941. Type. *Heterolejeunea javanica* Schiffner.

Plants 1–4 cm long × 0.8–2 mm wide, glossy (rarely dull), usually blackish pigmented, creeping and often forming dense mats on bark or rock. *Branching predominantly Lejeunea*-type, occasionally *Frullania*-type, flagelliform branches sometimes present. *Stems* with hyalodermis, epidermal cells 1–2× larger than medullary cells, all cell walls colorless or slightly brownish, usually somewhat thickened; ventral merophyte four cell rows wide in neotropical species. *Leaves* widely spreading when dry, apex rounded to acute-apiculate, plane or recurved, margins usually plane and entire; leaf cells isodiametric-hexagonal to slightly elongate, averaging 25–40 μm in diam., walls usually with blackish pigmentation, trigones simple-triangular or radiate, intermediate thickenings frequent, one per wall, oil bodies homogeneous, Massula-type, ocelli lacking. *Lobules* 1/4–1/2× lobe length, sometimes reduced, inflated and often strongly gibbous in the lower half, with 0–2 ill-defined teeth, keel arched; hyaline papilla positioned below the proximal base of the apical tooth. *Underleaves* 2–9× stem width, apex rounded, margins entire, bases cuneate or rounded, insertion line weakly curved to arched (less than 100 μm deep); underleaf base at the rhizoid disc bistratose, with four superior central cells. *Androecia* in short or long spikes on branches, bracts somewhat smaller than leaves, lobule large, elongated beyond the keel, hypostatic, underleaves present throughout, slightly smaller than ordinary underleaves; antheridia two per bract. Gynoecia without true subfloral innovations, occasionally with a pseudo-innovation of the *Lejeunea*-type originating just below the bracts, bracts in (1–)2 series, slightly larger than leaves, with rounded to acute apex and toothed margins (entire in some palaeotropical species), lobules reduced or well-developed, bracteoles conspicuously larger than underleaves, undivided or short bifid, entire or toothed. *Perianths* immersed or exserted, with 4–5 sharp, ± winged and dentate-laciniate (rarely smooth) keels: 2 lateral, 2 ventral and 0–1 dorsal. *Sporophyte:* seta articulate; elaters 34 per capsule (van Slageren, 1985); otherwise as in the tribe. *Vegetative reproduction* not observed. *Terpenoids:* 5-hydroxycalamene.

Distribution. The genus *Lopholejeunea* is the largest genus of the Ptychanthoideae and the taxonomy of the species is poorly understood. More than 45 species are recognized, almost all of them in the palaeotropics. Four species occur in tropical America, three of which have a pantropical distribution. The species of *Lopholejeunea* are common at lowland and submontane elevations in the humid portions of tropical America and grow on bark and rock in primary and secondary forests and in plantations, often in rather sunny locations.

A fossil species of *Lopholejeunea* has been found in Miocenic amber of the Dominican Republic (see FOSSILS).

The neotropical species of *Lopholejeunea* are creeping plants which usually form blackish patches on bark or rock. Dark pigmentation of the cell walls is a characteristic feature of the genus although not all species exhibit this character. In *L. quelchii*, for instance, which is usually dark brown in color, the pigmentation of the cell walls is barely developed. Further characteristics of *Lopholejeunea* include the discrete hyaloderm, the isodiametric leaf cells with ± radiate trigones and small, homogeneous oil bodies, the lobule which is often strongly inflated-gibbose and has only 1–2 obscure teeth which may be lacking altogether, and the gynoecium which lacks subfloral innovations and has a perianth with 4–5 sharp, dentate-laciniate (rarely entire) keels. The terpenoid 5-hydroxycalamene is a chemical marker of the genus (Gradstein et al., 1988).

Schuster (1980) recognized two sections among the North American species: (1) sect. *Lopholejeunea* (for *L. subfusca*), characterized by the immersed, 4-keeled perianth and the reduced female bract lobule and 2) sect. *Muellerianae* Schust. (for *L. muelleriana*; synonym of *L. nigricans*), characterized by a long exserted, 5-keeled perianth and long female bract lobule. As shown in the present treatment, the gynoecial differences among these two sections are by no means stable. Variation is particularly strong in *L. nigricans*, which may produce perianths with 4 or 5 keels and female bracts with large or reduced lobules. As I have not found any other significant morphological differences among the neotropical species warranting the recognition of sections, an infrageneric classification of the species is not proposed in this treatment.

Key to the Species of *Lopholejeunea*

1. Underleaves about 2x wider than long (length measured from rhizoid disc to apex), 5–10x stem width; female bracteole toothed.
   2. Leaf apex mostly recurved; female bracteole more than 1 mm long, orbicular, apex undivided, usually recurved; lobule of female bracts more than 1/2x lobe length, toothed to laciniate; Cocos I., northern South America. . . . . 1. *L. eulopha.*
   2. Leaf apex mostly plane; female bracteole smaller, up to 1 mm long, ovate, apex bifid, plane; lobule of female bracts 1/4–1/2x lobe length, entire or with 1–2 small teeth; West Indies, northern South America. . . . . 3. *L. quelchii.*
1. Underleaves 1–1.5x wider than long, 2–5(–6)x stem width; female bracteole entire or with a few small teeth.
   3. Perianth immersed (rarely slightly emergent), hidden behind the bracteole except for the large, crowded laciniae; apex of female bracts broadly rounded; lobules when well-developed almost entirely inflated-gibbous, distal end of the free margin often truncate and connate to lobe surface across 2–3 cells; leaf apex rounded; throughout tropical America, lowland-submontane. . . 4. *L. subfusca.*
   3. Perianth distinctly emergent, laciniae not crowded; apex of female bracts acute-acuminate, rarely rounded; lobules usually partially flattened, distal end of the free margin always acute and attached to lobe surface by only one cell; leaf apex apiculate or rounded.
      4. Female bracteole entire (rarely with a few teeth), apex rounded or truncate; plants glossy brown-green to blackish; throughout tropical America, lowland-lower montane. . . . . 2. *L. nigricans.*
      4. Female bracteole sharply toothed, apex short bifid; plants dull brown; West Indies, northern South America. . . . . 3. *L. quelchii.*

1. Lopholejeunea eulopha (Taylor) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; *Lejeunea eulopha* Taylor, London J. Bot. **5:** 391. 1846; *Phragmicoma eulopha* (Taylor) Mitten *in* Seeman, Fl. Vitiensis 413. 1871; *Symbiezidium eulophum* (Taylor) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877. Type. "Pacific Islands," *Nightingale s.n.* (holotype, FH; isotype, NY).

Lopholejeunea cocosensis Clark, Proc. Calif. Acad. Sci. Ser. 4, **27:** 605, Pl. 40. 1953. Type. Costa Rica. Cocos I.: Wafer Bay, *Howell 231* (holotype, CAS; isotype, WTU), *syn. nov.*

Autoicous. *Plants* ca. 2 cm long x 1.0–1.8 mm wide, glossy, blackish brown when dry. *Branching* sparse, *Lejeunea*-type, flagelliform branches lacking. *Stems* in cross section 6–7 cells across, composed of 13–15 epidermal cells surrounding a similar number of smaller medullary cells, epidermis subsymmetric, dorsal epidermal as large as or slightly larger than ventral epidermal cells, walls of epidermal cells thin or slightly thickened, inner walls more strongly thickened, all cell walls brownish pigmented. *Leaves* imbricate, dorsal lobe asymmetrically ovate-suborbicular, ca. 0.6–0.9 x 0.7–0.75 mm, somewhat falcate, apex rounded, usually recurved, margins entire, dorsal base rounded, ventral margin forming an angle of 100–150° with the keel; leaf cells in mid-leaf 20–45 µm, trigones large, radiate, intermediate thickenings frequent, conspicuous; oil bodies not observed. *Lobules* ovoid, not reduced, ca. 0.3 mm long, 1/3x lobe length, strongly inflated-gibbous, abruptly flattened and folded at apex, free margin without distinct teeth. *Underleaves* imbricate, reniform, ca. 0.3–0.45 mm long x 0.6–1.0 mm wide, 6–9x stem width, apex recurved or plane, bases rounded, insertion line curved. *Androecia* intercalary on long shoots, bracts in 3–4 series. *Gynoecia* on long branches, pseudo-innovations not observed, bract lobes asymmetrically ovate, acute, margins dentate-laciniate above, lobule lanceolate, distinctly extended beyond the keel, 1/2–2/3 x lobe length, margins toothed to laciniate; bracteoles suborbicular, ca. 1.2 mm long, apex rounded, usually recurved, rarely plane, margins dentate-laciniate above. *Perianths* immersed to emergent, obpyriform, in upper half with 4–5 sharp, unwinged, laciniate keels: 2 lateral keels, 2 ventral keels and usually a low dorsal keel; beak ca. 4 cells long, not recessed. *Sporophyte* not observed.

Terpenoids: 5-hydroxycalamene is the major component of this species (Gradstein et al., 1985).

Illustration. Mizutani, J. Hattori Bot. Lab. **45:** 376, Fig. 1. 1979; VandenBerghen, Bull. Jard.

Bot. Belg. **54:** 428-432, Figs. 15–17. 1984; Thiers & Gradstein, Mem. New York Bot. Garden **53:** 26, Fig. 8. 1989.

Distribution. Pantropical but rare in the neotropics (Northern South America, Cocos I.), at low elevations, up to 100 m. *Lopholejeunea eulopha* was first recorded from Cocos I. by Clark (1953), as *L. cocosensis* Clark, and subsequently from Guyana by Gradstein (1990).

In Guyana and in the Amazon basin *Lopholejeunea eulopha* occurs on bark in virgin, dry evergreen forest on white sand. In Guyana it was found in walaba forest on the trunks and lower canopy branches of *Eperua grandiflora* trees. The Amazonian specimen came from tree trunks in campina forest.

Specimens examined. COSTA RICA. Cocos I., type of *Lopholejeunea cocosensis.*

COLOMBIA. "Andes Bogotenses", *Weir s.n. (NY).*

TRINIDAD. *Fendler s.n.* (NY); Valencia, Toco Rd., *Britton et al. 1879* (US).

GUYANA. Mabura Hill, ca. 120 km S of Georgetown, *Cornelissen & ter Steege C579, C807* (U).

BRAZIL. AMAZONAS: road Manaus-Caracarai km 60, *Griffin et al. 552* (FLAS, U).

Lopholejeunea eulopha is readily recognized by the recurved leaf apices, the broad, reniform underleaves and the large, rounded, dentate-laciniate female bracteole with undivided and usually recurved apex. Although known from only few neotropical collections, considerable variation is seen in the diagnostic features of this species. The degree of recurving of the apex of leaves and underleaves, for instance, varies and in some specimens they are barely recurved (e.g., type of *L. cocosensis*). The lobules of the female bracts are laciniate in the collections from Guyana but in other specimens they are subentire. The margins of the female bracteoles may be plane or strongly recurved.

Lopholejeunea eulopha is most closely related to *L. quelchii*. Differences are discussed under the latter.

2. **Lopholejeunea nigricans** (Lindenberg) Schiffner, Consp. Hep. Archip. Ind. 293. 1898; Mizutani, J. Hattori Bot. Lab. **45:** 385, Fig. 7 (1979); *Lejeunea nigricans* Lindenberg, Syn. Hep. 316. 1845; *Symbiezidium nigricans* (Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877. Type. Java, *unknown collector* (holotype, W; isotype, G). Fig. 30.

?*Phragmicoma fischeriana* Nees, Repert. Pharm **76:** 44. 1842; *Lejeunea fischeriana* (Nees) Nees, Syn. Hep. 320. 1845; *Symbiezidium fischerianum* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Archilejeunea fischeriana* (Nees) Stephani, Spec. Hep. 4: 713. 1911, *nom. dubium.* Type. Brazil. Rio de Janeiro: on bark of "Páo Pereira," *Naumann s.n.* (holotype, STR). The type material of *Lejeunea fischeriana* Nees consists of a few sterile, somewhat etiolated stems. The leaves are elongated, with rounded tips, the lobules are small, tending to become reduced, and the underleaves are small and distant. Because of its asymmetric epidermis (two dorsal cells distinctly smaller than ventral cells) the plant should probably be placed in the synonymy of *Lopholejeunea nigricans. Lejeunea fischeriana* has also been recorded from Pernambuco by Herzog (Hedwigia **67:** 251. 1927) and São Paulo (Schiffner & Arnell, 1964). The collections from São Paulo belong to *Lopholejeunea subfusca* (*Schiffner 1676*) and *Schiffneriolejeunea polycarpa* (*Schiffner 1788*).

Lopholejeunea muelleriana (Gottsche) Schiffner, Bot. Jahrb. **23:** 599. 1897; Evans, Bull. Torrey Bot. Club **34:** 27, Pl. 4. 1907; Schuster, Hep. Anth. N. America IV: 743, Figs. 648–649. 1980; Thiers & Gradstein, Mem. N.Y. Bot. Garden **52:** 31, Fig. 11. 1989; *Lejeunea muelleriana* Gottsche, Mex. Leverm. 280. 1863. Type. Mexico. Veracruz: Orizaba, *Müller s.n.* (holotype, B, destroyed; isotype, G), *syn. nov.*

Lejeunea abortiva Mitten, Phil. Trans. Roy. Soc. London **168:** 399. 1879; *Lopholejeunea abortiva* (Mitten) Stephani, Spec. Hep. **5:** 70. 1912; VandenBerghen, Bull. Jard. Bot. Nat. Belg. **54:** 416, Figs. 9–13. 1984. Type (VandenBerghen, 1984). Africa. Rodriguez I., *Balfour 057* (holotype, NY, n.v.), *syn. nov.*

Lejeunea mariei Bescherelle & Spruce, Bull. Soc. Bot. France **36:** 179. 1890 "1889"; *Lopholejeunea mariei* (Bescherelle & Spruce) Stephani, Spec. Hep. 5: 72. 1912. Type. Guadeloupe. Marie s.n. (holotype, MANCH), *syn. nov.*

Lejeunea rusbyi Spruce, Mem. Torrey Bot. Club **1:** 122. 1890; *Lopholejeunea rusbyi* (Spruce) Stephani, Spec. Hep. **5:** 71. 1912. Type. Bolivia. La Paz: Mapiri, *Rusby 3077, 3078, 3081* (holotype, MANCH, one packet), *syn. nov.*

Lejeunea atroviridis Spruce, J. Linn. Soc., Bot. **30:** 355. 1895; *Lopholejeunea atroviridis* (Spruce) Evans, Bryologist **14:** 88. 1911; *Acrolejeunea atroviridis* (Spruce) Bonner, Index Hep. 1, **2:** 15. 1962. Type. St. Vincent. Richmond Valley, *Elliott 219* (holotype, MANCH; isotype, BM), *syn. nov.*

Lopholejeunea andersonii Stephani, Hedwigia **35:** 108. 1896. Type. Ecuador. Galapagos Is., "inter Radulam," *Andersson s.n. (holotype, G 17877), syn. nov.*

This name was earlier treated as a synonym of *Mar-*

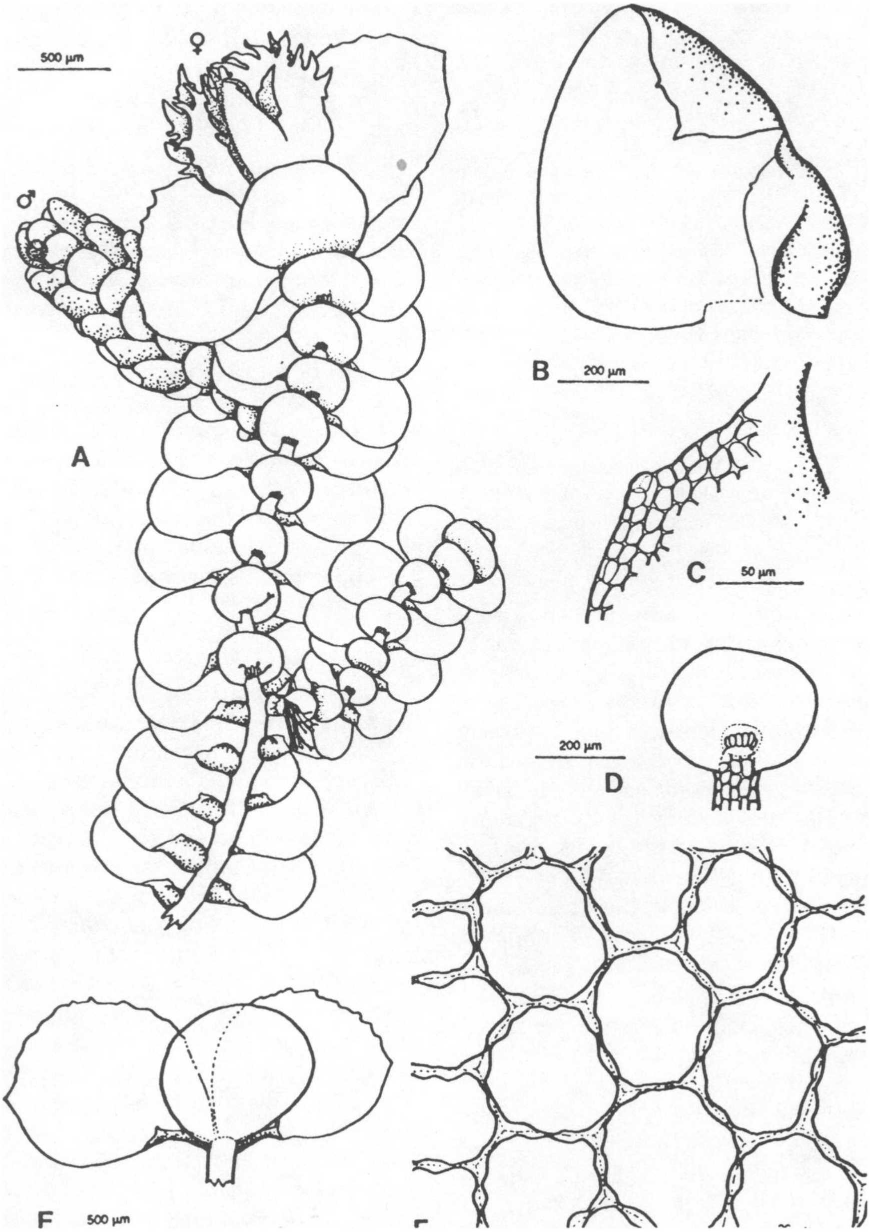

FIG. 30. *Lopholejeunea nigricans.* **A.** Habit, with gynoecium and androecial branch; note hypostatic lobules of male bracts. **B.** Leaf with acute apex. **C.** Lobule apex. **D.** Underleaf. **E.** Gynoecial bracts and bracteole. **F.** Leaf cells. A, C–F from Colombia, *Van Reenen & Griffin 1910.* B from Brazil, *Schäfer-Verwimp 8255.*

chesinia brachiata by Gradstein and Weber (1982). I am grateful to Dr. Patricia Geissler, Geneva, for calling my attention to this error.

Lopholejeunea rivularis Stephani, Hedwigia **35:** 111. 1896. Type. Brazil. São Francisco, *Ule 147* (lectotype (nov.), G 23603). Paralectotype. Brazil. São Paulo: Apiahy, *Puiggari s.n.* (G), *syn. nov.* The Ule collection is chosen as the lectotype because it is the best specimen.

Lopholejeunea spinosa Stephani, Kongl. Svenska Vetenskapsakad. Handl. **46:** 87. 1911. Type. Chile. Juan Fernandez Is.: Masatierra, *Skottsberg s.n.* (holotype, G 17921; isotype, S), *syn. nov.*

Neurolejeunea lechleri Stephani, Spec. Hep. **4:** 697. 1911. Type. Peru. Tatauara, *Lechler s.n.* (holotype, G 22912).

Lopholejeunea fragilis Stephani, Spec. Hep. **5:** 65. 1912; *Lopholejeunea abortiva* (Mitten) Stephani var. *fragilis* (Stephani) VandenBerghen, Bull. Jard. Bot. Nat. Belg. **54:** 424, Fig. 11-13. 1984. Type (VandenBerghen 1984). Africa. Ivory Coast. *Jolly s.n.* (holotype, G, n.v.), *syn. nov.*

Lopholejeunea apiahyna Gottsche ex Stephani, Spec. Hep. **5:** 72. 1912. Type. Brazil. São Paulo: Apiahy, *Puiggari 268* (holotype, G 17878; isotypes, G, W), *syn. nov.*

Lopholejeunea muelleriana (Gottsche) Schiffner subsp. *puertoricensis* Schuster, Hep. Anth. N. America **4:** 749. 1980, nom. inval. (herbarium where type is kept not indicated). Material. Puerto Rico. El Yunque, *Evans 124* (n.v.), *syn. nov.*

Lopholejeunea muelleriana (Gottsche) Schiffner subsp. *floridana* Schuster, Hep. Anth. N. America **4:** 751. 1980. Type. U.S.A. Florida. Putnam: Orange Springs, *Schuster 42211* (isotype, C), *syn. nov.*

Autoicous or dioicous. *Plants* to 4 cm long × 0.8–1.4 mm wide, glossy, brown green to blackish when dry. *Branching* irregularly pinnate, usually *Lejeunea*-type, rarely *Frullania*-type, recurved flagelliform branchlets occasionally present on lower portions of stem. *Stems* in cross section ca. 7–10 cells across, composed of ca. 10–20 epidermal cells surrounding 15–40 medullary cells, all cells thin-walled with colorless walls, epidermis symmetric or asymmetric, dorsal epidermal cells as large as or smaller than ventral epidermal cells. *Leaves* contiguous to imbricate, dorsal lobe asymmetrically ovate-oblong, 0.5–1 × 0.3–0.7 mm, apex rounded, obtuse or acute-apiculate, plane or recurved, margins entire, occasionally slightly toothed above, dorsal base rounded, ventral margin forming an angle of 100–150° with the keel; leaf cells in mid-leaf ca. 20–35 μm, trigones small to medium-sized, simple triangular to radiate, intermediate thickenings frequent, small; oil bodies (Schuster, 1980) 8–20 per median leaf cell, homogeneous, small, *Massula-type*. *Lobules* ovoid-oblong, sometimes reduced, when well-developed 0.3–0.45 × 0.2–0.3 mm, up to 1/2x lobe length, weakly to strongly inflated along the keel, usually flattened distally, free margin without or with a one-celled tooth, at distal end attached to lobe surface by only one cell. *Underleaves* distant to subimbricate, transversally ovate to suborbicular, variable in size, ca. 0.2–0.5 mm long × 0.2–0.7 mm wide, 2–5× stem width, apex plane or recurved, bases cuneate or rounded, insertion line curved to arched (less than 100 μm deep). *Androecia* on short or long branches, bracts in 3–10 series. *Gynoecia* on short or long branches, without true subfloral innovations, occasionally with pseudo-innovation of the *Lejeunea*-type, bract lobes asymmetrically ovate-oblong, 0.8–1.2 × 0.6–0.8 mm, apex obtuse to acute-apiculate, rarely rounded, margin toothed to subentire above, lobule narrow rectangular-ligulate, hardly elongated beyond the keel, up to 2/3 × lobe length, sometimes reduced, margin entire or with a few teeth; bracteoles orbicular to oblong, rarely broadly ovate, 0.7–1 mm long, apex rounded or truncate-emarginate, margins plane or recurved, usually entire, rarely with a few teeth. *Perianths* exserted to 1/3–2/3, obpyriform, apex broad truncate, with 4–5 sharp, more or less winged, dentate-ciliate to laciniate keels: 2 lateral keels, 2 ventral keels and 1 dorsal keel which may be short or lacking altogether, teeth and laciniae up to 10 cells long (sometimes weak, perianth subentire), near perianth apex becoming randomly distributed, an additional row of lacinia sometimes developed on the dorsal side and on the ventral side between the two ventral keels; beak ca. 5 cells long. *Sporophyte* as in the genus.

Distribution (Fig. 31). Pantropical. In the neotropics a widespread species, reaching northwards to North Carolina, southwards to SE Brazil, Bolivia and Juan Fernandez, from sea level to 1800 m. The populations of *Lopholejeunea nigricans* from the Juan Fernandez Islands, where the species was known as *L. spinosa* Steph., constitute a remarkable disjunction of the species. *Lopholejeunea nigricans* is also common in Africa, where it has been known as *Lopholejeunea abortiva* (VandenBerghen, 1984), and in Southeast Asia (Mizutani, 1979). Thiers and Gradstein (1989) have recently recorded the species from Australia (as *L. muelleriana*).

Lopholejeunea nigricans grows on trunks, lianas, poles, and logs, mainly at forest edges and along creeks, in humid environments. The species is also common on rocks and boulders in meadows and streams.

The neotropical distribution of *Lopholejeunea nigricans* overlaps with that of *L. subfusca*, but the latter is basically a lowland species and rather xerophytic. *Lopholejeunea nigricans* is more common at higher elevations, above 300 m, and less tolerant of desiccation. Towards higher lati-

FIG. 31. Neotropical distribution of *Lopholejeunea nigricans* (dots) and distribution of *L. quelchii* (stars).

tudes, e.g., southeastern Brazil and the United States, *L. nigricans* also occurs at sea level and here the two species may grow side by side.

Selected specimens examined. MEXICO. CHIAPAS: Lacandon forest reserve along Río Lacantun, near Chajul Biological Station, *Gradstein 8136* (U).

COSTA RICA. COCOS ISLAND: Wafer bay, *Howell 241* (CAS).

PANAMA. PANAMÁ: Parque Nacional Altos de Campana, *Salazar & Gradstein 9454* (PMA, U); Cerro Jefe, *Salazar & Gradstein 9407* (PMA, U).

UNITED STATES. NORTH CAROLINA. Near Whiteville, *Schuster 29980a* (G, NY, U). **FLORIDA. LEVY:** Gulf Hammock, *Schuster F120* (G), *Griffin, Bryophytes of Florida 87* (FLAS, NY). **SEMINOLE:** Sanford, *Rapp s.n.* (NY, U, YU).

CUBA. ORIENTE: Sierra de La Gran Piedra, *Pócs et al. 9114/CZ* (HAC).

JAMAICA. Doll Wood, *Evans 501* (NY).

PUERTO RICO. Luquillo Mts., *Heller 783* (NY), El Yunque, *Evans 124, 165* (NY).

WINDWARD ISLANDS. GUADELOUPE. Type of *Lopholejeunea mariei.* **DOMINICA.** *Elliott 942, 1661* (G). **ST.VINCENT.** Mt. Bonhomme, *Elliott 80 p.p.* (MANCH).

COLOMBIA. CASANARE: Sácama, *Aguirre & Gradstein 2988, 3030, 3044, 3079, 3100* (COL, U). **META:** Río Guayabero, *Bischler 1613, 1615, 1625, 1628, 1633* (COL, U); near Villavicencio, *van Zanten & Gradstein 704A* (U). **RISARALDA:** near St. Rosa de Cabal, *van Reenen et al. 1834, 1839* (COL, U); Marsella, *van Reenen & Griffin 1901, 1910* (COL, U); San Antonio de Chami, Geguades, *Gradstein 8634* (COL, U). **SANTANDER:** Charalá, Virolín, *Castro et al. 236* (COL).

VENEZUELA. AMAZONAS: Cerro Neblina, 6 km NE of Pico Phelps, *Halling 4345* (NY). **MIRANDA:** Parque Nacional Guatopó, *Nee 17706* (NY).

TRINIDAD. *Fendler s.n.* (NY).

GUYANA. Upper Mazaruni District, Mt. Latipu near Kamarang, *Gradstein 5609* (U), Jawalla, *Gradstein 4841, 4866* (U), Mt. Roraima, *Gradstein 5250, 5445* (U).

SURINAME. NICKERIE: Kabalebo Dam project area, *Bekker 1743 p.p., 1748 p.p.* (U).

FRENCH GUIANA. Kourou, *Bekker 2008* (U); Kaw Mts., *Gradstein 5904, 5908* (U); Saül, *Bekker 2192* (U).

ECUADOR. PASTAZA: along Río Alpayacu W of Puyo, *Thiers 4693* (NY). **PICHINCHA:** NW of San Miguel de los Bancos, *Buck 10449, 10463* (NY). **GALÁPAGOS ISLANDS:** type of *Lopholejeunea andersonii.*

PERU. LORETO: Maynas, Río Yanayaco, *Hegewald 6384* (U). **SAN MARTÍN:** road Yurimaguas-Tarapoto km 95-107, *Frahm et al. 1392, 1393, 1464, 1465* (B, U).

BRAZIL. AMAZONAS: Rio Negro, *Spruce s.n., several colls.* (G, MANCH); Manaus, in igapó, *Griffin et al. 816* (FLAS, U), *Vital et al. 4415* (SP, U). **GOIAS:** Chapada dos Veadeiros, *Irwin et al. 33217* (NY, U); *Schäfer-Verwimp 8679* (U). **MATO GROSSO:** along Road BR 163, ca. 145 km N of Sinop, *Schäfer-Verwimp 11340* (U). **MINAS GERAIS:** Caldas, *Mosén s.n.* (G); Serra de Caparao, *Schäfer-Verwimp 8984* (U). **PARÁ:** *Spruce s.n.* (MANCH). **PARANÁ:** Curitiba, Serra Graciosa, *Schäfer-Verwimp 8255* (U). **SÃO PAULO:** Campo Grande, *Schiffner 777* (W); Itapetininga, *Schiffner 2187* (W); Peruibe, Morro do Gaurau, *Schäfer-Verwimp 7762* (U); Ubatuba, *Schäfer-Verwimp 7856, 9032, 9274* (U); Serra da Mantiqueira, *Schäfer-Verwimp 11835* (U).

BOLIVIA. BENI: Prov. Ballivian, Serranía del Pilón Lagas, *Gradstein 7142, 7147, 7259, 7280* (LPB, U). **COCHABAMBA:** road Cochabamba-Villa Tunari km 135, *Gradstein 7494a* (LPB, U).

CHILE. JUAN FERNANDEZ ISLAND: Masafuera, *Skottsberg H102, H143, H162* (S); Masatierra, *Skottsberg H38, H47* (S).

In the New World *Lopholejeunea nigricans* has commonly been known as *L. muelleriana.* Study of a number of collections of the Asiatic *L. nigricans* from the herbarium of Leiden has convinced me that the two are conspecific. I am indebted to Dr. Mizutani (pers. comm.) for confirming the conspecificity of the two. As the name *L. nigricans* antedates *L. muelleriana*, the former name has priority.

Lopholejeunea nigricans is the most widespread species of the genus in the neotropics and quite variable. It has been described in the past under many different names. The species can be distinguished most readily by its emergent perianth and its pointed female bracts. The perianth may be 4– or 5-keeled depending on whether a dorsal keel is developed, and the leaves may be rounded or acute. An interesting feature of neotropical *L. nigricans* not mentioned by previous authors, is the fact that the stem epidermis may be quite asymmetric, with one or two dorsal epidermal cells smaller than the ventral epidermal cells. Populations with symmetric epidermis (dorsal cells = ventral cells) do also occur, however.

Lopholejeunea nigricans is the only species of the genus *Lopholejeunea* in the neotropics which may produce populations with purely sharply acute-apiculate leaves (described as *L. apiahyna* Steph. and *L. muelleriana* subsp. *muelleriana* sensu Schuster, 1980). Acute leaves may also be observed in *L. quelchii*, but in that species they always occur mixed with rounded leaves. Occurrence of both rounded and acute leaves on a single plant is also common in *L. nigricans.* In addition, many populations have rounded leaves only (described as *L. rivularis* Steph. and *L. muelleriana* subsp. *puertoricensis* Schust.), including those from the United States and the West Indian islands.

Lopholejeunea abortiva (Mitt.) Steph. from tropical Africa is conspecific with *L. nigricans*, as was already suggested by VandenBerghen (1984). The African populations exhibit a variation somewhat similar as in the neotropics and two varieties were recognized by VandenBerghen: *L. abortiva* var. *abortiva* with a rounded leaf apex and perianth without dorsal keel, and *L. abortiva* var. *fragilis* (Steph.) VandenBerghen with a pointed or rounded leaf apex and a perianth furnished with a dorsal keel. The varieties apparently correspond with *L. muelleriana* subsp. *puertoricensis* Schust. and *L. muelleriana* subsp. *muelleriana*, except for the fact that female bracteoles are as a rule denticulate in African var. *fragilis*. In the neotropics female bracteoles are normally entire or sinuate and in only very few instances denticulate bracteoles have been observed in *L. nigricans.* Another difference seems to be the frequent occurrence in African populations of female bracts with entire margins and rounded apex. In tropical America rounded female bract apices are observed only very rarely (they are characteristic of *L. subfusca*!) and I have never seen forms with entire bract margins.

According to VandenBerghen (1984), the two African varieties of *L. abortiva* have a different geographical range, var. *abortiva* being a lowland plant whereas var. *fragilis* occurs at higher elevations. In tropical America, I have also noted that forms with pointed leaves occur at higher elevations only, whereas forms with rounded leaves are more common in lowland areas. As noted above, rounded and pointed leaves may often occur on single plants; in addition, the development of a dorsal perianth keel is subject to variation within single specimens. The entire range of variation can be seen in collections of *L. nigricans* from Casanare, Colombia, ca. 1150 m

(*Aguirre & Gradstein 3030, 3044, 3079*).

Thiers and Gradstein (1989) have recently reported *L. nigricans* (as *L. muelleriana*) from Australia. They recognized two varieties, var. *muelleriana* and var. *australis*, each with a different geographical range. The variation exhibited by the Australian plants largely falls within the range of variation in the New World except for the presence of almost smooth perianth keels in var. *australis*.

In this treatment I have chosen not to recognize infraspecific taxa in *Lopholejeunea nigricans* as the morphological differences observed among the neotropical populations are by no means sharp. A detailed biosystematic study of *L. nigricans* should be undertaken to assess the variation exhibited by this interesting taxon. As Vanden-Berghen (1984) has pointed out, such a study should focus on the entire range of the species, not just on the materials of one continent.

Lopholejeunea nigricans may be confused with *L. subfusca* and sterile material cannot always be identified with certainty. Differences between the two are discussed under *L. subfusca*.

3. **Lopholejeunea quelchii** Stephani, Malpighia **10:** 520. 1896. Type. Guyana. Georgetown, *Quelch s.n.* (holotype, G 17916).

Lopholejeunea howei Evans, Bull. Torrey Bot. Club **34:** 30. 1907. Type. Puerto Rico. Between Cayey and Caguas, *Howe 1413 p.p.* (holotype, YU).

Lopholejeunea herminieri Gottsche ex Stephani, Spec. Hep. **5:** 75. 1912. Type. Guadeloupe. *L'Herminier s.n.* (holotype, G 17895), *syn. nov.*

Autoicous. *Plants* to 4 cm long × 1.5–2.0 mm wide, dull, yellow brown to dark brown (not black) when dry. *Branching* irregularly pinnate, *Lejeunea*-type, flageliform branches lacking. *Stems* in cross section ca. 7–8 cells across, composed of ca. 10–15 epidermal cells surrounding ca. 20 medullary cells, cell walls colorless and thickened, those of the medulla more strongly than those of the epidermis, epidermis symmetric. *Leaves* contiguous to imbricate, dorsal lobe often convex, asymmetrically ovate-oblong, 0.5–1 × 0.3–0.7 mm, apex rounded to apiculate, plane or narrowly recurved, margins entire, dorsal base straight, ventral margin forming an angle of 120–170° with the keel; leaf cells in mid-leaf 25–50 µm, trigones strong, radiate, intermediate thickenings frequent, well-developed; oil bodies not observed. *Lobules* ovoid-triangular, sometimes reduced, when well-developed 0.25–0.35 × 0.2–0.3 mm, 1/4–1/2× lobe length, free margin without or with a rudimentary tooth. *Underleaves* distant to subimbricate, transversely ovate to reniform, ca. 0.3–0.4 mm long × 0.4.5–0.9 mm wide, (4–)5–8× stem width, apex plane, bases straight or rounded, sometimes decurrent, insertion line arched, to 100 µm deep. *Androecia* on specialized branches, bracts in 6–7 series. *Gynoecia* on short or long branches, without true subfloral innovations, occasionally with a pseudo-innovation of the *Lejeunea*-type, bract lobes plane or convex with incurved apex, asymmetrically oblong, acute-apiculate, dorsal margin strongly toothed above, ventral margin with a few teeth or entire, lobule narrow rectangular-ligulate, 1/3–1/2× lobe length, not extended beyond the keel, margin entire or with 1(–2) teeth near apex; bracteoles ovate, ca. 0.8 mm long × 0.8–1 mm wide, up to 1/2× perianth length, apex short bifid, margins dentate above, plane. *Perianths* exserted to 1/2 of its length, obpyriform, apex truncate, with 4–5 sharp keels: 2 lateral keels, 2 ventral keels and sometimes a low dorsal keel, lateral and ventral keels extending over 1/2–3/4 of perianth length, sparingly dentate above, dorsal keel entire, short or lacking short or lacking; beak low, ca. 3 cells long, not recessed. *Sporophyte* not observed.

Terpenoids: 5-hydroxycalamene is the major component of this species (Gradstein et al., 1985).

Illustration. Evans, Bull. Torrey Bot. Club **34:** 34, Pl. 4. 1907 (as *Lopholejeunea howei*).

Distribution (Fig. 31). West Indies (up to 1000 m), Guianas (up to 150 m). *Lopholejeunea quelchii* is an uncommon species which occurs in dry or moist lowland rain forest, usually near creeks. It grows on trunks and on branches in the lower canopy.

Specimens examined. CUBA. VILLA CLARA: Sierra del Escambray, Pico Potrerillo, *Pócs & Borhidi 9011/U* (EGR, U). ORIENTE: Baracoa, Loma del Yunque, *Bisse & Leopold 4977a* (JE); Sierra de Moa, *Bisse & Lippold 11194* (JE).

PUERTO RICO. Río de Maricao, *Britton 2507* (NY).

WINDWARD ISLANDS. SABA: *Van Slageren 277* (U). **GUADELOUPE.** Type of *Lopholejeunea herminieri*.

GUYANA. Mabura Hill, *Cornelissen & ter Steege 870, 877, 824, 885* (U); Kanuku Mts., Nappi Cr., *Jansen-Jacobs* *et al. 648* (U).

SURINAME. Jodensavanne, Mapane Cr., *Lindeman 3937* (U); Kabalebo Dam project area, *Bekker 1092, 1093, 1097, 1694* (U).

Conservation. *Lopholejeunea quelchii* may be considered a threatened taxon because of its rarity and its growth in undisturbed rain forest. Particularly the Caribbean populations may be considered endangered; those of the Guianas are less threatened because deforestation is not alarming there. The species has been classified as "at risk" by Gradstein (1992c).

Diagnostic characters of *Lopholejeunea quelchii* are its dull brown color, its reniform underleaves with arched insertion line, the longly exserted perianth and, in particular, the sharply toothed, bifid female bracteoles. Some variation is seen in the width of the underleaves, the leaf apex (rounded or apiculate), the degree of dentation of the female bracts and bracteole, and the depth of incision of the female bracteole apex. In the type specimen of *L. quelchii*, the female bracteole is almost undivided.

Lopholejeunea quelchii is very closely related to *L. eulopha* and the two may eventually prove conspecific. The latter differs mainly by the recurved apices of leaves and underleaves (but sometimes only weakly so: Trinidad, *Fendler s.n.*), the broader underleaves which are often almost as wide as the leafy stems, and the broadly rounded, undivided female bracteoles. Typical phases of *L. eulopha* also differ by the recurved female bracteole margins and laciniate female bract lobules but these characters are not stable and populations with plane bracteoles and subentire bract lobules do occur.

Lopholejeunea quelchii and *L. eulopha* also seem to differ in ecology. In Guyanan dry evergreen walaba forest, dominated by *Eperua falcata* and *E. grandiflora* trees (Legum.), *L. quelchii* grows on *Eperua falcata* whereas *L. eulopha* inhabits *Eperua grandiflora* trees. The latter tree species has a rather coarse bark and harbours an epiphytic bryophyte flora very different from that of *E. falcata* which has smooth bark (Cornelissen & Ter Steege, 1989).

4. Lopholejeunea subfusca (Nees) Schiffner, Bot. Jahrb. **23:** 593. 1897; Schuster, Hep. Anth. N. America IV: 751, Fig. 650. 1980; Vanden-Berghen, Bull. Jard. Bot. Nat. Belg. **54:** 440, Figs. 22–23. 1984; *Jungermannia subfusca* Nees, Enum. Pl. Crypt. Jav. 36. 1830; *Lejeunea subfusca* (Nees) Nees & Montagne, Ann Sci. Nat., Bot. (sér. 2) **5:** 61. 1836; *Phragmicoma subfusca* (Nees) Nees, Naturgesch. Eur. Leberm. **3:** 248. 1838; *Symbiezidium subfuscum* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877. Type. Java. *Blume s.n.* (holotype, STR, n.v.; isotype, W).

Lopholejeunea sagraeana (Montagne) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; Evans, Bull. Torrey Bot. Club **34:** 24, Pl. 3. 1907; *Phragmicoma sagraeana* Montagne *in* de la Sagra, Hist. Phys. Nat. Cuba (Bot. Pl. Cell.) 464. 1842; *Lejeunea sagraeana* (Montagne) Gottsche, Lindenberg & Nees, Syn. Hep. 314. 1845; *Symbiezidium sagraeanum* (Montagne) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877 *Lejeunea sagraeana* (Montagne) Gottsche, Lindenberg & Nees var. *montagnei* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 121. 1884. Type. Cuba. *De la Sagra s.n.* (holotype, PC-MONT., n.v.; isotype, W)

Phragmicoma cyclostipa Taylor, London J. Bot. **3:** 387. 1846; *Lejeunea cyclostipa* (Taylor) Taylor, Syn. Hep. 749. 1847; *Symbiezidium cyclostipum* (Taylor) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Archilejeunea cyclostipa* (Taylor) Stephani ex Bonner, Index Hep. **2:** 261. 1962; *Lejeunea sagraeana* (Montagne) Gottsche, Lindenberg & Nees var. *amazonica* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 121. 1884. Type. Brazil. Pará: "Cincinnati [!], Hook. 1443" (isotypes, MANCH).

Lejeunea sagraeana (Montagne) Gottsche, Lindenberg & Nees var. *grandiloba* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 121. 1884. Type. Venezuela. Amazonas: San Carlos del Río Negro, *Spruce s.n.* (holotype, MANCH), *syn. nov.*

Lejeunea sagraeana (Montagne) Gottsche, Lindenberg & Nees var. *pusilla* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 121. 1884. Type. Brazil. Amazonas: Rio Negro, São Gabriel, *Spruce L70* (lectotype, MANCH, here designated), *syn. nov.* A form with numerous gynoecia and poorly developed vegetative leaves.

Autoicous. *Plants* to 2 cm long × 0.8–1.5 mm wide, glossy, blackish green to blackish brown when dry. *Branching* irregularly pinnate, *Lejeunea*-type, recurved flagelliform branchlets frequently present. *Stems* with distinct hyalodermis, in cross section ca. 6–9 cells across, composed of ca. 10–15 epidermal cells surrounding 15–30 smaller medullary cells, all cells thin-walled with colorless walls, epidermis symmetric to subsymmetric, dorsal epidermal cells as large as or slightly larger than ventral epidermal cells.

Leaves widely spreading when dry, contiguous to imbricate, dorsal lobe asymmetrically ovate, 0.45–0.7 × 0.35–0.5 mm, often falcate, apex rounded, plane, margins entire, dorsal base straight, ventral margin forming an angle of 90–150° with the keel; leaf cells in mid-leaf 25–40 µm, trigones small to large, simple triangular to slightly radiate, intermediate thickenings ± frequent, often coalesced with the trigones; oil bodies (Schuster, 1980) 8–15(–20) per median leaf cell, homogeneous, small, *Massula*-type. *Lobules* ovoid, sometimes reduced, when well-developed up to 0.3 mm long, 1/3–2/5× lobe length, strongly inflated-gibbous in the lower half, inflated portion often obscuring the free margin, slightly flattened distally, free margin usually with one short, blunt tooth, apex truncate or oblique, the distal edge of the free margin often slightly connate with the lobe lamina over a width of 2–3 cells. *Underleaves* contiguous to imbricate, transversely ovate, ca. 0.2–0.3 × 0.25–0.6 mm, 3–6× stem width, apex plane or recurved, bases cuneate or rounded, insertion line curved to arched. *Androecia* on short or long branches, bracts in 3–15 series. *Gynoecia* on short or long branches, pseudoinnovations lacking, bract lobes broadly ovate-orbicular, 0.8–1 mm long, apex broadly rounded, dorsal margin sharply toothed, ventral margin weakly toothed or entire, lobule reduced to a very short fold; bracteole transversely ovate, very large, 0.6–1 mm long × 0.8–1.2 mm wide, usually covering the perianth, apex rounded, margins entire or obscurely sinuate. *Perianths* normally immersed, rarely slightly emergent, obovate, with 4 long, sharp, more or less winged, strongly laciniate keels: 2 lateral and 2 ventral keels, dorsal keel lacking, laciniae densely crowded and emerging beyong the bracteole, usually large, up to 25 cells long and 8 cells wide at base, with or without toothed margins; beak ca. 4 cells long. *Sporophyte* as in the genus.

Terpenoids: 5-hydroxycalamene is the major component of this species (Gradstein et al., 1985).

Illustration. Schuster, Hep. Anth. North America IV: 753, Fig. 650. 1980; VandenBerghen, Bull. Jard. Bot. Nat. Belg. **54:** 440–446, Figs. 22–24. 1984.

Distribution. Pantropical; throughout the warm, humid portions of tropical America, from sea level up to 1200 m. I have seen only very few specimens from Central America but presumably the species does occur there more widely. *Lopholejeunea subfusca* is a xerotolerant epiphyte and grows on bark in the high canopy and at the margins of virgin and disturbed rain forest, in low, scrubby vegetations and often in gardens and orchards; occasionally it may grow as an epiphyll on living leaves. The species is most common in lowland environments.

Selected specimens examined. MEXICO. CHIAPAS: Lacandon forest reserve, near Chajul Biological Station, *Gradstein 8077* (U). VERACRUZ: El Palmar, near Tezonapa, *Carlson 1325a* (US), *Sharp 1446b* (TENN).

HONDURAS. ATLÁNTIDA: Lancetilla valley, near Tela, *Standley 55353, 55515, 55559* (US).

UNITED STATES. FLORIDA. DADE: Everglades, Royal Palm Hammock, *Small et al. 6205* (NY, US); Addison Hammock, *Small 6214* (NY). HIGHLANDS: Highlands Hammock State Park, *Schuster 19952a* (NY), *Thiers 3161* (NY). SEMINOLE: Sanford, *Rapp 81* (NY, U, US).

BAHAMA ARCHIPELAGO. NEW PROVIDENCE: Maidenhead, *Britton 3254, 6554, 6577* (NY).

CUBA. HABANA: Sierra del Rosario, *Pócs & Reyes 9042* (EGR); I. de Pines, *Britton & Wilson 15214* (NY). ORIENTE: Holguin, Sao Redondo, *Pócs & Catasús 9023* (EGR, NY, U); Sierra Maestra, Pico Turquino, *Pócs & Duany* (HAC); Sierra Maestra, Gran Piedra, *Pócs & Reyes 9058* (EGR), *Buck 7665* (NY); Baracoa, El Yunque Mt., *Underwood & Earle 10 colls.* (NY); Guantánamo, Sierra del Purial, *Reyes 9186* (EGR, HAC). VILLA CLARA: Sierra de Escambray, *Pócs & Borhidi 9004* (EGR, HAC). Loma San Juan, *Hioram 12678/B* (HAC).

JAMAICA. Hollymount, Mt. Diabolo, *Maxon 2233* (US); Ocho Rios, Gradstein 6385 (MICH, U).

DOMINICAN REPUBLIC. Santo Domingo City, *Rose et al. 4467* (NY, US).

PUERTO RICO. Mayaguez, *Britton & Marble 649* (NY); Cordillera Central, above Villalba, *Gradstein 6502* (U), *Thiers 5324* (NY), Reserva Forestal Guillarte, *Buck 3923* (NY); Barranquitos, *Britton 5576* (NY).

WINDWARD ISLANDS. GUADELOUPE. Matelyane, *Duss 45* (NY). **MARTINIQUE.** Lower slopes of Mt. Pelée, *Duss 639, 683* (NY); summit of Calebasse, *Duss 36* (NY). **ST. LUCIA.** *King s.n.* (NY).

COLOMBIA. CASANARE: Sácama, *Aguirre & Gradstein 2946, 3089* (U). CHOCÓ: Mun. Nuqui, near Arusi, *Gradstein 8868, 1992* (COL, U). VALLE: road Buenaventura-Loboguerrero km 30, *Cleef 2705a* (COL, U).

VENEZUELA. AMAZONAS: San Carlos de Río Negro, *Spruce div. colls.* (MANCH). MIRANDA: Parque Nacional Guatopo, *Nee 17730* (NY). SUCRE: Río Sabacual-Guaraunos, *Griffin & Bermúdez s.n.* (FLAS, U).

TRINIDAD. North Post to Magueripe, *Britton et al. 930* (NY, US).

GUYANA. Mabura Hill, *Cornelissen & Ter Steege 671,* *674 697, 856, 897, 912* (U); Kanuku Mts., Maipaima, *Jansen-Jacobs et al. 1233* (U); Upper Mazaruni, Jawalla, *Gradstein 4883, 4946* (U).

SURINAME. Paramaribo, *Gradstein 1613* (U); Brownsberg, *Bekker 1062B* (U); Kabalebo Dam project area, *Bekker 1062, 1392, 1570A, 1753, 1760B* (U).

FRENCH GUIANA. Mt. Grand Matourey, SW of Cayenne, *Gradstein 5846* (U); Kaw Mts., *Cornelissen & Ter Steege 238* (U); Saül, *Bekker 2116, 2235* (U), *Montfoort & Ek 1010. 1011, 1013, 1014* (U), *Aptroot 15183, 15186* (U), *Gradstein 6095A, 6186* (U).

ECUADOR. Napo: Santa Clara between Puyo and Puerto Napo, *Steere E-83* (NY).

PERU. Huanuco: Tingo Maria, *Hegewald 7909* (U). **Junín:** San Ramón, *Hegewald 8392* (U). **Loreto:** Pucallpa, Yarinacocho, *Hegewald 8245* (U); Iquitos, Laguna Quistococha, *Hegewald 6340, 6351, 6355* (U). **San Martín:** road Yurimaguas-Tarapoto km 95-112, *Frahm et al. 1384, 1683, 1787, 1819* (B, U).

BRAZIL. Acre: SE of Rio Branco, *Nelson 621* (NY). **Amazonas:** Rio Negro, São Gabriel, *Spruce div. colls.* (MANCH), between Manaus and São Gabriel, *Schuster many colls.* (NY); Uaupés, *Spruce s.n.* (MANCH); Manaus, *Griffin et al. I-72* (FLAS, U). **Bahía:** Porto Seguro, *Schäfer-Verwimp 8780* (U). **Espírito Santo:** Vitoria, *Schäfer-Verwimp 8858* (U). **Pará:** Serra do Cachimbo, *Reese 16557* (NY). **Pernambuco:** Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). **Rondonia:** Alto Condeias, Mun. Ariquemes, *Fife et al. 4142, 4198* (NY). **São Paulo:** Reserva Biologica de Mogi Guacu, *Vital 2659* (SP, U); Ubatuba, *Schäfer-Verwimp 8276* (U).

BOLIVIA. Beni: near Guayaramerín, *Reese 12952* (NY, U); Prov. Ballívian, Serranía del Pilón Lagas, *Gradstein 7101, 7111, 7212, 7264, 7281* (LPB, U). **Cochabamba:** road Cochabamba–Villa Tunari km 135, *Gradstein 7494* (LPB, U).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Lopholejeunea subfusca is readily distinguished by its immersed laciniate perianth, hidden behind a large bracteole except for the laciniae which project beyond the bracteole apex. The laciniae are very coarse, up to 25 cells long and 8 cells wide, and densely crowded. The perianth characters are quite diagnostic although plants with somewhat emergent perianths do occur which may be confused with *L. nigricans*.

Other characters of *Lopholejeunea subfusca* are the strongly inflated-gibbous lobules and the truncate distal end of the lobule free margin (near the junction with the lobe), which is connate to the surface of the lobe by 2–3 cells. In other neotropical species of *Lopholejeunea* the distal end of the free margin is connected to the lobe by only one cell and never truncate. Not all lobules of *L. subfusca* have truncate free margin tips, however, and stems should be carefully searched for lobules with this feature.

Sterile plants of *Lopholejeunea subfusca* with reduced lobules may be very difficult to distinguish from *L. nigricans* although the two species usually differ in general appearance. *Lopholejeunea subfusca* always grows in dense mats on bark, tightly appressed to the substrate. The stems are short (1–2 cm long) and flagelliform branches may sprout from lower stem portions. *Lopholejeunea nigricans* is a more slender plant, up to 4 cm long, and usually grows more loosely. Flagelliform branches may occur in *L. nigricans* but are very rare. Unlike *L. subfusca*, the latter species is not restricted to bark but may also grow on rock.

11. Caudalejeunea (Stephani) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893; *Lejeunea* subgen. *Caudalejeunea* Stephani, Hedwigia **29:** 18. 1890. Type. *Caudalejeunea lehmanniana* (Gottsche) Evans. Genus named for its caudiform shoots.

Lejeunea subgen. *Callistolejeunea* Spruce *in* Pearson, Vidensk.-Selsk. Forh. Kristiania **8:** 7. 1892. Type. *Lejeunea harpaphylla* Spruce (= *Caudalejeunea lehmanniana* (Gottsche) Evans).

Plants green to brown, creeping or ascending. *Branching* *Lejeunea*-type, occasionally *Frullania*-type, flagelliform branches lacking. *Stems* with hyalodermis, epidermis symmetric, cell walls thickened and without brownish pigmentation; ventral merophyte four cell rows wide. *Leaves* spreading or weakly convoluted when dry, apex rounded to acute, margins entire or toothed; leaf cells elongate, trigones cordate, intermediate thickenings frequent, 1–3 per wall, oil bodies homogeneous, *Massula*-type, ocelli lacking. *Lobules* variable and sometimes reduced, when well-developed with 1-3 conspicuous teeth (in *Caudalejeunea cristiloba* with up to 10 or more ciliate teeth); hyaline papilla positioned on the margin or on the inner side of the lobule near the proximal base of the first tooth. *Underleaves* emarginate or short bifid, bases cuneate, insertion line shallowly curved; underleaf base bistratose; large, adhesive rhizoid discs at underleaves produced in epiphyllous plants. *Androecia* on short or elongated branches, bracts slightly smaller than leaves, lobules hypostatic, underleaves present throughout; antheridia two per bract. *Gynoecia* without subfloral innovations, pseudoinnovations sometimes present, bracts in 1–3 series, larger than leaves, usually with acute-acuminate apex, margins entire or toothed, lobules usually small and narrow; bracteoles short bifid, margins entire or toothed. *Perianths* compressed, with 1–2 ventral keels, rarely pluriplicate. *Sporophyte:* seta not articulate; elaters 72 (?) per capsule; otherwise as in the tribe. *Vegetative reproduction* by means of discoid gemmae from the dorsal surface of young or modified leaves.

Distribution. The genus *Caudalejeunea* is pantropical and contains about fifteen species, only one of which occurs in the neotropics. The center of diversity is tropical Africa with eleven species (VandenBerghen, 1984a). Schuster (1980) recognized three different subgenera: subgen. *Caudalejeunea*, subgen. *Vermilejeunea* Schust. and subgen. *Acaudalejeunea* Schust. The neotropical species is the type species of the genus, hence belongs to subgen. *Caudalejeunea.*

The unique feature of *Caudalejeunea*, by which it differs from all other genera of Ptychanthoideae, is the capacity of the species to reproduce asexually by means of discoid gemmae. The gemmae are produced on dorsal leaves surfaces, from the upper portions of ascending vegetative branches. In some species gemmae production is rare, however, and in the subgenus *Acaudalejeunea* gemmae are unknown.

Caudalejeunea is the only genus of Ptychanthoideae which is frequently epiphyllous. When growing on leaves it produces large adhesive rhizoid discs at the underleaf bases. These discs serve as a holdfast and are a characteristic morphological feature of epiphyllous Lejeuneaceae. The species also grow on bark but, characteristically, rhizoid discs are lacking in corticolous plants.

1. **Caudalejeunea lehmanniana** (Gottsche) Evans, Bull. Torrey Bot. Club **34:** 554, Pl. 33. 1907; Schuster, Hep. Anth. N. America IV: 779, Figs. 654, 655. 1980; *Lejeunea lehmanniana* Gottsche, Syn. Hep. 325. 1845. Type. Brazil. *Liebmann s.n.* (holotype, W; isotype, G). Fig. 32.

Lejeunea crescentiae Lindenberg & Gottsche, Syn. Hep. 752. 1847; *Caudalejeunea crescentiae* (Lindenberg & Gottsche) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893. Type. Mexico. Mirador, "in folio *Crescentiae,*" *Liebmann 273* (holotype, W; isotypes, C, G).

Lejeunea harpaphylla Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 123. 1884; *Caudalejeunea harpaphylla* (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893. Type. Ecuador. Río Bombonasa, *Spruce L173* (lectotype, MANCH; isolectotype, G).

Lejeunea harpaphylla Spruce fo. *breviloba* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 123. 1884. Type. Brazil. Amazonas: Rio Negro, São Gabriel, *Spruce s.n., Hepaticae Spruceanae: Amazonicae et Andinae* (lectotype, MANCH; isolectotypes, G, W), *syn. nov.*

Lejeunea harpaphylla Spruce fo. *longiloba* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 123. 1884. Type. Brazil. Amazonas: Rio Uaupés, Panuré, *Spruce s.n.* (holotype, MANCH), *syn. nov.*

Phragmicoma haenkeana Schiffner, Bot. Centralbl. **27:** 210. 1886; *Caudalejeunea haenkeana* (Schiffner) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 129. 1893. Type. Mexico. *Haencke s.n.* (n.v.), syn. fide Evans (1908).

Caudalejeunea leiboldii Stephani, Hedwigia **34:** 233. 1895; *Lejeunea leiboldii* Stephani, Hedwigia **29:** 19. 1890, nom. inval. Type. Cuba. *Leibold s.n., Hb. Stephani 417* (holotype, G, n.v.; isotype, MANCH).

Caudalejeunea tricarinata E. W. Jones, Trans. Brit. Bryol. Soc. **2:** 169, Fig. 2. 1953. Type. Africa. Nigeria. Okumé Forest Reserve, *Jones 33, 70 p.p., 190A* (syntypes, Hb. Jones, n.v.), syn. fide Schuster (1980).

Mastigolejeunea dentilobula Herzog, Rev. Bryol. Lichénol. **20:** 134. 1951. Type. Honduras. Atlantida: Lancetilla valley, near Tela, *Standley 48775a* (lectotype, JE; isolectotype, NY), *syn. nov.*

Thysananthus brasiliensis S. Arnell *in* Schiffner & Arnell, Oesterr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. **11:** 118. 1964. Type. Brazil. Paraná: Rio Paranapanema, near Salto Grande, *Schiffner 2199* (holotype, W), *syn. nov.*

Autoicous or dioicous. *Plants* to 4 cm long × 1.5–2.5 mm wide, dull bright green, becoming pale yellowish to brown when dry, loosely creeping to ascending and free from the substrate, on twigs or leaves. *Branching* irregularly pinnate, *Lejeunea*-type, microphyllous branches lacking. *Stems* 0.15–0.2 mm in diam., in cross section composed of ca. 12–15 epidermal cells surrounding ca. 20–30 smaller medullary cells, epidermis symmetric, all cell walls slightly thickened, colorless; ventral merophyte four cell rows wide. *Leaves* distant to subimbricate, obliquely spreading and somewhat falcate, convex or plane, not squarrose, when dry flat and variable in position, some leaves spreading-falcate with a sheathing base, others (sub)erect and appressed to the stem

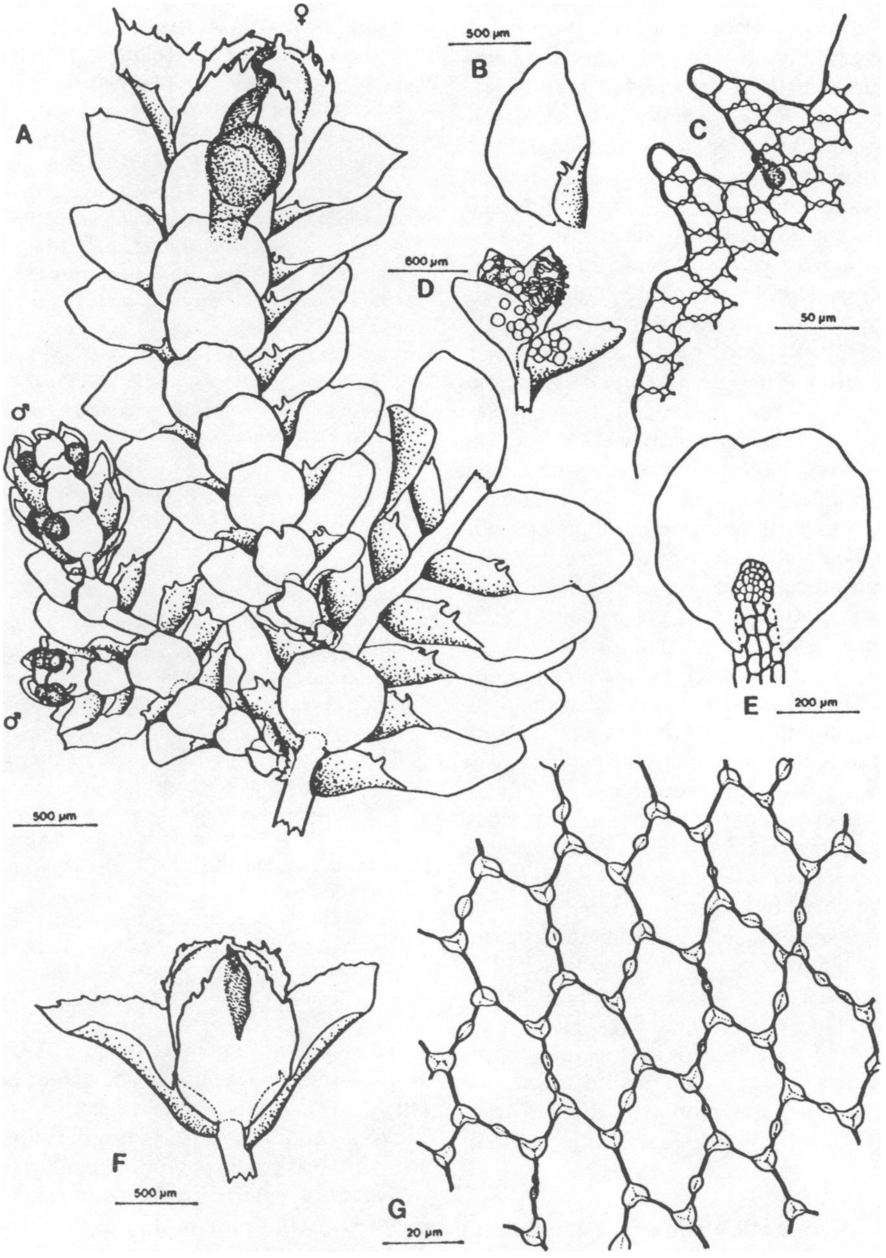

FIG. 32. *Caudalejeunea lehmanniana*. **A.** Habit, with gynoecium and two androecial branches; note *Lejeunea*-type branching. **B.** Leaf. **C.** Lobule apex. **D.** Gemmae. **E.** Underleaf. **F.** Gynoecium. **G.** Leaf cells. From Brazil, *Vital 1373-b*.

but not convoluted, dorsal lobe ovate-oblong to narrowly oblong, 0.8–1.5 × 0.5–0.8 mm, apex rounded to acute, plane, margins entire or weakly toothed near apex, ventral margin plane, forming a straight line or very wide angle with the keel; cells in mid-leaf ca. 30–45 × 20–25 µm, trigones usually conspicuous, intermediate thickenings 1–2(–3) per wall. *Lobules* ovate-oblong, 3.0–5.5 ×

0.1.5–2.5 mm, sometimes reduced to a small fold, inflated, keel curved or straight, apex acute and short continuing into the ventral margin of the lobe, free margin incurved proximally, towards apex plane and with 1–2(–3) teeth, first tooth coarse, 3–6 cells long and 2–3 cells wide at base, second tooth shorter, sometimes reduced. *Underleaves* distant to imbricate, plane or gibbose, broadly obovate-obcuneate, 0.35–0.5 mm long × 0.35–0.6 mm wide, 2–5× stem width, apex truncate or emarginate, plane, margins entire, bases short decurrent, insertion line curved; epiphyllous plants with a large, circular rhizoid disc originating from the base of the underleaves. *Androecia* usually terminal on elongated branches, bracts in 4–15 series. *Gynoecia* with 1–2 series of bracts, inner bracts obliquely spreading, lobe ovate-lanceolate, up to 1.5 mm long, apex acute-acuminate, margins entire or weakly toothed above, lobule reduced to a small, narrow fold, up to 0.5 mm long; inner bracteole as long as or slightly shorter than the bracts, narrowly oblong, up to 1.3 mm long, tapering to a short bifid apex, margins entire or weakly toothed above. *Perianths* exserted to 1/2 or less, obovate-obconical, up to 1.5 mm long, with very broad, truncate-retuse apex and three long, narrow keels: two sharp lateral keels and one rather sharp ventral keel, lateral keels smooth or irregularly toothed-winged above, ventral keel smooth; beak 3–5 cells long. *Sporophyte* as in the genus.

Distribution. Scattered throughout Tropical America, from sea level to about 1000 m; also recorded from West Africa (as *Caudalejeunea tricarinata* E. W. Jones). *Caudalejeunea lehmanniana* grows on living leaves, twigs or branchlets in scrub, swamps, or in rain forest in rather open situations, e.g., in the high canopy, in gaps and at forest margins. The plants usually grow in small tufts and never form extensive mats.

Specimens examined. MEXICO. CHIAPAS: Palenque, *Eggers & Frahm MX22,6* (JE); Lacandon forest reserve, near Chajul Biological Station, *Gradstein 8049* (U). VERACRUZ: Mirador, *Liebmann 242* (C).

BELIZE. Orange Walk District, near Lamanai, *Hebda B5* (NY).

HONDURAS. Copán, archeological site, *Hape 50949* (US).

COSTA RICA. St. Domingo de Golfo Dulce, *Tonduz 15601* (G).

PANAMA. Barro Colorado I., *Machado 32* (NY).

UNITED STATES. FLORIDA. COLLIER: Collier-Seminole State Park, *Schuster 26130a* (G), *20428, 26148* (NY). DADE: Everglades Nat. Park, *Small & Lowe 7041, 7044, 7059* (NY), *Small & Mosier 5285, 6174, 6188* (US), *Schuster 22810* (NY), *Buck B799* (NY).

BAHAMA ARCHIPELAGO. NEW PROVIDENCE: Maidenhead, *Britton 257* (NY).

CUBA. LAS VILLAS: Peninsula Zapata, *Boruvka s.n.* (JE, PRC). MATANZAS: *Underwood 2136* (G). ORIENTE: Sierra del Escambray, Pico Potrerillo, *Pócs & Borhidi 9011/CB* (EGR). PIÑAR DEL RÍO: Peninsula Guanahacabibes, *Schubert M1* (JE).

JAMAICA. Ocho Rios, *Britton 739* (NY), *Gradstein 6390* (MICH, U).

PUERTO RICO. Santurce, *Heller 838* (US); Arecibo, Reserva Forestal Cambalache, *Buck 16168* (NY).

WINDWARD ISLANDS. MARTINIQUE. Fort de France, Bois Lezard, *Maurice 120* (CINC, U).

VENEZUELA. FALCÓN: Coro, Cerro Buenos Aires, *Wingfield 13480B* (U).

GUYANA. Mabura Hill, 180 km S of Georgetown, *Cornelissen & ter Steege C563* (U).

SURINAME. NICKERIE: Kabalebo Dam project area, *Bekker 1451b, 1529a* (U), *Lindeman 888a* (U).

ECUDADOR. Type of *Lejeunea harpaphylla*.

PERU. LORETO: near Iquitos, laguna Quistococha, *Hegewald 6353a, 6358* (U).

BRAZIL. AMAZONAS: Rio Negro, São Luis, *Schuster 79-4-121* (NY), Ilha da Costa Arirarrá, *Schuster 79-5-135* (NY). ESPIRITO SANTO: Juguaré, *Schäfer-Verwimp 8821* (hb. Schäfer-Verwimp). MATO GROSSO: Mun. Barra do Garcas, *Vital 1373B* (JE, SP, U). PARÁ: Santarem, *Schäfer-Verwimp 2716* (JE); Serra do Cachimbo, *Reese 16515, 16699* (NY). PARANÁ: type of *Thysananthus brasiliensis*. PERNAMBUCO: Rio Formosos, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). RIO GRANDE DO SUL: Reserva Florestal do Turvo, *Lorscheitter-Baptista s.n.* (ICN 12846, U). RONDONIA: Rio Pacaás Novos, first rapids, *Reese 13562a, 13649* (NY, U). SANTA CATARINA: Blumenau, *unknown coll.* (G). SÃO PAULO: Bertioga, *Schäfer-Verwimp 8536* (JE).

PARAGUAY. ALTO PARANÁ: 80 km N of Hernandarías, *Geissler 14642* (G).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993). Material from the Galapagos Islands identified as *Caudalejeunea lehmanniana* by Clark (1953) belongs to *Dicranolejeunea axillaris*.

Caudalejeunea lehmanniana is easily recognized by its elongated, obliquely spreading and somewhat falcate leaves which are barely overlapping, its emarginate, entire underleaves, and by its elongated leaf lobules with two conspicuous teeth. The plants are usually fertile and produce innovation-free gynoecia with narrow oblong-lanceolate, acuminate bracts, short bifid bracteoles and obconical perianths with three sharp keels. Variation is seen in the overall size of the plants, in the leaf apex which may be rounded or narrow subacute, and in the margins of leaves, female involucre and perianth which may be entire or somewhat toothed.

12. Acrolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; Gradstein, Bryophyt. Biblioth. **4:** 1-162, Pls. I-XXIV; *Lejeunea* subgen. *Acrolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 115. 1884. Lectotype (Gradstein, 1974). *Acrolejeunea torulosa* (Lehmann & Lindenberg) Schiffner. Genus named for the gynoecia terminal on elongated shoots, without innovations.

Ptychocoleus Evans, Bull. Torrey Bot. Club **35:** 161. 1908, non Trevisan 1877. Lectotype (Evans, 1908). *Acrolejeunea aulacophora* (Montagne) Stephani (= *Ptychocoleus aulacophorus* (Montagne) Trevisan).

Plants 1–4 cm long × 1–2 mm wide, glossy (yellow) green when alive, dull yellow brown to gray brown in the dried condition, loosely creeping or forming dense mats, on bark. *Branching* predominantly *Lejeunea-type, occasionally Frullania*-type, irregularly pinnate, often with tiny upright flagelliform shoots producing caducous leaves. *Stems* with hyalodermis, dorsal epidermal cells slightly larger than ventral epidermal cells in neotropical species, epidermal cells thinwalled, medullary cells slightly thickened, all cell walls ± colorless; ventral merophyte 4–6 cell rows wide. *Leaves* rather densely imbricated, strongly convoluted when dry, wide spreading and often somewhat squarrose when moist, dorsal margin plane, dorsal base cordate, apex rounded to obtuse, plane, margins entire; leaf cells elongate, trigones cordate, oil bodies homogeneous, *Massula*-type, ocelli lacking. *Lobules* 2/5–1/2× lobe length, never reduced, inflated along the keel, flattened towards the free margin, with (2–)3–8 teeth; hyaline papilla positioned on the inner side of the lobule 2–3 cells below the proximal base of the first tooth. *Underleaves* 3–4.5× stem width, apex rounded to truncate, plane in neotropical species, margins entire, bases cuneate to rounded, insertion line shallowly curved; underleaf base at the rhizoid disc bistratose, with four superior central cells. *Androecia on elongated branches, bracts little modified, lobule epistatic, underleaves present throughout; antheridia one per bract. Gynoecia* without true subfloral innovations, occasionally with small pseudo-innovations of the *Radula*-type (originating below the inner bracts), bracts in 2–6 series, with rounded to obtuse apex and entire margins, lobules large; inner bracteoles about as long as the bracts, ovate-oblong to suboribicular, apex undivided, plane or narrowly recurved, margins entire. *Perianths* with 5–10 smooth, rounded keels. *Sporophyte:* seta articulate; elaters 30(38) per capsule (van Slageren, 1985); otherwise as in the tribe. *Vegetative reproduction* in all neotropical species by means of tiny caducous leaves produced on upright flagelliform shoots; flagellae devoid of leaves and with numerous small, appressed to squarrose underleaves. *Terpenoids:* pinguisanines.

Distribution. The genus *Acrolejeunea* is pantropical in distribution and contains 15 species (Gradstein, 1975). The center of diversity of the genus is Southeast Asia. Tropical America has only three species, all belonging to subgen. *Acrolejeunea.*

The neotropical species occur in lowland areas, up to about 1000 m, in relatively dry, open habitats: in plantations, pastures, savannas, savannah forests, scrub, gallery woodlands and in the canopy of primary and secondary rain forests. They usually grow on bark, rarely on rock. The genus is most common in northern South America and seems virtually lacking in the West Indies.

Acrolejeunea is recognized by its glossy green to yellow brown color, the lack of any trace of darkish pigmentation in the cell walls, the very densely imbricated leaves, the almost straight underleaf insertion line, the unmodified male bracts which resemble vegetative leaves, the lack of subfloral innovations, and the perianth which has many keels (usually 6–10).

Gradstein (1975) distinguished two subgenera, subgen. *Acrolejeunea* characterized by the presence of vegetative reproduction by means of caducous leaves, and subgen. *Isolejeunea* Gradst. which lacks vegetative reproduction. All neotropical species produce caducous leaves and belong in the subgenus *Acrolejeunea.* The caducous leaves originate from the apex of tiny, upright flagelliform shoots and are usually very small, about 0.2–0.3 mm long. In *A. torulosa* they are highly modified, with subequal lobe and lobule and a long subapical rhizoid; in the other species caducous leaves resemble young branch leaves, possessing rather small lobules and lacking a long subapical rhizoid. The flagelliform shoots are 1–5 mm long, devoid of leaves (except near the apex) and with tiny, densily imbricated underleaves.

Acrolejeunea is most closely related to *Frullanoides*. Differences are discussed under the latter.

Key to the Species of *Acrolejeunea*

1. Lobule with 2–3(–4) teeth, the teeth erect; lobule free margin semicircular, undulating between the teeth; northern South America. . . . . 1. *A. emergens.*
1. Lobule with 5–8 teeth, the first tooth curved outwards (rarely erect); lobule free margin straight or slightly curved, not undulate.
    2. First tooth of the lobule longer than the other teeth, 2–4 cells long; caducous leaves very small, with a lobule almost as long as the lobe and with a long, subapical rhizoid; northern South America, common. . . . . 2. *A. torulosa.*
    2. First tooth of the lobule not longer than the other teeth, all teeth consisting of a single, inflexed cell; lobule of caducous leaves up to half the length of the lobe, subapical rhizoid lacking; Florida, Central America, Greater Antilles, uncommon. . . . . 3. *A. heterophylla.*

1. **Acrolejeunea emergens** (Mitten) Stephani *in* Engler, Die Pflanzenwelt Ostafrikas C: 65. 1895; Gradstein, Bryophyt. Biblioth. **4:** 71. 1975; *Phragmicoma emergens* Mitten, Philos. Trans. **168:** 397. 1879; *Lejeunea emergens* (Mitten) Stephani, Bull. Soc. Roy. Bot. Belg. **32:** 119. 1894; *Ptychocoleus emergens* (Miten) Stephani, Spec. Hep. **5:** 24. 1912. Type. Africa. Rodriguez I., *Balfour s.n.* (holotype, NY; isotype, BM).

Ptychocoleus grossispicus Stephani, Spec. Hep. **5:** 34. 1912. Type. French Guiana. St. Jean, *unknown collector* (holotype, G).

Autoicous or dioicous. *Plants* 1–3 cm long × 1.2–2 mm wide. *Branching Lejeunea*-type, occasionally *Frullania*-type, flagelliform shoots frequently present. *Stems* 0.12–0.2 mm in diam., in cross section composed of 15–20 thin-walled epidermal cells surrounding 25–35 smaller, slightly thick-walled medullary cells; ventral merophyte 4–6 cell rows wide. *Leaves:* dorsal lobe ovate-suborbicular, 0.7–1.2 × 0.6–0.9 mm, apex rounded or subobtuse, ventral margin plane or curved upwards, when spread out forming an angle of 150–180° with the keel; median cells 25–35 × 17–24 μm, trigones small to medium-sized, intermediate thickenings usually scarce; oil bodies homogeneous, small, ellipsoid to fusiform, 2–3 × 6–8 μm, 9–20 in median leaf cells, more numerous in basal leaf cells, shorter and fewer in margins cells. *Lobules* ovate-semiorbicular, 0.35–0.5 × 0.25–0.35 mm, 2/5–1/2× lobe length, apex oblique to truncate, keel straight, curved near the base, free margin plane, ± semicircular in outline, often waving between the teeth, with 2–4 erect or somewhat inflexed teeth, the first tooth 2-3 cells long, the other teeth 1–2 cells long, the teeth rather widely separated from each other (by 4–7 margin cells). *Underleaves* broadly ovate-obovate, 0.3–0.4 × 0.5–0.65 mm, 3–4.5× stem width, margins plane or weakly recurved. *Androecia* with bracts in 4–13 series. *Gynoecia* with bracts and bracteoles in 2–3(–4) series, inner bracts suberect or squarrose above, bifid to 1/3, keel sharp or broadly rounded, lobes obovate, 1,1–1,4 mm long, apex widely rounded, lobules narrow oblong, 3/4× lobe length, apex rounded or notched; bracteoles as in the genus. *Perianths* immersed or (when stalked) exserted to 1/3, obovoid to obpyriform, 0.8–1.4 mm long, entirely inflated or compressed above, 5–10-keeled in the upper half with 2–5 ventral, two lateral and 1–3 small dorsal keels, beak 3–8 cells long. *Sporophyte* as in the genus. *Caducous leaves* basically similar to branch leaves but about 3–4× smaller, lobule up to half the size of the lobe, with 1–3 short teeth, a few short rhizoids arising from cells along the keel, long subapical rhizoid lacking.

Illustration. Gradstein, Bryophyt. Biblioth. **4:** Pl. IX, X. 1975.

Distribution. Throughout the neotropics but particularly northern South America; also in tropical Africa (where the species is very common) and Sri Lanka. Isolated records from Mexico, Jamaica (a tiny fragment!) and southern Bolivia indicate that *Acrolejeunea emergens* is very widespread in the neotropics even though the number of collections is still rather low. The species grows mainly in scrubby secondary vegetation and cultivated areas.

Specimens examined. MEXICO. OAXACA: between Tuxtepec and Chiltepec, *Clayton B483* (F).

PANAMA. DARIÉN: trail El Real-Pirre, *Salazar & Gradstein 9197* (PMA, U). PANAMÁ: Madden Dam and near Alahuela, *Dodge 16872* (hb. Fulford).

JAMAICA. St. Elisabeth, near Ipswich, *Maxon & Killip 1499 p.p.* (US).

VENEZUELA. GUARICO: Calabozo, *Goodland s.n.* (US).

GUYANA. Kanuku Mts., Nappi Cr., *Jansen-Jacobs et al. 604* (U).

SURINAME. Paramaribo, *Kegel s.n.* (BM, U, W).

FRENCH GUIANA. Cayenne, *Broadway 843* (FH, NY, U, US, YU), *Gradstein 5767, Bryoph. Neotrop. Exsicc.* 131 (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PAN, QCA, S, SP, U, USJ, XAL).

BRAZIL. AMAZONAS: Rio Negro, São Gabriel, *Spruce s.n.* (MANCH); road Manaus- Itacoatiara, *Griffin 212* (FLAS, U); road Manaus-Caracarai, *Griffin et al. 48* (FLAS, U). BAHIA: near Mun. Morro de Chapeu, *Vital 6062* (SP, U), *Boom & Mori 1259, 1283* (NY). GOIÁS: Mun. Formoso, *Vital 8527* (SP, U). MATO GROSSO: São Joao, *Lindman 544* (M, S); Camapua, *Vital 6424* (SP, U). PARÁ: Serra do Cachimbo, *Reese 16199, 16207, 16293* (NY); Rio Cururu, *Sioli 40* (GRO). RONDÔNIA: Rio Pacaás Novos, near first rapids, *Reese 13351* (NY, U). SÃO PAULO: Res. Biol. de Mogi-Guacu, *Vital 2647, 2666* (SP, U); Nova Independência, near Andradino, *Vital 2088* (NICH, SP, U); Mun. Onda Verde, *Vital 5001* (SP, U).

BOLIVIA. BENI: near Guayaramerín, *Reese 12730, 12976* (NY, U). SANTA CRUZ: Prov. Ichilo, 3 km N of Buena Vista, *Gradstein 7727, 7728* (LPB, U).

Acrolejeunea emergens is closely related to *A. torulosa* and differs from the latter mainly by its lobule, which is somewhat broader and has 2–3 (–4) teeth set along a semicircular free margin and with U-shaped sinuses between the teeth, and by the more simple caducous leaves, which resemble small branch leaves. Moreover, the keel in *A. emergens* usually forms an almost straight line with the ventral leaf margin whereas in *A. torulosa* an angle of 140–160° is observed. Occasionally the two species grow mixed.

2. Acrolejeunea heterophylla (Evans) Grolle & Gradstein *in* Gradstein, J. Hattori Bot. Lab. **38:** 332. 1974; Gradstein, Bryophyt. Biblioth. **4:** 68. 1975; Schuster, Hep. Anth. N. America IV: 794, Fig. 657. 1980; *Ptychocoleus heterophyllus* Evans, Amer. J. Bot. **5:** 44, Fig. 5. 1918. Type. United States. Florida. Seminole: Robinson's spring 8 km of Sanford, on live oak, *Rapp. s.n.* (holotype, YU).

Dioicous. *Plants* 1–3 cm long × 1–1.5 mm wide. *Branching Lejeunea*-type, occasionally *Frullania*-type, flagelliform shoots occasionally present. *Stems* 0.1–0.15 mm in diam., in cross section composed of 13–20 thin-walled epidermal cells surrounding more numerous smaller, slightly thick-walled medullary cells; ventral merophyte four cell rows wide. *Leaves*: dorsal lobe ovate-suborbicular, 0.6–1 × 0.45–0.8 mm, apex (sub)obtuse, ventral margin ± plane, when spread out forming an angle of 90–140° with the keel; median cells 25–35 × 17–23 μm; trigones medium-sized, intermediate thickenings frequently present on the longer walls, one per wall; oil bodies (Schuster, 1954) homogeneous, small, bacilliform to narrowly fusiform, more rarely ovoid to broad-ellipsoid, 2(–3) × 3–5(–8) μm, 7–12 in median leaf cells. *Lobules* ovate-triangular, 0.35–0.5 × 0.25–0.3 mm, ca. 1/2× lobe length, apex oblique, keel slightly curved, free margin plane or curved upwards, gradually curved to the apex and not or shortly continuing into the ventral margin of the lobe, with (4–)5–7 teeth, the teeth entirely or partly inflexed, consisting of only one sphaerical cell attached to an enlarged margin cell, closely spatiated, separated from each other by only 1–2 margin cells (the first tooth sometimes more widely separated). *Underleaves* orbicular to broadly ovate, 0.3–0.4 × 0.35–0.5 mm, 3× stem width, margins plane. *Androecia* with bracts in 6–15 series. *Gynoecia* with bracts and bracteoles in 3–5 series, inner bracts wide spreading to squarrose above, bifid to 1/4, lobes ovate, ca. 1.2 mm long, the margins tapering to an obtuse to subacute apex, lobules oblong, almost as long as the lobe length, apex obtuse; inner bracteoles as in the genus. *Perianths* not exserted, obovoid, averaging 1 × 0.7 mm, compressed above, 6–10-keeled in the upper half with 5–6 unequal or ca. 10 subequal keels, beak 5–6 cells long. *Sporophyte* unknown. *Caducous leaves* as in *A. emergens*.

Illustration. Gradstein, Bryophyt. Biblioth. **4:** Pl. VII. 1975; Schuster, Hep. Anth. N. America IV: 795, Fig. 657. 1980.

Distribution (Fig. 34). Central Florida, the Caribbean side of Central America (Mexico to Costa Rica) and Greater Antilles (Dominican Republic), uncommon. The habitat of *Acrolejeunea heterophylla* is as in the genus.

Specimens examined. MEXICO. VERACRUZ: Estación Biologica "Los Tuxtlas," *Gentry et al. 32567 (MO, U).*

GUATEMALA. IZABAL: Puerto Barrios, *Steyermark 39828* (F, hb. Fulford).

BELIZE. Punta Gorda, *unknown collector* (hb. Fulford).

HONDURAS. Morazán, La Montanita, *Stanley 12355* (F).

NICARAGUA. Sandy Bay, *Hamilton 224, 225* (DUKE, FH, YU).

COSTA RICA. Turrialba, *Schultes 11885* (NY).

UNITED STATES. FLORIDA. DADE: Royal Palm Park, *Taylor s.n.* (YU); Everglades, Gumbo Limbo trail, *Redfearn 31591a* (U). **MARION:** Ocala Nat. Forest, Juniper Springs, *Schuster 22090* (NY), ibid. *31910b* (ABSH, H, NY), ibid. *31940* (DUKE). **SEMINOLE:** Sanford, *Rapp, Hep. Flor. 38* (ABSH, BM, FH, K, NY, PRC, U, US).

DOMINICAN REPUBLIC. Prov. La Vega, Jarabacoa, *Buck 8533* (NY).

Acrolejeunea heterophylla is the only dioicous species of the genus in the neotropics and stands out by its northern distribution. The species is lacking in South America where it is replaced by *A. torulosa* and *A. emergens*.

Acrolejeunea heterophylla is easily recognized by the 4–8 more or less inflexed lobule teeth which all consist of only one rounded cell, and by the rather narrow, obtuse leaf apex. The caducous leaf is small and little modified (as in *A. emergens*), with a few short rhizoids arising from the keel. *A. heterophylla* may be confused with *A. torulosa* but the latter has a longer apical tooth (2–4 cells long), a broader leaf apex, and more strongly modified caducous leaves. Moreover, the two species have very different geographical distributions.

3. Acrolejeunea torulosa (Lehmann & Lindenberg) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. 1, **3(1):** 128. 1893; Gradstein, Bryophyt. Biblioth. **4:** 63, Pl. VIII. 1975; *Jungermannia torulosa* Lehmann & Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **6:** 41. 1834; *Phragmicoma torulosa* (Lehmann & Lindenberg) Lehmann & Lindenberg, Syn. Hep. 294. 1845; *Ptychocoleus torulosus* (Lehmann & Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 405. 1877; *Lejeunea torulosa* (Lehmann & Lindenberg) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 117. 1884; *Marchesinia torulosa* (Lehmann & Lindenberg) Kuntze, Revis. Gen. Pl. **2:** 837. 1891. Type. Guianas. "hb. Hooker" (holotype, S; isotypes, BM, FH, MANCH, NY, PC, W, YU). Fig. 33.

Lejeunea polyphylla Taylor, London J. Bot. **5:** 390. 1846; *Symbiezidium polyphyllum* (Taylor) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Lejeunea torulosa* var. *polyphylla* (Taylor) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 118. 1884; *Archilejeunea polyphylla* (Taylor) Stephani, Spec. Hep. **4:** 717. 1911. Type. Brazil. Pará: Belém, on bark of coffee trees, *Richard s.n.* (holotype, FH-TAYL; isotypes, BM, MANCH, W).

Acrolejeunea torulosa var. *obtusa* Gradst., Bryophyt. Biblioth. **4:** 67. 1975. Type. Guyana. Rupununi river basin, near mouth of Chairwair creek, *Smith 2397* (holotype, NY; isotypes, FH, hb. Fulford, K, S, U, US), *syn. nov.*

Autoicous or dioicous. *Plants* up to 4 cm long × 1.2–1.8 mm wide. *Branching Lejeunea*-type, occasionally *Frullania*-type, flagelliform shoots frequently present. *Stems* 0.12–0.17 mm in diam., in cross section composed of 16–22 thin-walled epidermal cells surrounding 24–34 smaller, slightly thick-walled medullary cells; ventral merophyte 4(–6) cell rows wide. *Leaves* dorsal lobe ovate-orbicular, 0.7–1.2 × 0.7–1 mm, apex rounded or subobtuse, ventral margin plane or curved upwards, when spread out forming an angle of 140–160° with the keel; median cells 25–35 × 16–27 µm; trigones small to medium-sized, intermediate thickenings usually scarce; oil bodies homogeneous, small, ellipsoid to fusiform, 2 × 4–7(–9) µm, 7–15 in median leaf cells. *Lobules* ovate-triangular, 0.35–0.5 × 0.25–0.35 mm, 2/5–1/2× lobe length, apex oblique, keel almost straight, curved near the base, free margin plane or curved upwards, straight or slightly curved to the apex and shortly continuing into the ventral margin of the lobe, with 5–7 teeth, the first tooth 2–4 cells long, curved outwardly, occasionally erect or inflexed, separated from the second tooth by 3–5 margin cells, the other teeth 1–2 cells long, erect or inflexed, separated from each other by 1–3 margin cells. *Underleaves* broadly ovate to obovate, 0.25–0.5 × 0.5–0.8 mm, 3–4.5× stem width, margins plane. *Androecia* with bracts in 6–10 series. *Gynoecia* with bracts and bracteoles in 3–6 series, inner bracts squarrose above, bifid to 1/3, lobes obovate, 1,1–1,4 mm long, apex widely rounded, rarely narrow obtuse (var. *obtusa* Gradst.), lobules narrow oblong, 2/3–3/4× lobe length, apex rounded, obtuse or notched; inner bracteoles as in the genus. *Perianths* not

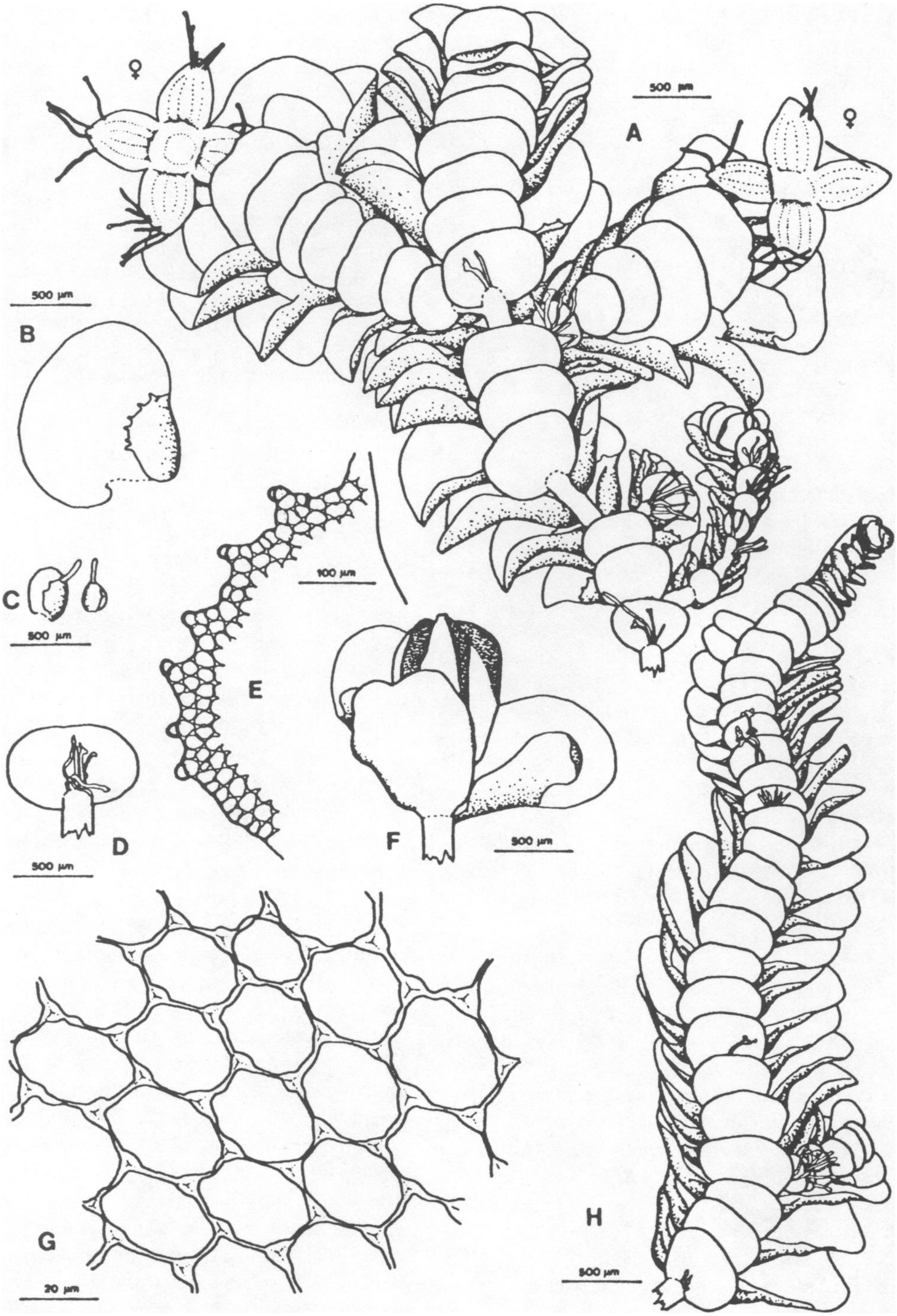

FIG. 33. *Acrolejeunea torulosa*. **A.** Habit, with two gynoecia. **B.** Leaf. **C.** Caducous leaves. **D.** Underleaf. **E.** Lobule free margin. **F.** Gynoecium. **G.** Leaf cells. **H.** Stem terminating in flagella producing caducous leaves. From Brazil, *Lisboa et al. 2951*.

exserted, obovoid, averaging 1 × 0.7 mm, weakly compressed above, 5–10-keeled in the upper half with 2–5 ventral, two lateral and 1–3 small dorsal keels, beak 6–7 cells long. *Sporophyte*: spores 40–50 m long, covered with numerous short, bluntish papillae and a few rosettes; elaters 350–400 × 14 µm, with one brown, ca. 4 µm wide spiral. *Caducous leaves* usually minute, about 4–6× smaller than branch leaves, with subequal lobe and lobule, lobule with 2 teeth, a long apical rhizoid arising from the sinus at the apex of the keel (in colls. *Vital 2109, 1846* from Brazil caducous leaves larger, resembling those of *Acrolejeunea emergens*).

Terpenoids: trans-ß-farnesene and various pinguisanines (hydroxypinguisanine, pinguisanolide) have been detected as main compounds of this species (Gradstein et al., 1985).

Distribution (Fig. 34). Northern South America, common. Habitat as in the genus.

Selected specimens examined. NETHERLANDS ANTILLES. CURAÇAO: Christoffelberg region, *van Slageren & Stoffers 8130, 8155, 8222, 8225* (U).

TRINIDAD. Piarco Savanna, *E.G. Britton et al. 119* (FH, NY, US, YU); Princestown, *Broadway 9137* (hb. Fulford).

COLOMBIA. AMAZONAS: Araracuara, *Sipman & Duivenvoorden 28152, 28167* (B, U). CUNDINAMARCA: Mun. Medina, *Aguirre 6688* (COL). META: Villavicencio, *Rangel & Cala 1966* (COL). NARIÑO: Mun. Mosquera, Parque Nacional Sanguianga, *Linares 40, 41, 67* (COL, U). RISARALDA: St. Cecilia, *Gradstein 9019* (COL, U). VAUPÉS: San José del Guaviare, *Schultes 11122* (COL).

VENEZUELA. AMAZONAS: San Carlos, *Halling 4367* (NY); near Puerto Ayacucho, *Davidse & Gonzales 15273, 15288* (MO, U); Upper Orinoco, Esmeralda, *Lützelburg 22552* (JE), *Mägdefrau 188a* (U); Cerro Neblina, *Buck 11415* (NY). APURE: Muñoz, Caño Guaritico, *Davidse & Gonzales 14832* (MO, U); Pedro Camejo, 14 km SW of Urañon, *Davidse & Gonzales 12738* (MO, U), Río Meta 22 km NW of Buena Vista, *Davidse & Gonzales 14299* (MO, U); San Fernando, Río Arauca & Río Orinoco, *Davidse & Gonzales 192, 13257, 13273* (MO, U). GUARICO: San Carlos, *Rudd 407* (hb. Fulford). LARA: road Gamelotal-Yaritagua, El Altar, *Griffin et al. 210* (FLAS, U). MONAGAS: 15 km S of Maturín airport, *Nee 17343* (NY).

GUYANA. Georgetown, *Aptroot 15717* (U), *Gradstein 4705a* (U); Timehri, *Gradstein 4717* (U); Mabura Hill, *Cornelissen & ter Steege 118, 716, 745, 906* (U); Kanuku Mts., Maipaima, *Jansen-Jacobs 1150* (U); Upper Mazaruni, near Waramadan, *Gradstein 5668, 5685* (U).

SURINAME. Paramaribo, Palmgarden, *Gradstein 4610, 4625* (U); Charlesburg, *Lanjouw 124, Verdoorn, Hep. Crit. Sel. 436* (BM, FH, JE, L, MANCH, NY, S, US, W, YU); Berg en Dal, *Suringar s.n.* (L); Brownsberg, *Gradstein 4691* (U); Kabalebo Dam project area, *Bekker 1484, 1493, 1524, 1564, 1575, 1763* (U).

FRENCH GUIANA. Kourou, *Bekker 2035* (U); St. Jean de Marouni, *Rey 38* (PC); Saül, *Cremers 6885* (CAY, U), *Gradstein 6118* (U), *Montfoort 828-832* (U).

PERU. LORETO: near Iquitos, *Hegewald 6322, 6354* (U), *Timme 5350* (NY).

BRAZIL. ACRE: road Rio Branco–Brasileia km 33, *Reese & McPherson 13249* (NY, U); Cruzeiro do Sul, *Prance et al. 11967* (NY, U). AMAZONAS: Rio Negro, Mt. Canapuna, *Spruce L95* (MANCH); along Rio Negro between Manaus and São Gabriel, *Schuster 13 colls.* (NY); Manaus, Estrada Mauá, *Smith et al. P11728* (NY, U); road Manaus-Caracarai, *Griffin et al. 48* (FLAS, U); road Manaus-Itacoatiara km 12, *Griffin 212* (FLAS, U); Rio Uatumã, *Buck 2784, 2963* (NY). BAHIA: Serra da Agua de Rega, Rio Riachao, *Irwin et al. 31048* (NY, U); Rio das Ondas, near Mun. Barreiras, *Irwin et al. 31421* (NY, U); Rio de Contas, Mun. Cachoeira da Fraga, *Harley et al. 27623, 27626* (K, U), *Prance et al. 11364, 11384* (NY, U). ESPÍRITO SANTO: Piuma, Lake Piabanha, *Vital 2846* (SP, U). MARANHÃO: Mun. de Codó, *Vital 88420* (SP, U). MATO GROSSO: Mun. Aripuana, *Lisboa et al. 602* (MG, U); Rio Aripuana, Humboldt Center, *Prance et al. 18341* (NY, U). PARÁ: Serra do Cachimbo, *Reese 16243* (NY); Rio Cururu, *Sioli 40* (GRO). RONDÔNIA: road Pimenta Buena-Roulim de Moura, Jaboti, *Lisboa et al. 2951* (MG, U). RORAIMA: Boca da Mata, 216 km N of Boa Vista, *Buck et al. 1960* (NY, U). SÃO PAULO: Nova Independencia, near Andradino, *Vital 2085, 2086* (NICH, SP, U); Rancharia, *Vital 2109* (NICH, SP, U).

BOLIVIA. BENI: near Guayaramerín, *Reese 13084* (NY, U).

Acrolejeunea torulosa is easily distinguished from its allies by its lobule with 5–8 teeth and by its very small caducous leaves with subequal lobe and lobule and a long subapical rhizoid. Gradstein (1975) recorded a few collections from coastal Brazil (*Vital 2109, 2846*) with less strongly modified caducous leaves, resembling those found in *A. emergens*. *Acrolejeunea torulosa* is the most common species of *Acrolejeunea* in the neotropics. In Amazonia the species has been found growing intermingled with *A. emergens*. The more flattened appearance of *A. emergens* in these mixed collections serves to distinguish the two species almost by the naked eye.

Acrolejeunea torulosa may be confused with pale-colored phases of *Frullanoides corticalis*. For differences see under the latter.

FIG. 34. Distribution of *Acrolejeunea heterophylla* (stars) and *A. torulosa* (dots).

Excluded Species

(see Gradstein, 1975: 125–131)

Ptychocoleus reflexus Winkler, Rev. Bryol. Lichénol. **35:** 329. 1968. Type. San Salvador, *Winkler B/6/d8* (hb. Winkler, n.v.) = ?

The type material has not been made available. Judging from the original description this species does not belong to *Acrolejeunea.*

Ptychocoleus subfalcatus Herzog *in* Standley, Field Mus. Nat. Hist. Bot. **10:** 61. 1931, nom. nud. = ?

The material could not be located.

13. Frullanoides Raddi, Critt. Bras. 13. 1822; Ptychocoleus Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 404. 1877. Lectotype (Trevisan, 1877). *Frullanoides densifolia* Raddi. Genus named for its *Frullania*-like appearance.

Brachiolejeunea subgen. *Plicolejeunea* Schuster, Beih. Nova Hedwigia 9: 104. 1963; *Trocholejeunea* subgen. *Plicolejeunea* (Schuster) Schuster, J. Hattori Bot. Lab. **72:** 200. 1992. Type. *Brachiolejeunea bahamensis* Evans (= *Frullanoides bahamensis* (Evans) van Slageren).

Plants 1.5–12 cm long × 1–3 mm wide, green to black when alive, usually darkish brown to black in the dried condition, creeping or ascending, rarely pendent. *Branching Frullania- or Lejeunea*-type, irregular or forked due to paired, floriferous innovations; microphyllous branches lacking. *Stems* with a hyalodermis, epidermal cells larger (at least dorsally) and much thinner-walled than the medullary cells, dorsal epidermal cells as large as or larger than the ventral epidermal cells, cells walls with brownish pigmentation especially in the medulla; ventral merophyte 4–10(–14) cell rows wide. *Leaves* convoluted when dry, apex rounded to acute-apiculate, margins entire or toothed (*Frullanoides laciniatiflora*); leaf cells elongate, walls often with darkish pigmentation, trigones cordate, small to medium-sized, intermediate thickenings usually scarce, oil bodies homogeneous, *Massula*-type, ocelli lacking. *Lobules* 1/3–2/3× lobe length, never reduced, inflated along the keel, flattened towards the free margin, with (3–)5–9(–11) teeth; hyaline papilla positioned on the inner side of the lobule below the proximal base of the first tooth. *Underleaves 3–6*× stem width, margins entire, bases auriculate or rounded, insertion line arched or almost straight; underleaf base at the rhizoid disc bistratose, with 4–8 superior central cells. *Androecia* on elongated shoots, bracts resembling leaves but smaller, lobules more strongly inflated, epistatic or hypostatic (*F. corticalis*), underleaves present throughout; antheridia 1–2 per bract. *Gynoecia* on main stems or on branches, always with two pycnolejeuneoid subfloral innovations, bracts in one series, larger than leaves, with rounded to apiculate apex and entire or toothed margins, the keel usually with a conspicuous wing (inserted partially on the associated innovation), lobules 1/3–3/4× lobe length, bracteoles undivided or short bifid, entire or toothed. *Perianths* with 5–11 smooth, rounded keels. *Sporophyte:* seta articulate; elaters 30–68 per capsule (van Slageren, 1985); otherwise as in the tribe. *Vegetative reproduction* not observed. *Terpenoids:* pinguisanines.

Distribution. *Frullanoides* Raddi is the largest genus of Ptychanthoideae in tropical America. All seven species recognized in the genus (van Slageren, 1985) occur in tropical America; one of them, *F. tristis*, extends into the palaeotropics. This treatment follows the revision by van Slageren. The species of *Frullanoides* are drought tolerant and grow on bark, rock or soil, from sea level to the forest line, in dry or moist woodlands, scrubby vegetations, savannas, plantations, and along road sides. When growing in virgin rain forest, the species are usually restricted to the crowns of the trees.

Frullanoides is a well-defined genus, with relationships to *Acrolejeunea* and to the Asiatic genus *Trocholejeunea*. The presence of large quantities of pinguisanine-type sesquiterpenes is a characteristic chemical feature of the species of these genera (Gradstein et al., 1988). The species of *Frullanoides* can be readily distinguished from *Acrolejeunea* by their somewhat blackish pigmentation, auriculate underleaves (except *F. corticalis* and *F. bahamensis*), distinctly swollen male bracts with (1–)2 antheridia and the presence of innovations. Moreover, the flagelliform branches producing caducous leaves, characteristic of neotropical *Acrolejeunea*, are never found in *Frullanoides*.

The genus *Trocholejeunea* is considerably different from *Frullanoides* based on characters of both gametophyte and sporophyte: the lack of blackish secondary pigmentation, the unique, *Frullania*-type innovation, the scarcely swollen male bracts as in *Acrolejeunea*, and the seta which is not articulate and is made up of more than 20 cell rows (as in *Bryopteris* and *Marchesinia*). The occurrence of a fossil species of *Trocholejeunea* in Eocenic amber of Europe (*Trocholejeunea contorta* (Göppert & Berendt) Grolle & Gradst.) shows that *Trocholejeunea* is one of the oldest extant genera of Lejeuneaceae.

Frullanoides resembles *Mastigolejeunea* in habit. For differences see under the latter.

Key to the Species of *Frullanoides*

1. Leaf margins toothed near apex; high Andes of Peru. . . . . 4. *F. laciniatiflora.*
1. Leaf margins entire.
2. Leaf apex acute-apiculate to (narrowly) rounded; underleaves distinctly auriculate (auricles 0.1–0.3 long, appressed to the stem), insertion line deeply arched, margins recurved; Central and South America, montane. . . . . 3. *F. densifolia.*
2. Leaf apex broadly rounded (occasionally apiculate in *F. tristis*); underleaves not or slightly auriculate (auricles less than 0.1 mm long), insertion line straight or curved, margins plane.
3. Plants (1–)1.5–3 mm wide; underleaves slightly auriculate; lobule with 3–11 teeth; submontane-montane.
    4. Lobule with 9–11 small teeth consisting of only one cell; Mexico, Honduras, Costa Rica. . . . . 6. *F. mexicana.*
    4. Lobule with 3–9 teeth consisting of 1–4 cells.
        5. Lobule with 3–4(–5) teeth, each tooth 1(2) cells long, positioned on a triangular segment of the waving free margin; dioicous, antheridia two per bract. . . . . 5. *F. liebmanniana.*
        5. Lobule with (4–)6–9 teeth, each tooth 2–3 cells long, free margin not waving; paroicous; antheridium one per bract. . . . . . 7. *F. tristis.*
3. Plants 1-1.5 mm wide; underleaves not auriculate; lobule with (3–)4–6 teeth; coastal areas up to 600 m.
    6. Lobule teeth 1–2 cells long, the first tooth situated in the sinus, at the junction with the ventral leaf

margin (tooth often incurved and inconspicuous!); usually dioicous; male bracts hypostatic; widespread. . . . . 2. *F. corticalis*.
6. Lobule teeth 3 cells long, the first tooth not situated in the sinus; monoicous; male bracts epistatic; Florida, Bahamas, Cuba. . . . . . . 1. *F. bahamensis*.

1. **Frullanoides bahamensis** (Evans) van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 81. 1985; *Brachiolejeunea bahamensis* Evans, Bull. Torrey Bot. Club **35:** 383. 1908; *Trocholejeunea bahamensis* (Evans) Schuster, J. Hattori Bot. Lab. **72:** 201. 1992. Type. Bahama Archipelago. Crooked I.: Coppice, *Brace 4816* (holotype, YU).

Brachiolejeunea longispica Stephani, Spec. Hep. **5:** 125. 1912. Type. Cuba. *Wright 1086* (holotype, G).

Autoicous (rarely paroicous). *Plants* up to 1,5 cm long × 1–1.6 mm wide, olive green to black when alive, becoming dark brown to black in the dried condition. *Branching Lejeunea-type, occasionally Frullania*-type. *Stems* 0.1–0.15 mm in diam., in cross section composed of 11–15 epidermal cells surrounding 17–26 smaller, thicker-walled medullary cells, dorsal epidermal cells about as large as the ventral epidermal cells or larger; ventral merophyte four cell rows wide. *Leaves* imbricate, dorsal lobe ovate-oblong, 0.5-0.8 × 0.4–0.55 mm, apex rounded, ± plane, dorsal margin straight at base, ventral margin plane or curved upwards, when spread out forming an angle of 150–170° with the keel; median cells 28–36 × 18–28 μm, base cells larger, margin cells subquadrate, 11–22 μm high; oil bodies homogeneous, small, ellipsoid to fusiform, 2 × 3–6(–8) μm, 15–30 per cell. *Lobules* ovate, averaging 0.3 × 0.25 mm, 2/5–1/2× lobe length, apex oblique, keel slightly curved, free margin plane, gradually curved to the apex, with 5–6 teeth, separated from each other by (1–)3–4 margin cells, the teeth 2–3 cells long, erect with the upper cell inflexed. *Underleaves* imbricate, suborbicular, 0.3–0.4 mm, ca. 3× stem width, apex rounded, plane, margins plane, bases rounded, auricles ± lacking, insertion line almost straight. *Androecia on long Lejeunea*-type branches, bracts in 4–12 series, below the gynoecium in 1–5 series only, epistatic, antheridia 1–2 per bract. *Gynoecial* bracts bifid to 1/4–1/2, keel usually winged, lobes obovate-oblong, 0.8–1 mm long, slightly concave, apex narrowly rounded, lobules ± narrow rectangular, 1/2–3/4× lobe length, apex acute; bracteoles erect, spathulate, 0.6–0.7 mm long, apex rounded, plane or slightly recurved, margins plane. *Perianths* exserted to 1/4, occasionally stalked, (ob)ovoid-cylindrical, 0.8–1.1 mm long, with 9–10 keels extending over the upper 1/2–3/4, beak 5–7 cells long. *Spores* ca. 60 μm long; elaters 30 per capsule, 260–360 × 18 μm, with a single brown, ca. 4 m wide spiral.

Illustration. Schuster, Hep. Anth. N. America IV: Figs. 652, 653. 1980 (as *Brachiolejeunea bahamensis*); van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pls. XIV, XV. 1985.

Distribution. Southern Florida, Cuba, Bahamas, Puerto Rico (Mona I.), from sea level up to 350 m. *Frullanoides bahamensis* grows on bark and on rock in mesic, rather open woodlands and swamps. The species is apparently tolerant of salt spray.

Selected specimens examined. UNITED STATES. FLORIDA. DADE: Madeira Bay, *Small 7557* (FH, NY, YU). **MONROE:** Big Pine Key, *Schuster 51748* (G), *42083* (S).

BAHAMA ARCHIPELAGO. ABACO: Old Kerr's Point, *Brace 2027* (YU). **CROOKED ISLAND:** *Britton 3191* (U, YU). **PROVIDENCE:** Fox Hill, *Britton & Millspaugh 2090* (YU); Grantstown, *Britton 562* (YU).

CUBA. MATANZAS: Playa, *Britton & Wilson 81* (YU). **ORIENTE:** Holguin, *Pócs 9040/B, 9041/B* (HAC, U); Sierra Maestra, *Pócs 9056 p.p.* (HAC, U). **PINAR DEL RÍO:** Carabelita, *Schubert M32* (JE).

PUERTO RICO. Mona Island, *Britton et al. 1798* (YU).

2. **Frullanoides corticalis** (Lehmann & Lindenberg) van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 84. 1985; *Jungermannia corticalis* Lehmann & Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **4:** 50. 1832; *Phragmicoma corticalis* (Lehmann & Lindenberg) Lehmann & Lindenberg, Syn. Hep. 297. 1845; *Ptychocoleus corticalis* (Lehmann & Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 405. 1877; *Lejeunea corticalis* (Lehmann & Lindenberg) Stephani, Hedwigia **28:** 167. 1889; *Marchesinia corticalis* (Lehmann & Lindenberg) Kuntze, Revis. Gen. Pl. 2: 836. 1891; *Brachiolejeunea corticalis* (Lehmann & Lindenberg) Schiffner, Hedwigia **33:** 180. 1894; *Trocholejeunea corticalis* (Lehmann & Lindenberg) Schuster, J. Hattori Bot. Lab. **72:** 201. 1992. Type. Ja-

maica. *Lehmann s.n.* (holotype, S; isotypes, G, W).

Frullania leprieurii Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **14:** 333. 1840; *Phragmicoma leprieurii* (Nees & Montagne) Montagne, Syll. Gen. Spec. Crypt. 86. 1856. Type. French Guiana. Near Cayenne, *Leprieur 273, 277* (syntypes, PC).

Lejeunea linguaefolia Taylor, London J. Bot. **5:** 390. 1846; *Acrolejeunea linguaefolia* (Taylor) Bonner, Index Hep. **2:** 19. 1962. Type. Virgin Is. St. Thomas: *Richard s.n.* (isotypes, BM, G, MANCH, PC, S, W).

Brachiolejeunea surinamensis Stephani. Spec. Hep. **5:** 124. 1912. Type. French Guiana. *Leprieur 115* (holotype, G).

Dioicous (rarely autoicous). *Plants* up to 2,5 cm long × 1,2–1.7 mm wide, brown green to black when alive, becoming dark brown to black in the dried condition. *Branching Lejeunea-type, occasionally Frullania*-type. *Stems* 0.15–0.2 mm in diam., in cross section composed of 11–14 epidermal cells surrounding 17–40 smaller, thicker-walled medullary cells, dorsal epidermal cells slightly larger than the ventral epidermal cells; ventral merophyte four cell rows wide. *Leaves* imbricate, dorsal lobe ovate to ovate-oblong, 0.6–0.9 x 0.5–0.6 mm, apex rounded, plane or recurved, dorsal margin straight to cordate at base, ventral margin plane, when spread out forming an angle of 150–170° with the keel; median cells 30–40 × 18–30 μm, base cells larger, margin cells subquadrate, 14–20 μm high; oil bodies not observed. *Lobules narrowly ovate, averaging 0.4* × 0.25 mm, 2/5–1/2x lobe length, apex oblique, keel slightly curved, free margin plane, straight except at the base, with 3–6 teeth, separated from each other by 2–4 margin cells (except the second and third tooth which are 3–8 cells apart), the teeth 1–3 cells long, inflexed, the first tooth rather inconspicuous, located in the sinus at the extreme end of the lobule; hyaline papilla near the base of the 2nd tooth. *Underleaves imbricate, suborbicular to broadly ovate, 0.35–0.45* × 0.4–0.55 mm, ca. 3–4x stem width, apex rounded to truncate, plane, margins plane, bases rounded, auricles lacking, insertion line arched or almost straight. *Androecia on long or short branches, bracts in 4–15(–22) series, hypostatic except in the basal and apical series, antheridia two per bract. Gynoecial* bracts bifid to 1/4–1/2, keel winged, lobes obovate-oblong, 0.9–1.2 mm long, concave or squarrose, apex narrowly rounded, lobules narrow rectangular, 1/2–3/4x lobe length, apex acute or rounded; bracteoles erect, gibbous, rectangular, 0.7–1 mm long, apex rounded to truncate-emarginate, slightly recurved, margins plane. *Perianths exserted to 1/5–1/3, occasionally stalked, ovoid-cylindrical, 0.7–1.3 mm long, with 5–8(–10) keels restricted to the upper half of the perianth, beak 4–7 cells long. Spores* 50–60 μm long; elaters 30 per capsule, 290–400 × 15 μm, with a single brown, ca. 4 μm wide spiral.

Illustration. Schuster, Hep. Anth. N. America IV: Fig. 651. 1980 (as *Brachiolejeunea corticalis*); van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pls. XVII, XVIII. 1985.

Distribution (Fig. 36). West Indies and coastal regions of Central and South America, ranging from sea level up to about 600 m on Cuba. *Frullanoides corticalis* is a drought-tolerant species which grows on bark or rock in coastal areas: in mesic to xeric woodlands, in swamps and mangroves, in plantations, and on isolated trees in towns and villages. The species may locally be very common and may form extensive black mats on bark of trees along the beach. Like *F. bahamensis*, the species is tolerant of salt spray. Although *F. corticalis* has similar habitat preferences as *F. bahamensis*, the two species apparently do not grow mixed when occurring in the same general area (Schuster, 1980).

Selected specimens examined. MEXICO. VERACRUZ : Hac. Mirador, *Liebmann s.n.* (S, W).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley 54496* (JE).

BELIZE. *Spellman & Stoddart B127b, B128b, B129b* (HAC, U).

NICARAGUA. CHONTALES: La Gateada near Highway 7, *Stevens & Krukoff 2862d* (MO, U). Puerto Cabezas, *Seymour s.n.* (MO, U).

COSTA RICA. Golfo Dulce, *Taylor 39-754* (herb. Fulford).

PANAMA. PANAMÁ: Lake Gatún, *Howe s.n.* (NY, YU).

UNITED STATES. FLORIDA. DADE: Brogdon Hammock, *Small & Mosier 6230* (NY, US). **LEE:** Fort Myers, *Standley 12995a* (US).

BAHAMA ARCHIPELAGO. CAT ISLAND: *Britton & Millspaugh 5899* (YU). **GREATBAHAMA:** Golden Grove, *Britton & Millspaugh* (YU).

CUBA. HABANA: I. de Pines, Siguanea, *Britton et al. 15389, 15428* (YU). **LAS VILLAS:** Santa Clara, *León & Loustalot 9574* (HAC, U). **ORIENTE:** Baracoa, *Reyes 699, 719, 732* (HAC, U), *Lippold 10106, 10114, 10118* (JE), *Underwood & Earle 313* (YU); Sierra Maestra, Gran Piedra, *Reyes 733* (HAC, U).

JAMAICA. Mansfield, near Bath, *Evans 337* (B, BM, US, YU); Portland, *Orcutt 4549* (hb. Fulford); Castleton Botanic Garden, *van der Porten 286, 287* (WTU).

HAITI. Tortue Island, *Leonard 11613, 12542* (JE, NY).

DOMINICAN REPUBLIC. *Eggers s.n.* (BM).

PUERTO RICO. Vieques Island, *Schäfer 2989b* (YU).

VIRGIN ISLANDS. ST. THOMAS. Type of *Lejeunea linguaefolia* Tayl.

WINDWARD ISLANDS. GUADELOUPE. Without loc., *Marie s.n.* (BM). **ST. LUCIA.** Road Castries-Morne Fortuné, *Evans 84b* (YU).

LEEWARD ISLANDS. CURAÇAO. Christoffelberg, *Suringar s.n.* (L), *Florschütz 3456a* (U), *van Slageren & Stoffers 8129, 8133a, 8151b, 8401* (U).

COLOMBIA. **Chocó:** Mun. Nuqui, *Gradstein 9022, 9023* (COL, U). **Nariño:** Mun. Mosquera, Parque Nacional Sanguianga, *Linares 27, 33, 40, 57* (COL). I. de Providencia, *Ramirez 014* (COL, U).

TRINIDAD. North Post Road, *Britton et al. 788* (US, YU); Manzanilla, *Britton 2203* (US); Biscayne Bay, Monos I., *Britton et al. 1734* (NY).

GUYANA. Near Berbice, *Aiken s.n.* (BM, BP, U).

SURINAME. Paramaribo, Palmgarden, *Kegel s.n.* (U, W), *Gradstein 4605, 4611, 4616* (U).

FRENCH GUIANA. Cayenne, Jardin Botanique, *Cremers 3811* (CAY, U), *Gradstein 5753, 5772, 6272* (U), *Bekker 2054* (U); Place des Palmistes, *Aptroot 15077* (U); Matabon, Reservoir Hill, *Broadway 790* (NY, US).

BRAZIL. **MinasGerais:** Sierra d'Estrella, *Beyrich 21 (BM, G, S, W)*. **Rio de Janeiro:** *Ule 94* (BM, G).

Pale phases of *Frullanoides corticalis*, without blackish pigmentation, bear close resemblance to *Acrolejeunea* spp. They differ from *Acrolejeunea*, when sterile, by the presence of a small tooth at the extreme end of the free margin of the lobule, where it meets with the ventral margin of the leaf. Sometimes this tooth is incurved and inconspicuous, however. The lack of the tiny, upright flagelliform shoots, characteristic for the neotropical species of *Acrolejeunea*, is another character to distinguish sterile plants of *F. corticalis* from *Acrolejeunea*.

3. Frullanoides densifolia Raddi, Critt. Bras.: 14. 1822; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 90. 1985.

Key to the Subspecies of *Frullanoides densifolia*

1\. Lobule with 6–10 teeth, each tooth (1)2–3 cells long; dioicous; male bracts modified, smaller than leaves and with reduced lobule teeth, diandrous; mainland South America and Central America..
. . . . 3a. *F. densifolia* subsp. *densifolia*.

1\. Lobule with 5–6 teeth, each tooth 3–4 cells long; paroicous; male bracts unmodified, resembling leaves, monandrous; Galapagos Islands.
. . . . 3b. *F. densifolia* subsp. *grandidentata*.

3a. Frullanoides densifolia Raddi subspecies **densifolia**; *Ptychocoleus densifolius* (Raddi) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 405. 1877; *Brachiolejeunea densifolia* (Raddi) Evans, Bull. Torrey Bot. Club **35:** 158. 1908; *Trocholejeunea densifolia* (Raddi) Schuster, J. Hattori Bot. Lab. **72:** 201. 1992. Type. Brazil. Rio de Janeiro: Mt. Corcovado, *Raddi s.n.* (holotype, PI; isotypes, BM, FH-TAYL, PC, NY). Fig. 35.

Jungermannia bicolor Nees *in* Martius, Fl. Bras. **1 (1):** 349. 1833; *Lejeunea bicolor* (Nees) Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **5:** 59. 1836; *Phragmicoma bicolor* (Nees) Nees, Syn. Hep. 294. 1845; *Brachiolejeunea bicolor* (Nees) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893. Type. Brazil. Minas Geraes, *Martius s.n.* (isotypes, FH, M, S, W).

Phragmicoma rupestris Gottsche, Ann. Sci. Nat., Bot. (sér. 5) **1:** 146. 1864; *Brachiolejeunea rupestris* (Gottsche) Stephani, Spec. Hep. **5:** 122. 1912. Type. Colombia. Padua, *Lindig 224* (B, G).

Lejeunea succisa Stephani, Hedwigia **28:** 168. 1889; *Brachiolejeunea succisa* (Stephani) Stephani, Hedwigia **34:** 65. 1895. Type. Ecuador. Ex hb. *Renauld* (holotype, G).

Brachiolejeunea canaliculata Stephani, Spec. Hep. **5:** 117. 1912. Type. Mexico. *Unknown collector* (holotype, G).

Marchesinia coniloba Stephani, Spec. Hep. **5:** 147. 1912. Type. Costa Rica. Cartago, *Werckle s.n.* (holotype, G).

Mastigolejeunea decurrens Stephani, Biblioth. Bot. **87:** 249. 1916. Syntypes. Bolivia. *Herzog 3695, 3697, 4089, 4094* (G).

Ptychanthus boliviensis Stephani, Biblioth. Bot. **87**: 249. 1916. Type. Bolivia. Río Tocorani, *Herzog 4113* (holotype, G).

Ptychocoleus boliviensis Stephani, Biblioth. Bot. **87:** 250. 1916, nom. nud. Material. Bolivia. Florida de San Mateo, *Herzog 3639* (B, G, L, M, MANCH, S, W).

Dicranolejeunea boliviensis Stephani, Biblioth. Bot. **87:** 253. 1916. Type. Bolivia. Cochabamba: Incacorral, *Herzog 4971* (holotype, G; isotype, L).

Dicranolejeunea nudiflora Stephani, Biblioth. Bot. **87:** 254. 1916. Type. Bolivia. Corani valley, *Herzog 4753* (holotype, G; isotype, L).

Brachiolejeunea appendiculistipa Stephani, Spec. Hep. **6:** 381. 1923. Type. Bolivia. *Herzog 3365* (holotype, G).

Brachiolejeunea columbica Stephani, Spec. Hep. **6:** 382. 1923. Type. Ex hb. Cardot (holotype, G).

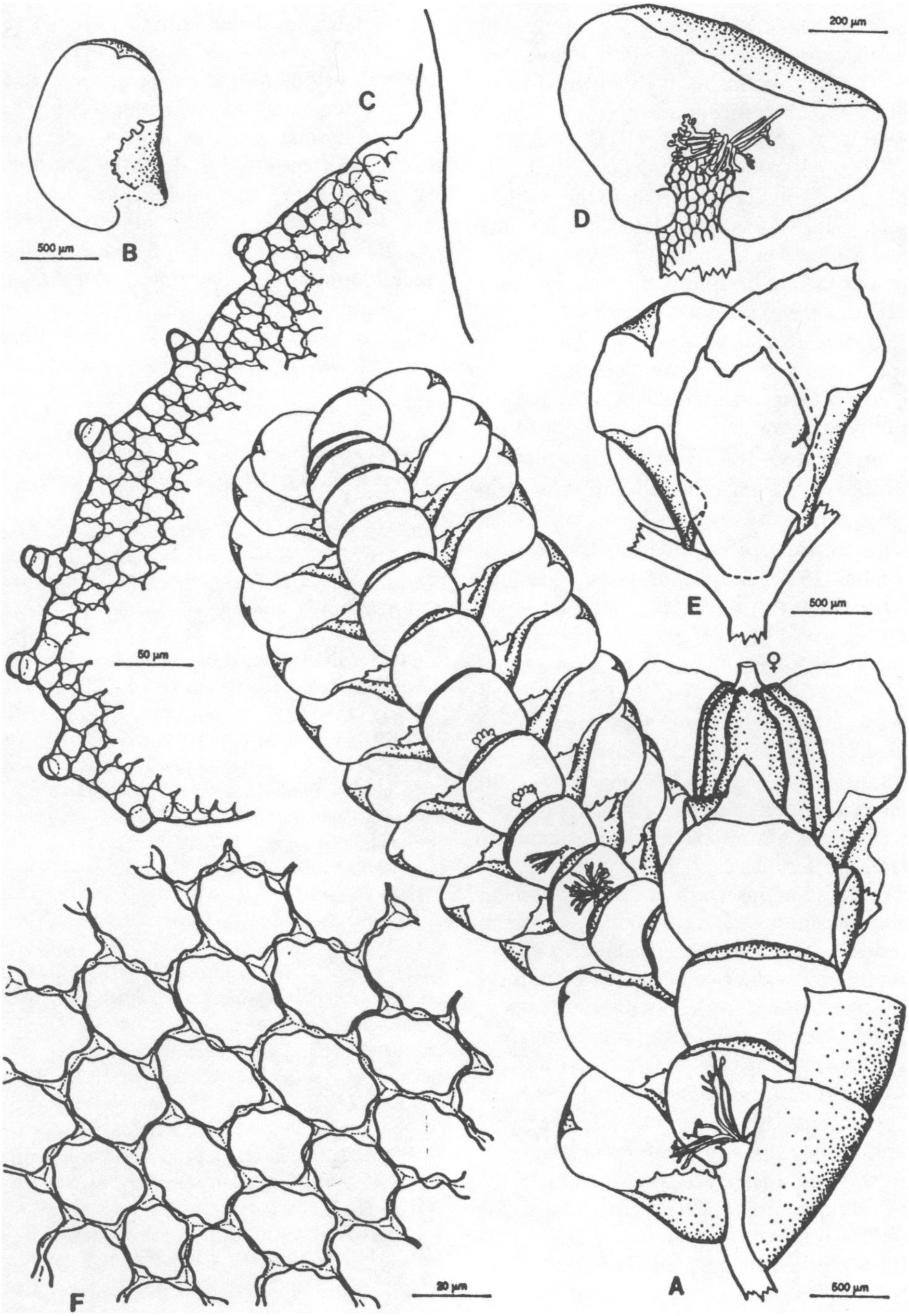

FIG. 35. ***Frullanoides densifolia*****. A.** Habit, with gynoecium; note that right-hand innovation is omitted. **B.** Leaf. **C.** Lobule free margin. **D.** Underleaf. **E.** Gynoecial bracts and bracteole; wing of bracts not shown. **F.** Leaf cells. A from Peru, *Hegewald 7323*. B–E from Costa Rica, *Griffin & Eakin 222*.

Dioicous. *Plants* 3–12 cm long × 2–3 mm wide, green to black when alive, becoming dark brown to black in the dried condition. *Branching Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.15–0.3 mm in diam., in cross section composed of 20–35 epidermal cells surrounding ca. 50–100 smaller medullary cells, dorsal epidermal cells distinctly larger than the ventral epidermal cells, dorsal and lateral epidermis rather thinwalled, ventral epidermis and medulla strongly thickwalled; ventral merophyte 8–10 (–14) cell rows wide. *Leaves* imbricate, dorsal lobe ovate-falcate, 1–1.8 × 0.8–1.4 mm, apex acute-apiculate or narrowly rounded, usually recurved, dorsal margin auriculate at base, ventral margin curved upwards, when spread out forming an angle of 160–180° with the keel; median cells 25–40 x 18–32 µm, base cells larger, margin cells subquadrate, 14–22 µm high; oil bodies homogeneous, small, ellipsoid to fusiform, ca. 2 x 3–6 µm, 15–25 per cell. *Lobules* ovate-triangular, 0.5–0.8 x 0.3–0,7 mm, 2/5–1/2x lobe length, apex oblique, keel almost straight, free margin plane, with 6–10 teeth, the teeth 1–3 cells long, longest and more widely spatiated towards the apex of the lobule, erect with the upper cell(s) inflexed. *Underleaves* imbricate, broadly ovate-subquadrate, 0.5–1.1 × 0.8–1.3 mm, 4–5x stem width, apex rounded to truncate, recurved, margins recurved or almost plane, bases distinctly auriculate, the auricles ca. 0.1–0.3 mm long, appressed to the stem, insertion line deeply arched. *Androecia* on short or long branches, bracts in 3–20 series, lobule swollen, epistatic, with reduced teeth; antheridia two per bract. *Gynoecial* bracts bifid to 1/2 or more, keel with a large wing, lobes ovate-obovate, ca. 2 mm long, squarrose, apex acute-apiculate or narrowly rounded, lobules narrow rectangular, 1/3–1/2x lobe length, apex acute; bracteoles erect, rectangular, 1–1.4 mm long, apex truncate-emarginate to short bifid, plane or slightly recurved, margins plane. *Perianths* immersed, occasionally exserted to 1/4, obovoid-cylindrical, 1.2–1.7 mm long, 10–keeled over much of its length, beak 8–10 cells long. *Spores* ca. 45–55 µm long; elaters 68 per capsule, 435–550 × 18 µm, with a single brown, ca. 4 µm wide spiral.

Chemistry: the sesquiterpenes bicyclogermacrene, ß-caryophyllene and various pinguisanines, and the free flavonol aglycone kaempferol-3-methylether are the main secondary metabolites detected in this species (Kruijt et al., 1986; Asakawa & Inoue, 1987).

Distribution. Mexico, Costa Rica, Panama, Andes (Venezuela to Argentina), SE Brazil; a common montane species, occurring at altitudes of 500–3500 m in the Andes and Central America, in SE Brazil approaching sea level. *Frullanoides densifolia* grows in rather open, exposed habitats on bark, rock or soil in natural and degraded submontane and montane forests, scrubby vegetations, meadows, along roads and in rather dry cerrado vegetation of southeast Brazil. In dense forests the species is restricted to canopy branches.

Selected specimens examined. MEXICO. VERACRUZ: Fortin de las Flores, *Düll 2/102* (DUIS, JE, U).

COSTA RICA. CARTAGO: Tapanti Forest Reserve, *Griffin & Eakin 244* (B, FLAS, HAC, U). PUNTARENAS: San Vito, *Sipman 11941* (U). SAN JOSÉ: Santa Maria de Dota, *Standley & Valerio 43158* (JE, S, US).

PANAMA. CHIRIQUÍ: Volcán, *Salazar 5279* (PMA, U).

COLOMBIA. ANTIOQUIA: Montanita à San Pedro, *Onraedt 83A10317* (U); Llanos de Quivá, *Onraedt 83A10196* (U). BOYACÁ: road Chiquinqui-Paun, *vanderHammen et al. 2474* (COL, U). CASANARE: Sácama, *Aguirre & Gradstein 2952* (COL, U). CUNDINAMARCA: Tequendama, *Lindig s.n.* (S); Choacha, *Lindig s.n.* (BM); Pacho, *Lindig 198* (G); Laguna de Pedro-Palo, *Bischler 2216* (COL, PC, U); páramo de Sumapaz, *Aguirre 2317* (COL, U). HUILA: La Plata, Merenberg, *Aguirre & Gradstein 6363, Bryoph. Neotrop. Exsicc. (ed. Gradstein) 139* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL). MAGDALENA: Sierra Nevada de Santa Marta, *Winkler C166, C183, C186, C313* (ULM). RISARALDA: Santa Rosa de Cabal, *van Reenen et al. 1559* (COL, U). SANTANDER: near Charta, *Killip & Smith 19337* (JE, NY); Charalá, Virolin, *Castro et al. 194* (COL, U). TOLIMA: Santa Isabel, *Aguirre & Gradstein 1669* (COL, U).

VENEZUELA. LARA: Parque Nacional Yacambú, *Griffin & Lopez 363* (FLAS, U). MÉRIDA: Mucuy, *Onraedt 78V5599* (JE, U). TACHIRA: páramo de Tamá, *Griffin et al. 772, 874, 949* (FLAS, U); near Delicias, *Steyermark & Liesner 118352* (MO, U).

ECUADOR. CARCHI: road Tulcan-Maldonado, *Gradstein et al. 6829* (U). CHIMBORAZO: *Spruce L117* (MANCH). PICHINCHA: Quito, *Jameson s.n.* (MANCH, NY); páramo Guamani, *Gradstein & Frahm 6923* (U). Cuenca, *Harling 2200a, 2205, 2206* (JE, S).

PERU. AMAZONAS: Bongará, Pomacochas, *Hegewald 7058, 7073, 7077, 7102* (U); Leimebamba, *Frahm et al. 1148* (B, BA, BM, COL, F, FLAS, G, H, MEXU, NY, S, SP, TNS, U, USJ). CAJAMARCA: Cerro Huayllaconga, *Hege-*

wald 6556 (U). **CUZCO:** San Miquel, *Foote 8* (YU); Paucartambo, *Jay 104* (NY, YU), *Inoue 33986* (TNS, U); Macchu Picchu, *Hegewald 5578* (U). **HUANUCOT:** Churubamba, *Mexia 8246a* (NY). **SAN MARTIN:** Mt. Lamas, *Spruce L174* (MANCH); above Rioja, *Frahm et al. 1312* (B, G, U).

BRAZIL. BAHIA: Lugar, Tapero Garazinho, *Sehnem 5700* (U). **ESPÍRITO SANTO:** Morro do Cruzeiro, *Schäfer-Verwimp 10219* (hb. Schäfer-Verwimp). **MINAS GERAIS:** Serra de Caldas, *Mosén s.n.* (G, S, US), *Lindberg 31, 33* (S). **RIO DE JANEIRO:** *Glaziou 5620* (NY), *Schiffner 595* (S, W); Sierra Itatiaia, *Dusén 54* (NY). **PARANA:** *Dusén 12077* (S, W). **RIO GRANDE DO SUL:** Sarandi, *Vital 5712, 5715* (SP, U). **SANTA CATARINA:** Campos Novos, *Reitz & Klein 16367* (US). **SÃO PAULO:** Apiahy, *Souza 1410* (G), *Puiggari 883, 884* (G); Campos de Jordão, *Vital 9593* (JE, SP, U); São Bernardo, *Schiffner 16* (S, W); Itapetininga, *Schiffner 265* (S, W); Itapecirica, *Schiffner 1337, 1475, 1522, 2069* (S, W).

BOLIVIA. BENI: Ballívian, Serranía del Pilón Lagas, *Gradstein several colls.* (LPB, U). **COCHABAMBA:** Corani, *Herzog 3375* (B, L, MANCH, S, W); Tablas, *Herzog s.n.* (S); Incacorral, *Gradstein & Lewis 7550, Bryoph. Neotrop. Exsicc. 238* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL); Chaparé, *Hermann 24677* (G, NY). **LA PAZ:** Unduavi, *Pearce s.n.* (BM, G, NY, U); Comarapa, *Herzog s.n.* (B, JE, NY, S); Lagunillas, *Brooke 6163B* (BM); Paucartambo, *Jay 20* (NY, U, YU). **SANTA CRUZ:** Florida, Río Colorado y Río Elvira, *Lewis 85-1526* (LPB, U).

ARGENTINA. SALTA: Río Serro near San Andrès, Oran, *Lorentz s.n.* (B, BM, G, S, U). **TUCUMÁN:** Horco Molle, above city of Tucumân, *Steere 60-3* (NY).

Frullanoides densifolia subsp. *densifolia* varies considerably in size and plants from high altitudes tend to be more robust. Small plants from low altitudes often have a narrowly rounded leaf apex and rather small underleaf auricles and may therefore be confused with *F. liebmanniana*. The latter may be recognized, however, by the fewer lobule teeth and the thin-walled ventral epidermal cells.

3b. **Frullanoides densifolia** subspecies **grandidentata** (Clark) van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 95. 1985; *Brachiolejeunea grandidentata* Clark, Proc. California Acad. Sci. **27:** 595. 1953. Type. Ecuador. Galapagos Islands: Isabela, Villamíl, *Howell 211a* (holotype, CAS; isotype, WTU).

Paroicous. *Plants* rather long and slender, ca. 4–5 cm long, green to black when alive, becoming dark brown to black in the dried condition. *Branching Frullania*-type, *Lejeunea*-type branches not observed. *Stems* averaging 0.2 mm in diam., in cross section composed of 18–25 epidermal cells surrounding ca. 45–70 smaller medullary cells; ventral merophyte 8 cell rows wide. *Leaves* loosely imbricate, dorsal lobe ovate, 1–1.2 x 0.6–0.8 mm, apex apiculate, recurved. *Lobules ovate-triangular*, 0.4–0.5 x 0.3–0.4 mm, with 5–6 teeth, the teeth (2–)3–4 cells long, erect with the upper cell(s) inflexed. *Underleaves* contiguous to subimbricate, suborbicular, averaging 0.7–0.8 mm wide, with rather small auricles and deeply arched insertion line. *Androecia* located a few leaf cycles below the gynoecium, bracts in 3–6 series, similar to leaves, lobule tooth not reduced, antheridia one per bract. *Gynoecia* as in *F. densifolia* spp. *densifolia*. *Sporophyte* not observed.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pl. XXI. 1985.

Distribution. Endemic to the Galapagos Islands, where it grows pendent from bark in humid, evergreen woodland and pampa in rather open situations, at 450–750 m.

Specimens examined. ECUADOR. GALÁPAGOS ISLANDS: Isabela, Cerro Azul, *Gradstein & Sipman H454* (U); San Cristobal, El Junco, *Gradstein & Lanier H254* (U); Santa Cruz, Mt. Crocker, *Gradstein & Weber H11* (BM, COLO, FLAS, U), Cerro Maternidad, *vanderWerff 1777* (U), Media Luna, *Gradstein & Weber H105* (U); Pinzón, *Gradstein & Sipman H485* (U), *VanderWerff 2363* (U).

Frullanoides densifolia subsp. *grandidentata* is a slender plant with rather distant leaves and underleaves, probably due to pendent growth. The male bracts, situated directly below the gynoecium, are easily overlooked as they resemble vegetative leaves except for the presence of an antheridium in the lobule.

4. **Frullanoides laciniatiflora** (Loitlesberger) van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 100. 1985; *Lejeunea laciniatiflora* Loitlesberger *in* Szyszylowicz, Diss. Cl. Math. Phys. Acad. Litt. Cracow **29:** 233. 1894; *Brachiolejeunea laciniatiflora* (Loitlesberger) Stephani, Spec. Hep. **5:** 120. 1912. Type. Peru. Cajamarca: Cutervo, *Jelski 536* (holotype, W; isotypes, G, H, JE, S, U).

Dioicous. *Plants* 4–5 cm long x 1.7–3 mm wide, green to black when alive, becoming dark brown to black in the dried condition. *Branching Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.15–0.3 mm in diam., in cross section composed of 16–35 epidermal cells surrounding ca. 40–90 smaller medullary cells, dorsal epidermal cells distinctly larger than the ventral epidermal cells, dorsal and lateral epidermis rather thin-walled, ventral epidermis and medulla strongly thickwalled; ventral merophyte 8–10(–14) cell rows wide. *Leaves* imbricate, dorsal lobe ovate-falcate, 1–1.7 x 0.6–1 mm, apex apiculate to short acuminate, plane or recurved, margin near the apex more or less toothed, dorsal margin auriculate at base, ventral margin curved upwards, when spread out forming an angle of 160–180° with the keel; median cells 20–40 x 20–25 µm, base cells larger, margin cells subquadrate, 14–20 µm high; oil bodies not observed. *Lobules* ovate-triangular, 0.4–0.8 x 0.3–0,5 mm, 2/5–1/2x lobe length, apex oblique, keel almost straight, free margin plane, with 7–9 teeth, the teeth 1–3 cells long, longest and more widely spatiated towards the apex of the lobule, erect with the upper cell(s) inflexed. *Underleaves* imbricate, broadly ovate-subquadrate, ca. 0.6–1 mm, 4x stem width, apex rounded to truncate, recurved, margins plane, bases distinctly auriculate, the auricles ca. 0.15–0.25 mm long, appressed to the ventro-lateral side of the stem, insertion line deeply arched. *Androecia* on short or long branches, bracts in 3–12 series, epistatic, antheridia two per bract. *Gynoecial bracts* bifid to over 1/2, keel with a large wing, lobes obovate-oblong, ca. 2 mm long, squarrose, apex acute-apiculate, the margin in the upper half strongly toothed-laciniate, lobules narrow rectangular, rather small, 1/4–1/3x lobe length, apex acute; bracteoles erect, rectangular, 1–1.5 mm long, apex truncate-emarginate to short bifid, the apical margin toothed, plane or slightly recurved, margins plane. *Perianths* immersed, obovoid-cylindrical, ca. 1.3 mm long, 10-keeled over part of its length. Spores ca. 40–55 µm long; elaters 68 per capsule, 18 µm wide, with a single brown, ca. 4 µm wide spiral.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pls. XXI, XXII. 1985.

Distribution (Fig. 36). A rare species from the Andes of Peru, 2000–3200 m. *Frullanoides laciniatiflora* has been found growing on bark at forest edges and in scrubby vegetation, sometimes mixed with *F. densifolia*.

Specimens examined. PERU. AMAZONAS: road Chachapoyas-Balsas, above Leimebamba, *Frahm et al. 744, 975* (B, U). AYACUCHO: Pampalca, between Huanta and Río Apurimac, *Killip & Smith 22229* (JE, NY).

Frullanoides laciniatiflora is closely related to *Fr. densifolia* but differs by the toothed margins of leaves and female bracts and bracteoles. In *F. densifolia* the margins of the female bracts may occasionally possess a few blunt teeth (e.g. Peru, *Inoue 33986*) but the leaves in the latter are always entire.

5. **Frullanoides liebmanniana** (Lindenberg & Gottsche) van Slageren, Meded. Bot. Mus. Herb. **544:** 102. 1985; *Phragmicoma liebmanniana* Lindenberg & Gottsche, Syn. Hep. 744. 1847; *Lejeunea liebmanniana* (Lindenberg & Gottsche) Stephani, Hedwigia **29:** 8. 1890; *Brachiolejeunea liebmanniana* (Lindenberg & Gottsche) Schiffner, Hedwigia **33:** 183. 1894. Type. Mexico. Comaltepec, *Liebmann 197* (holotype, W; isotypes, B, BM, C, FH. G, S).

Brachiolejeunea anguliloba Stephani, Spec. Hep. **5:** 128. 1912. Type. Bolivia. *Herzog 5851* (holotype, G).

Dicranolejeunea gigantea Stephani, Spec. Hep. **5:** 160. 1912. Type. Bolivia. Cochabamba: Incacorral, *Herzog s.n.* (holotype, G).

Dioicous. *Plants* 2–4 cm long x 1,7–2.3 mm wide, dull brown green when alive, becoming light to dark brown to black when dry. *Branching Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.2–0.3 mm in diam., in cross section composed of 18–25 rather thin-walled epidermal cells surrounding ca. 50–80 smaller, thick-walled medullary cells, dorsal epidermal cells larger than the ventral epidermal cells; ventral merophyte 4–8 cell rows wide. *Leaves* imbricate, dorsal lobe ovate, sometimes falcate, 0.9–1.5 x 0.8–1.1 mm, rounded or obtuse, plane or recurved, dorsal margin cordate at base, ventral margin plane, when spread out forming an angle of 170–180° with the keel; median cells 30–45 x 18–32 µm; oil bodies homogeneous, small, fusiform, ca. 2–3 x 6–8 µm, 10–25 per cell. *Lobules very large, ovate, 0.5–0.8* x 0.3–0,6 mm, 1/2–2/3x lobe length, apex oblique, keel almost straight, free margin plane, waving and with 3–5 teeth, the

FIG. 36. Distribution of *Frullanoides corticalis* (dots), *F. laciniatiflora* (diamonds) and *F. mexicana* (stars).

teeth 1(–2) cells long, usually inflexed. *Underleaves* imbricate, broadly ovate, 0.5–0.7 × 0.6–0.9 mm, about 4× stem width, apex rounded to truncate, recurved, margins plane, bases broadly rounded and slightly auriculate, insertion line shallowly arched up to 0.12 mm deep. *Androecia* on short or long branches, bracts in 5–10 series, lobules swollen, epistatic, teeth somewhat reduced; antheridia 2 (or 1?) per bract. *Gynoecial* bracts on average bifid to 1/2, keel with or without wing, lobes ovate-obovate, ca. 1.1–1.3 mm long, squarrose, apex obtuse, lobules ± narrow rectangular, 1/2–2/3× lobe length, apex rounded or acute; bracteoles erect, rectangular, 0.8–1.1 mm long, apex rounded to emarginate, plane or slightly recurved, margins plane. *Perianths* slightly exserted, occasionally stalked, obovoid-cylindrical, ca. 1.3 mm long, 10-keeled over 1/3–1/2 of its length, beak 5–17 cells long. *Spores* 45–65 µm long; elaters 68 per capsule, 300–500 × 20–25 µm, with 1(–2) brown, ca. 4 µm wide spirals.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pls. XXIII, XXIV. 1985.

Distribution. Scattered throughout tropical America, at submontane elevations (200–1000 m). *Frullanoides liebmanniana* grows on bark or rock in rather open, dry habitats: in the canopy and at the margins of evergreen forests, in scrub, orchards and on isolated trees.

Selected specimens examined. MEXICO. Type of *Frullanoides liebmanniana.*

PANAMA. DARIÉN: trail El Real-Pirre, *Salazar & Gradstein 9199* (PMA).

JAMAICA. Montego Bay, Cataclupe, *Hegewald s.n.* (U).

COLOMBIA. CUNDINAMARCA: road Fusagasuga-Melgar, *vanderHammen et al. 2147* (COL, U). SANTANDER: San Gil, *Micholitz s.n.* (G, U). TOLIMA: Venadillo, *van Reenen 2508, 2530* (COL, U).

VENEZUELA. LARA: road Gamelotal-Yaritagua, *Griffin 130* (FLAS, U).

TRINIDAD. Without loc., *Fendler s.n.* (NY).

GUYANA. Kanuku Mts., Maipama, *Jansen-Jacobs 1175a* (U), Nappi Creek, *Jansen-Jacobs 605, 606* (U).

PERU. SAN MARTÍN: road Yurimaguas-Tarapoto, Lamas, *Frahm et al. 1833* (B, G, U).

BRAZIL. GOIÁS: Morrinhue, *Vital 6148* (SP, U). MATO GROSSO: Bonito, Vital 8596 (SP, U). MINAS GERAIS: near Cimento Tocantins, *Irwin et al. 31670* (NY, U); Paracatu, *Vital 6250* (SP, U). PARANÁ: Rio Paranapanema, *Schiffner 134, 2231* (SP, UPP, W).

BOLIVIA. COCHABAMBA: Type of *Brachiolejeunea gigantea* Herz. SANTA CRUZ: Prov. Ichilo, 15 S of Buena Vista, Estancia San Rafael de Amboró, *Gradstein 7729* (LPB, U).

PARAGUAY. AMAMBAY: Parque Nacional Cerro Corá, *Geissler 14812, 14813, 14816* (G).

Frullanoides liebmanniana is most closely related to *F. tristis* and the two were synonymized by Gradstein (1990). The two species differ, however, by the larger size of *F. liebmanniana*, its plane ventral leaf margins (upcurved in *F. tristis*), the dioicous inflorescence, usually two antheridia per bract (one in *F. tristis*) and, in particular, by the very large lobules (1/2 or more of leaf length) with only 3–5 short teeth and a somewhat waving free margin. The lobules of *F. tristis* are smaller and have (4–)6–9 distinct teeth, each 2–3 cells long and inserted on an almost straight free margin. Populations of *F. tristis* from the Galapagos Islands resemble *F. liebmanniana* by having only 4–6 lobule teeth. By their smaller dimensions and other features discussed above, these plants are typical *F. tristis*, however.

6. Frullanoides mexicana van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 106. 1985. Type. Mexico. Chiapas: Palenque, *Eggers & Frahm MX22.7* (holotype, hb. Eggers; isotypes, hb. Frahm, U).

Dioicous. *Plants* 2–4 cm long x 2–2.7 mm wide, dull green when alive, becoming dark green to black in the dried condition. *Branching Frullania*-type, rarely *Lejeunea*-type. *Stems* 0.2–0.35 mm in diam., in cross section composed of 20–30 rather thin-walled epidermal cells surrounding ca. 70–115 smaller, thick-walled medullary cells, dorsal epidermal cells distinctly larger than the ventral epidermal cells; ventral merophyte 6–8 cell rows wide. *Leaves* densely imbricate, dorsal lobe ovate, 1.1–1.7 x 0.9–1.3 mm, rounded or obtuse, plane or slightly recurved, dorsal margin weakly auriculate at base, ventral margin plane, when spread out forming an angle of 150–160° with the keel; median cells 30–50 x 20–25 μm, base cells larger, margin cells subquadrate, 15–28 μm high; oil bodies not observed. *Lobules* narrow triangular to rectangular, 0.7–0.8 x 0.3–0,4 mm, about 1/2– lobe length, apex oblique, keel almost straight, free margin straight, with 8–11 teeth consisting of only one thicker-walled cell slightly protruding from the margin. *Underleaves* imbricate, obtrapezioid, 0.6–0.8 x 0.8–1.1 mm, about 4x stem width, apex rounded to truncate, plane or slightly recurved, margins plane or slightly recurved, bases slightly auriculate, the auricles up to 0.1 mm long, insertion line arched up to 0.15 mm deep. *Androecia* on short or long branches, bracts in 8–20 series, epistatic, antheridia two per bract. *Gynoecial* bracts bifid to 1/2–2/3, keel without or with a short wing, lobes obovate-oblong, ca. 1.7–2 mm long, squarrose, apex obtuse or rounded, lobules narrow rectangular, 1/3–1/2x lobe length, apex rounded with a one-celled tooth; bracteoles erect, rectangular, 1–1.2 mm long, apex rounded to emarginate, plane or slightly recurved, margins plane. *Perianths* immersed, obovoid-cylindrical, 1.4–2 mm long, 5–6-keeled in the upper half, the ventral keels sometimes extending further downwards, beak 8–10 cells long. *Spores* 45–65 μm long; elaters 68 (?) per capsule, 400–450 x 20 μm, with one brown, ca. 4 μm wide spiral.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** Pls. XXIV-XXVI. 1985.

Distribution (Fig. 36). A rare Central American endemic known from southern Mexico (Chiapas), Honduras and Costa Rica, occurring from sea level to about 600 m. *Frullanoides mexicana* grows on trunks of large, mature trees in rather open situations: at forest margins and on isolated trees along rivers and at beaches. The species forms very extensive, blackish mats on the tree trunks where it occurs and is a very conspicuous plant. It is therefore surprising that the species has been so little collected.

Specimens examined. MEXICO. CHIAPAS: Agua Azul, between Palenque and Ocosingo, *Eggers & Frahm 792625* (hb. Frahm, U), *Gradstein 8253, 8255* (U); Palenque, *Gradstein 8233, 8238* (U).

HONDURAS. ATLÁNTIDA: Lancetilla valley, near Tela, *Standley 54358, 54372, 54423, 54496, 54526, 55295, 55428, 56075a* (JE).

COSTA RICA. LIMÓN: road Limón-Cahuita, *Sipman 12298a* (U); beach near Cahuita, *Maas 7934* (CR, MO, U).

Frullanoides mexicana is closely related to *F. tristis* and may grow mixed with the latter. The two species can easily be separated by their very different lobules and by the fewer perianth keels in *F. mexicana*.

7. **Frullanoides tristis** (Stephani) van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 110. 1985; *Lejeunea tristis* Stephani, Hedwigia **29:** 8. 1890; *Brachiolejeunea tristis* (Stephani) Stephani, Spec. Hep. **5:** 112. 1912. Type. Ethiopia. Ex hb. Hampe (holotype, G; isotypes, S, W).

Phragmicoma bicolor (Nees) Nees var. *chinantlana* Gottsche, Mex. Leverm. 268. 1863; *Lejeunea bicolor* (Nees) Montagne var. *chinantlana* (Gottsche) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 132. 1884; *Brachiolejeunea chinantlana* (Gottsche) Schiffner, Hedwigia **33:** 180. 1894. Type (van Slageren, 1985). Mexico. Chinantla, *Liebmann 456b* (lectotype, C; isolectotypes, FH, G, S, W).

Brachiolejeunea insularis Evans, Bull. Torrey Bot. Club **35:** 159. 1908. Type. Puerto Rico. Cayey, *Evans 97* (holotype, YU).

Brachiolejeunea jackii Stephani, Spec. Hep. **5:** 119. 1912. Type. Mexico. Tiapacoyo, *Liebmann s.n.* (holotype, G)

Brachiolejeunea wrightii Stephani, Spec. Hep. **5:** 123. 1912. Type. Cuba. *Wright 1186* (holotype, G).

Brachiolejeunea mohriana Stephani, Spec. Hep. **5:** 125. 1912. Type. Mexico. Huatusco, *Mohr 35* (holotype, G).

Brachiolejeunea parva Herzog, Rev. Bryol. Lichénol. **20:** 125. 1951. Type. Honduras. Lancetilla valley, near Tela, *Standley 56075a* (holotype, JE).

Paroicous. *Plants* 2–4 cm long × 1,4–2 mm wide, dull brown green when alive, becoming light to dark brown to black when dry. *Branching Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.15–0.25 mm in diam., in cross section composed of 14–20 rather thin-walled epidermal cells surrounding ca. 25–50 smaller, thick-walled medullary cells, dorsal epidermal cells somewhat larger than the ventral epidermal cells; ventral merophyte 4–6 cell rows wide. *Leaves* imbricate, dorsal lobe ovate, sometimes falcate, 0.7–1.3 × 0.5–0.9 mm, rounded or obtuse, occasionally ± apiculate, plane or recurved, dorsal margin cordate at base, ventral margin curved upwards, when spread out forming an angle of 150–170° with the keel; median cells 25–45 × 15–32 μm; oil bodies not observed. *Lobules* ovate-oblong, 0.5–0.8 × 0.3–0.6 mm, 2/5–1/2x lobe length, apex oblique, keel almost straight, free margin plane, with (4–)6–9 regularly spatiated teeth, the teeth 2–4 cells long, erect with the upper cell(s) usually inflexed, the first tooth sometimes broadened and very blunt. *Underleaves* imbricate, broadly ovate to suborbicular, 0.4–0.7 × 0.5–0.8 mm, about 4× stem width, apex rounded, slightly recurved, margins plane or recurved, bases broadly rounded and slightly auriculate, insertion line shallowly arched up to 0.1 mm deep. *Androecia* on stems just below the gynoecium, bracts in 2–4 series, lobule swollen, epistatic, antheridia one per bract. *Gynoecial* bracts on average bifid to 1/2, keel narrowly winged, lobes ovate-obovate, ca. 1.1–1.5 mm long, squarrose, apex obtuse or minutely apiculate, lobules ± narrow rectangular, 1/3–1/2x lobe length, apex rounded or acute; bracteoles erect, rectangular, 0.8–1.1 mm long, apex rounded to truncate-emarginate, plane or slightly recurved, margins plane. *Perianths* immersed or exserted, occasionally stalked, obovoid-cylindrical, 1.2–1.5 mm long, 10-keeled over 1/2–2/3 of its length, beak 5–10 cells long. *Spores* 45–65 μm long; elaters 68 per capsule, 300–400 × 20 μm, with one brown, ca. 4 μm wide spirals.

Terpenoids: bicyclogermacrene and various pinguisanines (pinguisanolide, hydropinguisanolide, pinguisenal, etc.) are the main constituents of this species (Gradstein et al., 1981, as *Brachiolejeunea chinantlana*).

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:**Pls. XV, XVI. 1985.

Distribution. Throughout the neotropics, also in tropical Africa and India (rare). In tropical America *Frullanoides tristis* usually occurs at rather low elevations, from almost sea level to about 1000 m, rarely up to 2000 m. In Africa and in the Himalayas the species reaches much higher elevations (3000 m in the Himalayas). *Frullanoides tristis* grows on bark or rock in rather open, often secondary habitats: in dry or moist woodlands, scrub, on fruit trees, in plantations and on roadside trees. In virgin rain forest the species is restricted to the canopy.

Selected specimens examined. MEXICO. VERACRUZ: Orizaba, *Mohr 35* (MANCH), Düll 4/A52a (DUIS, JE);

Tlapacoyo, *Liebmann 563b* (C).

HONDURAS. Type of *Brachiolejeunea parva*.

COSTA RICA. Turrialba, Rio Reventazon, *Svihla 47–749, 47–778* (WTU).

PANAMA. **CHIRIQUÍ:** *Hélion 497* (G).

CUBA. **ORIENTE:** Valle Huerto, *Schubert M265* (JE); Sierra de Boniato, *Pócs 9102/F* (EGR, HAC, U); Monte Verde, *Wright s.n.* (BM, U, US); Baracoa, *Underwood & Earle 1144* (YU).

JAMAICA. Cinchona, *Evans 143d, 407* (YU), *Underwood 1105* YU); Troy, *Evans 638, 671* (YU); Castleton Botanical Garden, *Underwood 55* (YU); St. James, between Catadupe and Moche, *Hegewald 8208, 8220* (U).

PUERTO RICO. Mayaguez, *Heller 4463a* (YU); Caribe State Forest, *Griffin s.n.* (FLAS, U).

COLOMBIA. **CASANARE:** Sácama, *Aguirre & Gradstein 2970* (COL, U). **CUNDINAMARCA:** road Bogotá–La Calera, *Bischler 563* (COL, U). **MAGDALENA:** Sierra Nevada de Santa Marta, San Lorenzo, *Winkler C192* (ULM). **RISARALDA:** Santa Rosa de Cabal, *van Reenen 1857* (COL, U); Mun. San Antonio de Chami, Geguades, *Gradstein 8656* (COL, U).

VENEZUELA. **LARA:** Parque Nacional de Terepaima, *Griffin et al. 21* (FLAS, U). **MÉRIDA:** Mucuy, *Onraedt 78V6540* (JE, U).

TRINIDAD. Without loc., *Wallace s.n.* (NY).

SURINAME. Paramaribo, *Kegel s.n.* (FH, G, S, U, W).

FRENCH GUYANA. Cayenne, *Moen 115* (G); Saül, *Gradstein 6077, 6188* (U), *Montfoort 969* (U).

ECUADOR. **GALÁPAGOS ISLANDS:** Floreana, Cerro Pajas, *Gradstein H155* (U); Isabela, rim of volcán Alcedo, *Gradstein & Weber H227* (COLO, U), *vander Werff 1547b, 2013* (U); Isabela, Cerro Azul, *Gradstein & Sipman H373, H454* (U); Santa Cruz, trail to Bella Vista, *Gradstein & Weber H5* (COLO, U), *Weber B-13655* (COLO, JE); San Cristobal, El Progreso, *Gradstein & Lanier H327* (U).

PERU. **HUANUCO:** Tingo Maria, *Hegewald 7885* (U). **JUNÍN:** Tarma, San Ramón, *Hegewald 8395* (U).

BRAZIL. **BAHIA:** *Lützelburg 43* (G); Sergipe, Itabaiana, *Vital 2869* (SP, U). **PERNAMBUCO:** Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC).

BOLIVIA. **SANTA CRUZ:** Prov. Ichilo, 3 km N of Buena Vista, *Gradstein 7726* (LPB, U).

Frullanoides tristis is closely related to *F. liebmanniana*. Differences are discussed under the latter species.

LEJEUNEOIDEAE

BRACHIOLEJEUNEAE

van Slageren & Berendsen

Ptychanthoideae tribe Brachiolejeuneae van Slageren & Berendsen *in* Kruijt & Gradstein, Nova Hedwigia **43:** 306. 1986; Ptychanthoideae Mizut. p.p.; *Lejeuneae Holostipae* Spruce p.p. Type. *Brachiolejeunea* (Spruce) Schiffner.

Plants creeping, ascending or pendent, never dendroid. Vegetative branching *Lejeunea*-type or *Frullania*-type; flagelliform branches lacking. Stem with 2–16 cells wide ventral merophyte. Leaf insertion long, J-shaped. Hyaline papilla at lobule apex usually entally displaced. Underleaves undivided. Male bracts epistatic or hypostatic. Perianth usually with one rounded ventral keel. Sporophyte: seta usually articulate, with 16 outer rows of cells; capsule valves remaining suberect after dehiscence, pale-colored, inner and outer valves with ± nodulose cell thickenings, brownish sheeth of thickening on inner valve lacking; elaters 34 per capsule, upper ends attached to valve margins only, spiral rudimentary, pale-colored; spores elongate-rectangular, arranged in decussate tetrads, spore ornamentation variable (van Slageren, 1985), rosettes usually rudimentarily developed. Terpenoid chemistry: pinguisane-type sesquiterpenes rare.

Distribution. Pantropical. Thirty-five species in nine genera are recognized in the Brachiolejeuneae. All of the genera and about 80% of the species occur in the New World, which is the centre of diversity of this tribe.

The Brachiolejeuneae are referred here to the subfamily Lejeuneoideae because of their lejeuneoid capsules (see CLASSIFICATION). The cladistic analysis has revealed two main generic lines of evolution within the tribe: the Stictolejeuninae and the Brachiolejeuninae. The differences between these two subtribes are exclusively gametophytic.

Key to the Subtribes of Brachiolejeuneae

1. Stem epidermis cells not larger than medullary cells. Median leaf cells 10–25 μm long, their walls evenly thickened, trigones obscure or lacking; leaves frequently with ocelli. Perianth auriculate. . . . . . . Stictolejeuninae.
1. Stem epidermis cells larger than medullary cells. Median leaf cells more than 25 μm long, walls with trigones; ocelli lacking. Perianth not auriculate. . . . . Brachiolejeuninae (p.157).

STICTOLEJEUNINAE Gradstein subtribe nov.

Brachiolejeuneae subtribe *Stictolejeuninae* Gradstein. Type. *Stictolejeunea* (Spruce) Schiffn.

Caulis sine hyalodermis. Cellulae trigonis obscuris vel nullis, parietibus equaliter incrassitis. Ocelli saepe adsunt. Perianthia auriculata.

Stem epidermis cells ± brown, not larger than medullary cells; ventral merophyte 4–18 cells wide. Leaves ovate and with rounded apex, the margins entire. Median leaf cells isodiametrical, 10–25 µm in diameter, their walls ± evenly thickened, trigones obscure or lacking, oil bodies lacking or finely papillose; ocelli scattered throughout the leaf or in a row, lacking in *Neurolejeunea* sect. *Aneurolejeunea*. Underleaf base bistratose. Androecia with bracteoles limited to the base of the spike. *Perianths* keels expanded above into a large auricle.

Distribution. Pantropical. The subtribe Stictolejeuninae consists of two genera, *Stictolejeunea* and *Neurolejeunea*, both of which occur in the New World. The close relationship between these two genera has been recognized by all authors since Spruce (1884).

14. Stictolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893; Gradstein, Beih. Nova Hedwigia **80:** 195. 1985; *Lejeunea* subgen. *Stictolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 81. 1884. Type (Evans, 1907). *Stictolejeunea squamata* (Willdenow ex Weber) Schiffner. Named for its leaves dotted with ocelli.

Plants 1–15 cm long × 1–2.5 mm wide, somewhat glossy green to dull olive green when alive, retaining their color or becoming darker, brown to blackish in the dried condition, creeping, ascending or pendent. *Branching Frullania*-type or *Lejeunea* type, irregular or densely (bi-)pinnate, microphyllous branches lacking. *Stems* rigid, ca. 0.1–0.35 mm in diam., epidermal cells in 1–3 rows, equal in size or smaller than medullary cells, walls of epidermal cells thicker than those of medullary cells and usually brownish pigmented; ventral merophyte 4–18 cell rows wide. *Leaves* widely spreading and flat, little altered when dry, apex rounded or obtuse, often with a whitish border of larger, thin-walled dead cells, margins entire or crenulate by eroding border cells, dorsal margin curved, dorsal base straight or rounded, extending ± across the stem, ventral margin ± straight, curved at the junction with the keel, the keel very short or lacking; leaf cells rather small, subisodiametrical-hexagonal, ca. 10–25 µm long, their walls ± evenly thickened, intermediate thickenings lacking; oil bodies lacking in subg. *Stictolejeunea*; ocelli present, scattered in throughout leaves, underleaves, bracts and perianth, variable in number and size, ca. 20–200 per leaf, up to 2x cell size, isodiametric (never elongated), oil mass ± colorless. *Lobules* small, up to 1/4x leaf length, often reduced, inflated, straight or curved with the orifice turned backwards to stem base, with one short tooth, hyaline papilla on the inner lobule surface 1–3 cells below the proximal base of the tooth. *Underleaves* orbicular to reniform, apex rounded, margins entire, sometimes with a whitish border, insertion line straight to arched; underleaf base bistratose. *Androecia* on short-specialized or elongated branches, bracts in 2–10 series, strongly inflated and subglobose, much smaller than leaves, subequally bilobed, lobule hypostatic, underleaves limited to the base of the spike; antheridia two per bract. *Gynoecia* on very short *Lejeunea*-type branches, with or without one pycnolejeuneoid innovation, bracts in one series, suberect, ± smaller than leaves, unequal in size, the inner bract larger, with entire margins and rounded apex, keel without wing, lobules plane, ca. 1/4–1/2x lobe length, bracteoles undivided, entire, longer than underleaves, covering the lower half of the perianth. *Perianths* exserted, when mature standing upwards and visible only in dorsal view of the plant, compressed, the dorsal surface smooth and plane, the ventral surface weakly swollen, smooth or (rarely) with 1–2 low, narrow keels above, the lateral keels smooth, expanded above into large auricles, the margins often whitish-bordered. *Sporophyte:* seta not(?) articulate; capsule valves with nodulose to monofenestrate (*Stictolejeunea squamata*) thickenings on the inner wall; spores finely spinose, with rosettes; otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution. The genus *Stictolejeunea* is pantropical in distribution and contains three species, two of which occur in tropical America (Gradstein, 1985b). The neotropical species occur in lowland and lower montane areas, normally ranging from sea level up to 1500 m, in the Andes up to 2400 m. They are characteristic epiphytes of shade synusia in the understory of virgin or little disturbed rain forest and usually grow on bark, more rarely on living leaves or rock.

Stictolejeunea is a very well defined genus with many diagnostic features (Gradstein, 1985b). It is the only genus of the Brachiolejeuneae with scattered ocelli in leaves and underleaves. Scattered ocelli are more common in the tribe Lejeuneae, e.g., *Physantholejeunea*, *Lepidolejeunea*, *Luteolejeunea* and *Diplasiolejeunea*, but all of these genera have stems with a distinct hyaloderm and a ventral merophyte of only two cells wide (four cells wide in *Lepidolejeunea eluta*; this species has bifid underleaves, however). In *Stictolejeunea* enlarged epidermis cells are lacking and the stems are more robust, the ventral merophyte being at least 4 cells wide. Robust forms of *S. squamata* have a distinct 2–layered subepidermis of very thick-walled cells, but in smaller, creeping plants of this species and in the other species of the genus this subepidermis is not produced.

Further characteristic features of *Stictolejeunea* are the small, evenly thickened leaf cells, the frequent presence on leaves and perianths of whitish borders , consisting of dead cells, and the perianth which is dilated above into two conspicuous, rounded auricles. The size of these auricles varies considerably and in *S. balfourii* var. *bekkeri* they are very low. Peculiar features of the type species of the genus, *S. squamata*, are its curved lobules and the lack of oil bodies in chlorophyllose cells. Oil body data have not yet been published for the other species of the genus.

Schuster (1984) and Gradstein (1985b), independently, recognized two subgenera in *Stictolejeunea:* (1) subgen. *Stictolejeunea* for the neotropical *S. squamata*, and (2) subgen. *Leptostictolejeunea* Schust. (= subgen. *Parastictolejeunea* Gradst.) for *S. balfourii* and the rare Asiatic *S. iwatsukii*. Differences between the two groups include the different branching patterns (*Frullania*-type in subgen. *Stictolejeunea*, *Lejeunea*-type in subgen. *Leptostictolejeunea*) and the thinner stems, with four cells wide ventral merophytes and without subepidermis, of *Leptostictolejeunea*. Chemically, the two groups are also quite distinct (Gradstein et al., 1985). Recent observations show that the morphological differences are not constant, however. Vegetative *Lejeunea*-type branches have now also been observed in *Stictolejeunea squamata* (Fig. 37A) and Thiers (1985) has shown that *Frullania*-type branches do occur in *S. balfourii*. Moreover, thin stems with 4 cells wide merophytes like those of *Leptostictolejeunea* may occur in small lowland populations of *S. squamata*. Thus, it appears that by their branching and stem anatomy features *Stictolejeunea* and *Leptostictolejeunea* are less sharply defined than previously believed.

Neurolejeunea is the sister genus of *Stictolejeunea*. The two genera are not very closely related, however, as they differ in quite a number of morphological features, e.g., the presence of blackish pigmentation, the sharply toothed lobules, the elongated gynoecial shoot, the paired innovations, and the lack of scattered ocelli in *Neurolejeunea*.

Key to the Subgenera and Species of *Stictolejeunea*

1. Vegetative branches mostly of the *Frullania*-type (rarely *Lejeunea*-type); underleaves wider than long, (3)4–10× stem width; plants 1.2–2.5 mm wide, creeping, ascendent or pendent, regularly (bi-)pinnate or, when creeping, iregularly branched; common epiphyte in lowland and lower montane rain forest. . . . . . . 1. *S. squamata (S. subgen. Stictolejeunea).*

1. Vegetative branches mostly of the *Lejeunea*-type (rarely *Frullania*-type); underleaves suborbicular, 2–3× stem width; plants smaller, 1–1.3 mm wide, always creeping and irregularly branched; uncommon epiphyte in the understory of lowland rain forest, usually near running water. . . 2. *S. balfourii (S. subgen. Leptostictolejeunea).*

1. Stictolejeunea subgenus Stictolejeunea

For description see under *S. squamata*.

Distribution. Throughout tropical America. *Stictolejeunea* subgen. *Stictolejeunea* contains only one species, *S. squamata*.

1. Stictolejeunea squamata (Willdenow ex Weber) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893; Gradstein, Beih. Nova Hedwigia **80:** 204, Fig. 1. 1985; *Jungermannia squamata* Willdenow ex Weber, Hist. Musc. Hep. Prodr. 33. 1815; *Lejeunea squamata* (Willdenow ex Weber) Nees, Syn. Hep. 322. 1845; *Symbiezidium squamatum* (Willdenow ex Weber) Trevisan, Mem. Reale Ist. Lomb. Mat. Nat., ser. 3, **4:** 403. 1877; *Stictolejeunea squamata* (Willdenow ex Weber) Schiffner var. *macrior* (Spruce) Herzog, Rev. Bryol. Lichénol. **20:** 130. 1951. Type.

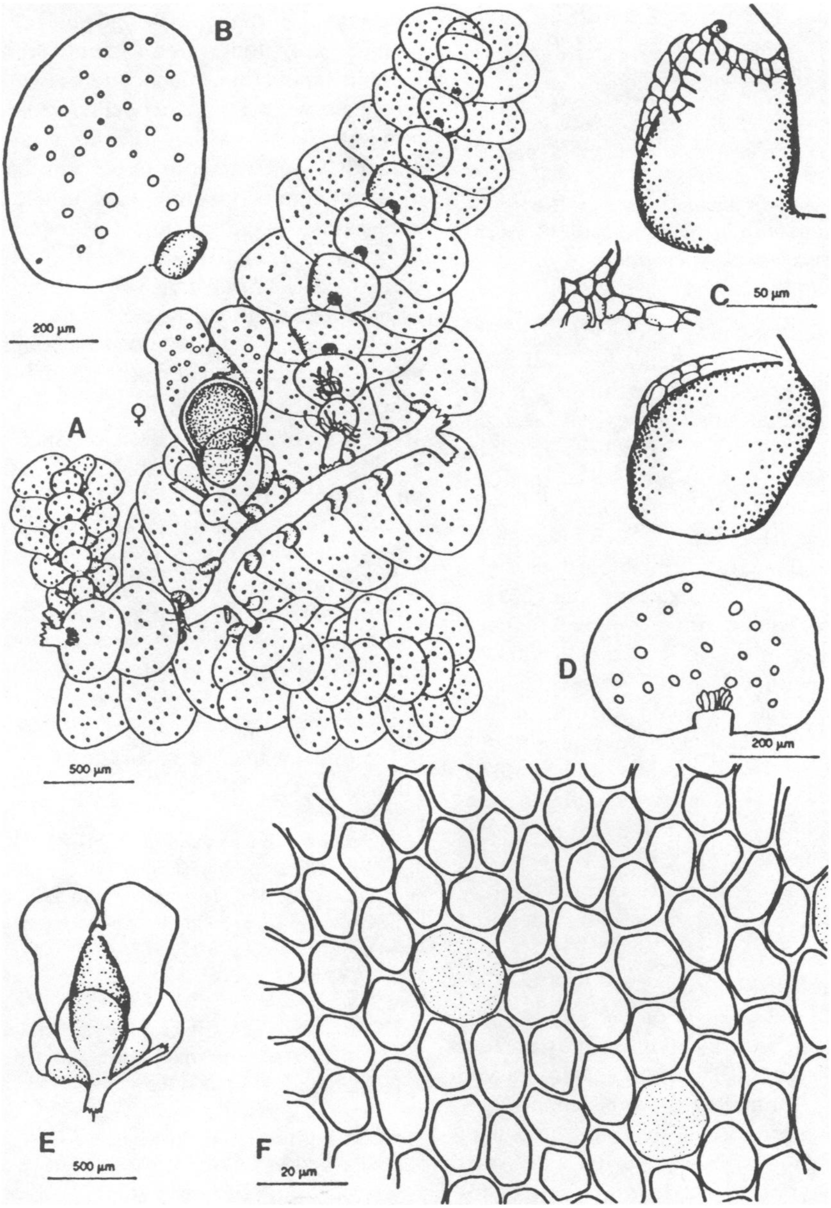

FIG. 37. *Stictolejeunea squamata.* **A.** Habit, with gynoecium; note vegetative branches of *Frullania*-type (below) and *Lejeunea*-type (above). **B.** Leaf. **C.** Lobules and lobule apex. **D.** Underleaf. **E.** Gynoecium. **F.** Leaf cells, showing two ocelli. From Brazil, *Maas et al. P13267.*

West. Indies. "In corticibus Myrti caryophyllatae," *unknown collector (S, STR, W).*

Figs. 9, 37.

Phragmicoma ocellulata Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **19:** 159. 1843. Type. Dominica. *Bory s.n.* (holotype, PC-MONT; isotype, STR).

Stictolejeunea kunzeana (Gottsche) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1** **(3):** 131. 1893; *Lejeunea squamata* (Willdenow ex Weber) Nees var. *kunzeana*

Gottsche, Syn. Hep. 322. 1845; *Lejeunea kunzeana* (Gottsche) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 83. 1884. Type (Gradstein, 1985b). Chile. *Pöppig s.n.* (lectotype, S; isolectotype, STR).

Lejeunea squamata (Willdenow ex Weber) Nees var. *neesii* Gottsche, Syn. Hep. 322. 1845. Type (Gradstein, 1985b). Brazil. Rio de Janeiro, *Sellow s.n.* (lectotype, STR; isolectotype, W).

? *Stictolejeunea rotundifolia* Stephani, Spec. Hep. **6:** 556. 1924. Type. West Indies. *Broadway s.n.* (n.v.; the material is not in G), syn. fide Gradstein (1985b).

Dioicous. *Plants* 1.5–15 cm long x 1.2–2.5 mm wide, glossy pale green when alive, dull green tinged with white or olive in the dried condition, ascending or pendent, small phases may be creeping. *Branching:* vegetative branches *Frullania*-type (very rarely *Lejeunea*-type), specialized sexual branches *Lejeunea*-type, branching pattern regularly (bi)pinnate, in creeping plants sometimes irregular, fertile plants usually with one to several short *Lejeunea*-type branches between two adjacent *Frullania*-type branches. *Stems* normally robust, 0,2–0,35 mm in diam., in cross section with (15–)25–75 brownish pigmented, strongly thick-walled epidermal cells in (1–)2–3 rows surrounding numerous thinner-walled, unpigmented medullary cells; ventral merophyte (4–)8–18 cell rows wide. *Leaves* ovate-suborbicular, 0.8–1.6 x 0.6–1.2 mm, apex rounded, often with a (1–)2–3 cell rows wide whitish border, margins entire or crenulate by eroding border cells, dorsal base often extending across the stem; median cells 14–24 x 10–16 μm, oil bodies lacking in green cells, ocelli ca. 20–150 per leaf, 20–30 μm in diam. *Lobules* up to 1/5(–1/4)x leaf length, on main stems usually smaller and often reduced, inflated and usually curved with the orifice turned backwards, more rarely straight, free margin usually incurved, apex with a 1–3 cells long tooth, the tooth usually incurved and invisible in optical view. *Underleaves* contiguous or imbricated, broadly ovate to reniform, 0.3–1 x 0.5–1.5 mm, (3–)4–7(–10)x stem width, apex rounded, plane or recurved and sometimes undulated, margins plane, sometimes with a 1–2 cell rows wide whitish border, bases straight, insertion line arched, up to 0.2 mm deep; brown adhesive rhizoid discs produced in epiphyllous plants. *Androecia* capitate or spicate, occupying a short-specialized *Lejeunea*-type branch or terminating a long *Frullania*-type branch (rarely intercalary). *Gynoecia* on a very short *Lejeunea*-type branch, usually with one short, vegetative (occasionally long, fertile) innovation, rarely without innovation, bracts and bracteoles as in the genus, with or without ocelli. *Perianths* 1.5–2 mm long, with or without ocelli, the lateral keels expanded as auricles up to 0.5 mm beyond the beak and almost touching each other, leaving a very narrow opening above the deeply recessed beak, auricles usually with a 2–10 cell rows wide whitish border. *Sporophyte* outer valve cells with irregularly nodulose thickenings, inner valve cells with irregularly nodulose thickenings which may become enlarged and confluent (van Slageren, 1985, p. 297, Fig.1); spores 20–50 x 15–25 μm; elaters 200–250 x 15 μm.

Chemistry: an oxygenated sesquiterpene and the flavonoid tricetin 6, 8-di-C-ß-D-glucopyranoside are chemical markers of this species (Gradstein et al., 1985, 1988).

Distribution. Common throughout the humid portions of tropical America, from sea level up to 2400 m. *Stictolejeunea squamata* grows in primary and disturbed rain forests on tree trunks, lianas, twigs, logs, living leaves, and occasionally on moist rock. Fossil *S. squamata* has been found in Miocenic amber of the Dominican Republic (see FOSSILS).

Selected specimens examined. MEXICO. CHIAPAS: *Munch s.n.* (S); Lacandon forest reserve along Río Lacantun, near Chajul Biological Station, *Gradstein 8087, 8153, 8168* (U); Marquez de Comillas region between Lacantun river and Guatemala border, *Gradstein 8181* (U).

GUATEMALA. Near Guatemala City, ex hb. Levier (BM, NY);

HONDURAS. Without loc., *Wilson 556a* (NY).

BELIZE. Near border with Guatemala, *Schipp 874* (NY).

NICARAGUA. BLUEFIELDS: base of Cerro San Isidro, *Proctor et al. 27218* (NY).

COSTA RICA. CARTAGO: Peji valley, *Standley & Valerio 47166* (JE). COCOS ISLAND: Chatham bay, *Weber 549* (COLO, U). GUANACASTE: Tilarán, *Standley & Valerio 45403* (JE). HEREDIA: Cerros de Zurqui, *Standley & Valerio 50623* (JE). LIMÓN: Tortuguero, *Steere CR-85* (NY).

PANAMA. CHIRIQUI: David, *Hélion s.n.* (L, S, U). DARIÉN: base of Cerro Pirre, *Salazar & Gradstein 9219* (PMA, U). Marragantí, *Williams 1082* (NY).

CUBA. GUANTÁNAMO: Baracoa, *Bisse & Köhler 6479* (JE), *Pócs & Reyes 9063* (HAC, U); El Yunque Mt., *Underwood & Earle 351, 811, 1103* (NY). SANTIAGO DE CUBA: Gran Piedra, *Ekman 8818* (S), *Reyes 830, 841, 842, 847, 850* (HAC); Sierra de Escambray, *Pócs & Borhidi 9005*

(HAC). **VILLA CLARA:** Mnts. de Banao, *Léon & Clemente 5556* (HAC, NY); Lomas de Banao, valle del Caracusey, *Léon & Roca 8351, 8353* (HAC).

JAMAICA. Mansfield near Bath, *Evans 339* (NY); Kempshot, *Britton 2444* (NY); Hollymount, *Marble 391* (NY).

HAITI. NE of Basse Terre, *Leonard 12481a* (JE, US); Port Margot, *Nash 193, 381* (NY); Faux Cap, *Orcutt 10118* (NY).

DOMINICAN REPUBLIC. Near Hato Mayor, *Thiers 5519* (NY).

PUERTO RICO. Cerrote, *Pagán 965* (HAC, NY); Utuado, Mt. Morales, *Howe 1100* (NY); Luquillo Mts., El Yunque, *Evans 173, 192, 195* (NY).

WINDWARD ISLANDS. ST. KITTS. *Breutel s.n.* (BM). **MONTSERRAT.** Sagra Mt., *Shafer 846, 859, 860* (NY). **GUADELOUPE.** Etang de Capesterre, *Le Gallo 633* (JE), *Duss 139, 451* (NY). **DOMINICA.** Rosalie, *Lloyd 695* (NY). **MARTINIQUE.** Bois des Deux-Choux, *Duss 376* (NY). **ST. VINCENT.** "misit Hooker" (W). **ST. LUCIA.** *King s.n.* **(NY).**

COLOMBIA. CHOCÓ: Quibdo, *Bischler 151, 155* (COL, JE, PC, U); Mun. Nuqui, near Arusi, *Gradstein 8827* (COL, U). **NARIÑO:** Mun. Mosquera, *Linares 73* (COL). **MAGDALENA:** Parque Nacional del Tayrona, *Diaz 4187* (COL). **VALLE:** Buenaventura, *Bischler 375* (COL, JE, PC, U), *Killip 11711, 11742* (NY); El Tambo, *von Sneidern s.n.* (S).

VENEZUELA. AMAZONAS: Atabapo, near Culebra, *Thiers 4910* (NY); Cerro Neblina, along Río Mawarinuma, *Halling 4149* (NY). **FALCÓN:** Santa Ana, *Steyermark & Braun 94548* (US). **ZULIA:** Topochalito, *Griffin 58* (FLAS, U).

TRINIDAD. Base of Mt. Tamana, *Britton et al. 1950* (NY, US).

GUYANA. Macouría river, *Jenman 2340, 2341* (NY); Rockstone, *Maas & Westra 3943* (U); Mabura Hill, *Cornelissen & ter Steege C.878, C.887* (U); Cuyuni river, *Tutin 321* (BM); Upper Mazaruni, Karowtipu, *Boom & Gopaul 7735* (NY), Kamarang, *Robinson 85-10* (U, US), Jawalla, *Gradstein 4896, 4903* (U).

SURINAME. Paramaribo, *Wullschlaegel s.n.* (BM); Brownsberg, *Florschütz 4757* (U), *Gradstein 4642* (U); Lely Mts., *Lindeman et al. 86a, 88a* (U); Kabalebo Dam project area, *Bekker 24 colls.* (BBS, U).

FRENCH GUIANA. Gabaret river, *Leprieur s.n.* (PC-MONT); confluent Sinnamary-crique Maroni, *Cremers 5471* (JE, U); Mts. de Kaw, *Gradstein 5890* (U); Saül, *Cremers 4160* (JE, U), *Gradstein 6108, 6109* (U), *Montfoort & Ek 1144-1149* (U).

ECUADOR. CHIMBORAZO: *Spruce s.n.* (BM, US). **ESMERALDAS:** Río San Miguel, *Harling 4670* (S), 4702 (NY), **PASTAZA:** W of Puyo, *Thiers 4658, 4767* (NY). **PICHINCHA:** NW of San Miguel de los Bancos, *Buck 10431* (NY). **SANTIAGO-ZAMORA:** Mendez, *Harling 2212a* (S).

PERU. LORETO: near Iquitos, *Hegewald 6277* (U), *Timme 4854* (US). **SAN MARTÍN:** road Yurimaguas-Tarapoto km 95, *Frahm et al. 1411, 1435, 1789* (B, U); road Chachapoyas-Moyabamba km 400, *Frahm et al. 20, 467, 1314, 2166* (B, U).

BRAZIL. ACRE: Cruzeiro do Sul, *Maas et al. P13267* (NY, U); near Sena Madureira, *Nelson et al. 495* (NY). **AMAPÁ:** Upper Rio Oyapock, *Lützelburg 20283, 20385, 21222* (JE, S). **AMAZONAS:** Manaus, *Griffin et al. 786* (FLAS, U); Rio Uatumã, *Buck 3035* (NY); Serra Curicuriari, *Schuster 79-15-539, 79-15-548* (NY). **BAHIA:** Mun. Ilhéus W of Olivença, *Boom & Mori 866* (NY). **PERNAMBUCO:** Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). **RIO DE JANEIRO:** *Hell 502* (JE). **SÃO PAULO:** Rio Branco, *Schiffner 1963* (S); Rio Mambu, *Schiffner 735* (S). **RIO GRANDE DO SUL:** Torres, *Vianna s.n.* (ICN, U).

BOLIVIA. COCHABAMBA: Chaparé, road Cochabamba–Villa Tunari km 112, *Gradstein 7511, 7517* (LPB, U). **LA PAZ:** Tutuhuancana, *Buchtien s.n.* (S).

CHILE. Type of *Stictolejeunea kunzeana.*

Stictolejeunea squamata is a variable species and some of the variation seems to be correlated with altitude (Gradstein, 1985b). Plants from lower altitudes tend to be small, creeping (more rarely pendent), densely branched and usually lack whitish perianth borders, whereas plants from higher altitudes are more robust, usually pendent, more laxly branched and with very conspicuous whitish perianth borders. The latter have been described as *S. kunzeana*. Whitish borders may also be present on leaves and/or underleaves but their presence is by no means constant and within single plants leaves or underleaves with or without hyaline borders may be observed.

Stictolejeunea squamata normally develops vegetative branches of the *Frullania*-type and sexual branches of the *Lejeunea*-type; its branching pattern is one of the main features distinguishing it from *S. balfourii* (subgen. *Leptostictolejeunea*). In small, creeping phases of *S. squamata* from lowland rain forest, however, vegetative *Lejeunea*-type branches may also be produced (Fig. 37A). Examples are collections from Brazil (*Maas et al. P13267*) and Colombia (*Gradstein 8827*).

2. Stictolejeunea subgenus Leptostictolejeunea Schuster, Phytologia 56: 70. 1984; *Leptostictolejeunea* (Schuster) Schuster, Trop. Bryol. 2: 252. 1990. Type. *Stictolejeunea iwatsukii* Mizutani.

Stictolejeunea subgen. *Parastictolejeunea* Gradstein, Beih. Nova Hedwigia **80:** 210. 1985. Type. *Stictolejeunea bal-*

fourii (Mitten) E.W. Jones.

For description see under *Stictolejeunea balfourii*.

Distribution. Pantropical. *Stictolejeunea* subgen. *Leptostictolejeunea* contains two species, one of which occurs in tropical America.

2. Stictolejeunea balfourii (Mitten) E. W. Jones, J. Bryol. **9:** 50. 1976; Gradstein, Beih. Nova Hedwigia **80:** 210, Figs. 2, 3. 1985.

Key to the Varieties of *Stictolejeunea balfourii*

1. Perianth auricles large, oblong, 1/3–2/5× perianth length, erect, approaching each other and leaving a very narrow opening above the beak; pantropical. . . . . 2a. *S. balfourii var. balfourii.*

1. Perianth auricles much lower, up to 1/5× perianth length, diverging, leaving a wide, v-shaped opening above the beak; Guianas. . . . . . 2b. *S. balfourii var. bekkeri.*

2a. Stictolejeunea balfourii var. **balfourii**; *Lejeunea balfourii* Mitten, Philos. Trans. Roy. Soc. London **168:** 398. 1879 (*"balfouri"*); *Symbiezidium balfourii (Mitten) Stephani, Spec. Hep. 5: 99. 1912. Type. Rodriguez I. Balfour s.n.* (holotype, NY; isotype, BM).

Stictolejeunea africana VandenBerghen, Bull. Jard. Bot. Etat (Bruxelles) **20:** 15. 1950. Type. Ivory Coast, *Chévalier 17* (syntype, PC).

Stictolejeunea richardsii Herzog, Trans. Brit. Bryol. Soc. **1:** 318. 1950. Type. Borneo. Sarawak: Mt. Dulit, *Richards 2618* (holotype, JE).

Monoicous. *Plants* creeping, forming small and strongly appressed, glossy blackish patches. *Branching Lejeunea*-type, an occasional vegetative *Frullania*-type branch present in vigorous plants, branching pattern irregular. *Stems* zigzag, thin, ca. 0.07–0.14 mm in diam., in cross section composed of 12–16 epidermal cells (in one row) surrounding a similar number of medullary cells, all stem cells moderately thickwalled, without pigmentation; ventral merophyte four cell rows wide; *Leaves* ovate to oblong, 0.5–0.9 × 0.3–0.7 mm, apex rounded to obtuse, a hyaline border of 1–2 cell rows sometimes present, dorsal base not extending across the stem; median cells 10–20 × 5–15 µm, oil bodies not observed, ocelli ca. 25–75 per leaf, up to 2× cell size. *Lobules* ovate-subquadrate, up to 1/4× leaf length, sometimes reduced, inflated, free margin almost plane, orifice directed towards leaf apex, apex truncate, with a 1–3 cells long tooth. *Underleaves* spatiated, appressed to the stem and on one side connate (by one single cell!) with the adjacent leaf, suborbicular, 0.2–0.35 mm wide, 2–3.5× stem width, apex rounded, margins plane, often with a 1–2 cell rows wide whitish border, bases and insertion line straight. *Androecia* capitate or spicate, occupying a short-specialized branch or innovation(!), occasionally terminating a longer, vegetative branch. *Gynoecia* on a very short lateral branch without innovation or with one very short androecial innovation, bracts and bracteoles as in the genus. *Perianths* with ocelli, ca. 1 mm long, with ocelli, the lateral keels expanded above into large, oblong auricles which are ca. 1/3–2/5× perianth length and almost touch each other, leaving a very narrow opening above the deeply recessed beak, auricles without whitish border. *Sporophyte* outer valve cells with small, cordate to confluent trigones, the inner valve cells thin-walled below and irregularly thickened in the upper half with nodulose thickenings; *spores* ca. 40 × 15 µm.

Illustration. Herzog, Trans. Brit. Bryol. Soc. **1:** 318. 1950 (as *Stictolejeunea richardsii*).

Distribution (Fig. 38). Mexico, Honduras (?, sterile), Colombia, Peru, tropical Africa, Malesia, Australia, New Caledonia, Caroline Island, Hawaii (?). *Stictolejeunea balfourii* var. *balfourii* grows in the understory of undisturbed, wet lowland and lower submontane rain forests, from sea level up to 800 m. It forms small, glossy blackish patches on tree bases, roots, lianas and logs close to the ground, or on rock in creeks. It prefers very moist, sheltered locations and may be locally common in periodically inundated forests. The species has been little collected and has probably been overlooked.

Specimens examined. MEXICO. CHIAPAS: Lacandon forest reserve, near Chajul Biological Station, *Gradstein 7923* (U).

HONDURAS. ATLÁNTIDA: Lancetilla valley, near Tela, *Standley 55741* (JE); identification doubtful because of poor condition of the material.

COLOMBIA. CAUCA: Gorgona I., *Schuster & Aguirre s.n.* (COL). CHOCÓ: Mun. Nuqui, El Amargal 5 km SW of Arusi, *Gradstein 8831, 8899* (COL, U). META: Villavicencio, forest of S.A. Bavaria, *Gradstein & van Zanten s.n.* (COL, GRO, U).

PERU. SAN MARTÍN: road Yurimaguas-Tarapoto km 95,

FIG. 38. Distribution of *Stictolejeunea balfourii* var. *balfourii* (dots) and var. *bekkeri* (stars).

Frahm et al. 1691b, 2046b (B, hb. Grolle, U).

2b. Stictolejeunea balfourii var. **bekkeri** Gradstein, Beih. Nova Hedwigia **80:** 214. 1985. Type: Suriname. Nickerie: Kabalebo Dam project area, line opposite camp road km 212, *Bekker 1619b* (holotype, U; isotypes, BBS, hb. Grolle).

Perianth auricles low, up to 1/5× perianth length, diverging.

Terpenoids: three unidentified bisbenzyl derivates have been dected as markers of this taxon (Gradstein et al., 1985).

Illustration. Gradstein, Beih. Nova Hedwigia **80:** 215, Fig. 3. 1985.

Distribution (Fig. 38). Guianas: Suriname, French Guiana. *Stictolejeunea balfourii* var. *bekkeri* inhabits the same general habitat as the typical variety and has been collected in mixed and periodically inundated rain forest, from sea level up to 150 m.

Specimens examined. SURINAME. NICKERIE: Kabalebo Dam project area, *Bekker 1314, 1593, 1659a 1693a, 1712a, 1713* (BBS, U).

FRENCH GUIANA. Saül, *Bekker 2153, 2188A, 2324C* (U), *Gradstein 6146, 6166* (U).

The characteristic features of this variety are the short perianth auricles, which are elevated to only ca. 0.2 mm above the beak and are distinctly diverging, leaving a wide, v-shaped sinus above the beak.

Excluded Taxa

(see Gradstein, 1985b: 217–220; Piippo, 1986)
Stictolejeunea herzogii Buchloh
= *Luteolejeunea herzogii* (Buchloh) Piippo
Stictolejeunea section *Macrocellularia* Schuster
= *Luteolejeunea* Piippo

15. Neurolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3)**: 131. 1893; *Lejeunea* subgen. *Neurolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 84. 1884. Type. *Neurolejeunea seminervis* (Spruce) Schiffner. Genus named for its ocelli in a row, forming a nerve.

Plants 1–2.5 cm long × 0.7–1.5 mm wide, glossy olive-green, brown to black, creeping, usually forming dense mats. *Branching Lejeunea*-type, irregularly to densely pinnate, when fertile sometimes forked by repeatedly floriferous innovations; flagelliform branches occasionally present. *Stems* slightly applanate, ca. 0.1 mm in diam., epidermal cells equal in size or smaller than medullary cells, walls of epidermal cells brown, thicker than those of medullary cells; ventral merophyte 4–6(–10) cell rows wide. *Leaves* spreading or slightly convoluted when dry, apex rounded or obtuse, plane or recurved, margins entire, plane, dorsal base straight or rounded; leaf cells (sub)isodiametrical, elongate towards leaf base, small, in mid-leaf ca. 10–20 μm long, walls more or less evenly thickened and often somewhat darkish pigmented, trigones obscure or lacking; intermediate thickenings lacking; oil bodies 4–8 per cell, globose to ellipsoid, *Jungermannia*-type, finely granulose to subhomogeneous with 1–2 small globules; ocelli present in leaf lobes, in a row, or lacking. *Lobules* often conspicuously darker in color than lobes, strongly inflated, flask-shaped, almost never reduced, free margin bordered by narrow rectangular cells, with 2 teeth, first tooth usually reduced, sometimes large, papilla-like (*Neurolejeunea sastreana*), second tooth (=apical tooth) long, curved outwardly; hyaline papilla distal of apical tooth on the inner side of free margin. *Underleaves* orbicular-obdeltoid or tranversely ovate, apex rounded or truncate, margins entire, insertion line straight to deeply arched; underleaf base bistratose. *Androecia* on short-specialized or elongated branches, bracts strongly inflated and subglobose, subequally bilobed, lobule hypostatic, underleaves limited to the base of the spike or present thoughout; antheridia two per bract. *Gynoecia* on elongated branches, with 1–2 pycnolejeuneoid innovations, bracts in one series, suberect, hardly larger than leaves, with entire margins and rounded or obtuse apex, keel with or without a narrow wing, lobules plane, ca. 1/2× lobe length, bracteoles undivided, entire. *Perianths* with 3–4 smooth or narrowly winged keels (always one ventral keel present), the lateral and ventral keels often horn-like expanded into auricles beyond the apex. *Sporophyte* seta articulate; spores with rosettes; otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution. *Neurolejeunea* is a small New World genus with four species in two sections. The species are restricted to tropical latitudes except *N. breutelii*, which extends into warm temperate latitudes, northwards to southeastern United States and southwards to Rio Grande do Sul, Brazil. The genus occurs mainly at lower elevations on bark and rock in rain forest, often in rather open situations. The highest records of *Neurolejeunea* are from the Andes of Colombia, where *N. breutelii* occurs in cloud forests up to 3000 m.

The genus *Neurolejeunea* is readily recognized by its rather dark, brown or black appearance, its small size, the lack of a stem hyaloderm, the flask-shaped lobules which are often darker in color than the lobe, almost never reduced and are provided with a long and slender apical tooth (sometimes incurved and visible only after dissection), its small leaf cells (less than 20 μm long) which are more or less evenly thickened, and by its 3-keeled perianth with lateral keels often expanded into auricles.

The hyaline papilla of the lobule is distal in position to the apical tooth which techically represents the second tooth. The first tooth, situated in the sinus at the position of the hyaline papilla, is lacking or rudimentary except in *N. sastreana* in which it is transformed into a large "papilla."

Sex distribution in *Neurolejeunea* is normally dioicous, and male and female plants usually occur as separate populations. In *N. breutelii* and *N. sastreana* plants of the two sexes sometimes grow intermingled, however, and in one collection of *N. breutelii* (Cuba, *Borhidi & Muniz 5027*) a single autoicous shoot was found (obs. R. Grolle). Technically, the latter species should therefore be considered polyoicous rather than dioicous. Monoicous and polyoicous species, which are more common in Lejeuneaceae than dioicous species (Gradstein, 1987), are predictably more widespread in general than dioicous species. The bisexual spores of the monoicous taxa are apparently a more favorable means of dispersal than the unisexual ones of the dioicous species. It would thus appear that the wide range of the *Neurolejeunea breutelii*, as compared with the other species of the genus all of which are strictly dioicous, has been enhanced by the occasional occurrence of bisexual spores in the species.

Neurolejeunea is most closely related to *Stictolejeunea*, especially to the subgenus *Leptostictolejeunea*. The latter, however, differs by its scattered ocelli in leaves and underleaves, its smaller lobule with reduced tooth, its frequent lack of innovations, etc.

Key to the Sections of *Neurolejeunea*

1. Leaf lobes with ocelli in a row, forming a distinct row of 7–22 cells long. . . . . . 1. *N.* sect. *Neurolejeunea*.
1. Leaf lobes lacking ocelli. . . . . 2. *N.* sect. *Aneurolejeunea*.

1. **Neurolejeunea** section **Neurolejeunea**

Plants olive-green or brown when dry, not turning blackish; leaf lobes plane or slightly convex, with ocelli in a row; lobules ovoid, flattened towards apex, never(?) reduced, apical tooth visible in situ; leaf cells evenly thickened, lacking trigones and usually without darkish pigmentation; dioicous; gynoecia with 1–2 sterile or fertile innovations; perianth 3–4-keeled, with or without dorsal keel.

Distribution (Fig. 40). Central America, West Indies, northern South America, at elevations ranging from sea level to 1200 m on the Caribbean islands.

Key to the Species of *Neurolejeunea* sect. *Neurolejeunea*

1. Leaf apex (at least on younger, branch leaves) capped by a whitish border of thin-walled cells in 2–4 rows, border fragile and breaking off in older leaves (leaf apex then becoming irregularly crenate); leaves oblong, 1.5–2 × longer than wide; West Indies. . . . . 1. *N. catenulata*.
1. Leaf apex entire, lacking a whitish border; leaves ovate, less than 1.5 × longer than wide; northern South America, Guatemala-Mexico. . . . 2. *N. seminervis*.

1. Neurolejeunea catenulata (Nees) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893; *Phragmicoma catenulata* Nees, Naturgesch. Eur. Leberm. **3:** 248. 1838, nom. nud.; *Lejeunea catenulata* Nees, Syn. Hep. 323. 1845; *Symbiezidium catenulatum* (Nees) Trevisan, Mem. Reale Ist. Lomb., Ser. 3, **4:** 403. 1877. Type (Evans, 1907). West Indies. "In . . . *Neckera abietina* Hook. Americae septentrionalis," *Sieber s.n.* (holotype, STR; isotype, W).

Dioicous. *Plants* 1–3 cm long × 1–1.5 mm wide, brownish-green when dry. *Stems* 0.1–0.12 in diam., in cross section composed of 16–20 epidermal cells surrounding 30–35 medullary cells; ventral merophyte 4–6 cell rows wide. *Leaves* subimbricate, plane, diverging from stem at an angle of 60°–75°(–90°), sometimes falcate, dorsal lobe asymmetrically oblong, 0.5–0.9 × 0.3–0.5 mm, apex broadly rounded, capped by a group of thin-walled, elongated, 20–25 µm long dead cells in 2–4 rows, forming a whitish border, border fragile, breaking off in older leaves, leaving an irregularly crenate leaf tip; ventral leaf margin straight, forming an almost continuous line (angle 160°–190°) with the keel except for a small indention at the sinus; row of ocelli 8–20 cells long, uniseriate throughout, separated from leaf base by 0–2 ordinary cells; oil bodies not observed. *Lobules* ovoid, ca. 0.15 × 0.1 mm, 1/5–1/3 leaf length, flattened towards free margin and apex, keel slightly curved, smooth, border cells of free margin colorless, apical tooth 3–5 cells long, 2 cells wide at base. *Underleaves* orbicular to transversely ovate, 0.2–0.3 mm long × 0.25–0.4 mm wide, 3–4× stem width, plane, insertion line straight or slightly curved. *Androecia* on short-specialized branches or terminal on elongated branches, bracts in 3–5 series, underleaves present throughout the spike but becoming smaller above. *Gynoecia* with 1–2 sterile or fertile innovations, bract lobules ovate-triangular, 2–4× longer than the keel, apex of lobules rounded to obtuse, keel with a 1 cell wide wing, row of ocelli short or rudimentary, consisting of a few groups of 1–3 ocelli separated from each other by 1–2 ordinary cells; bracteoles elongated obovate, 0,5 mm long × 0,4 mm wide, apex rounded. *Perianths* with or without distinct auricles, when with auricles obovate-oblong, distinctly emergent, ca. 1–1.2 mm long × 0.7–0.8 mm wide, apex deeply and narrowly retuse, lateral keels narrowly and interruptedly winged (wing 1–3 cells wide), especially on the auricles, ventral keel well-developed, rounded or with 2 (–3) folds in the upper half, sometimes horn-like expanded distally, dorsal keel low and narrow; when without auricles (e.g. Puerto Rico, *Evans 143*) obcuneate, 0.6–0.7 × 0.5–0.6 mm, apex truncate or shallowly emarginate, lateral keels unwinged or with rudimentary wings, ventral keel low, with two folds, dorsal keel lacking. *Sporophyte* not observed.

Illustration. Evans, Bull. Torrey Bot. Club **33**, Pl. 2. 1907.

Distribution (Fig. 40). West Indies, rare, occurring at elevations of 500–1200 m. *Neurolejeunea catenulata* grows on bark of trees or on logs in submontane rain forests.

Specimens examined. CUBA. ORIENTE: Loma San Juan, *Hioram 12625* (JE); Sierra de Moa, La Melba, *Bisse & Lippold 11156a* (JE), *Bisse 15457b* (JE).

JAMAICA. Mabess River, *Evans 313* (BM, NY, US, W, YU).

PUERTO RICO. Luquillo Mts., *Evans 119, 143, 144* (NY, YU).

WINDWARD ISLANDS. DOMINICA. Hampstead Valley, *Elliott 2326* (BM). **MARTINIQUE.** Piton Dumanze, *Degelius s.n.* (S).

Conservation. In view of the few collections of this species and the alarming deforestation rate in the Caribbean, *Neurolejeunea catenulata* is considered a threatened species (Gradstein, 1992c). In recent years, the species has only been recorded from eastern Cuba.

Neurolejeunea catenulata is a very distinct species. It is recognized by the rather long, oblong leaves and the presence of a whitish border of large, dead, thin-walled cells on the apex of the younger leaves. On older leaves this border is usually broken away, leaving an irregularly crenate margin.

2. Neurolejeunea seminervis (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893; *Lejeunea seminervis* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 84. 1884. Type. Venezuela. Amazonas: San Carlos del Río Negro, "Ad arboris in sylvis," *Spruce L403* "hb. 70" (lectotype, MANCH 17216, designated here). This specimen is chosen as the lectotype because it contains both male and female plants. Fig. 39.

Dioicous. *Plants* 1–3 cm long × 0.6–1 mm wide, olive-green to brown in the dried condition. *Stems* 0.06–0.1 mm in diam., in cross section composed of 15–20 epidermal cells surrounding 20–22 medullary cells; ventral merophyte four cell rows wide. *Leaves* imbricate, plane or slightly convex, diverging from the stem at an angle of 90°–100°, often falcate, dorsal lobe subsymmetrically ovate to oblong, 0.35–0.6 × 0.3–0.45 mm, apex rounded, without whitish border, ventral leaf margin straight, forming an angle of 90°–140° with the keel; row of ocelli 7–22 cells long, originating at leaf base, uniseriate, the tip sometimes two cells wide; oil bodies 4–8 per cell, ellipsoid, finely granulose to subhomogeneous. *Lobules* ovoid, ca. 0.15 × 0.1 mm, 1/4–1/2 leaf length, flattened towards free margin and apex, keel curved, smooth, border cells of free margin brownish or colorless, apical tooth 3–5 cells long, 2 cells wide at base. *Underleaves* obdeltoid, 0.1–0.25 mm long × 0.12–0.3 mm wide, 2–3× stem width, plane, insertion straight or slightly curved. *Androecia* on short-specialized branches or forming a terminal or intercalary spike on an elongated branch, bracts in 2–6 series, underleaves 1–2 limited to the base of the spike. *Gynoecia* with 1–2 sterile or fertile innovations, bract lobules obovate-oblong, up to 2× longer than the keel, apex of lobules obtuse, keel with a 1–3 cells wide wing of without wing, row of ocelli short or rudimentary, usually located in the centre of the lobe; bracteoles elongated obovate, 0.5 × 0.4 mm, apex rounded. *Perianths* as in *Neurolejeunea catenulata* but slightly smaller, not exceeding 1 mm in length. *Sporophyte* not observed.

Distribution (Fig. 40). *Neurolejeunea seminervis* has a rather remarkable, disjunct distribution and occurs in northern South America and in the Guatemala-southern Mexican region, at elevations fom sea level up to 500 m. In South America the species seems restricted to the up-

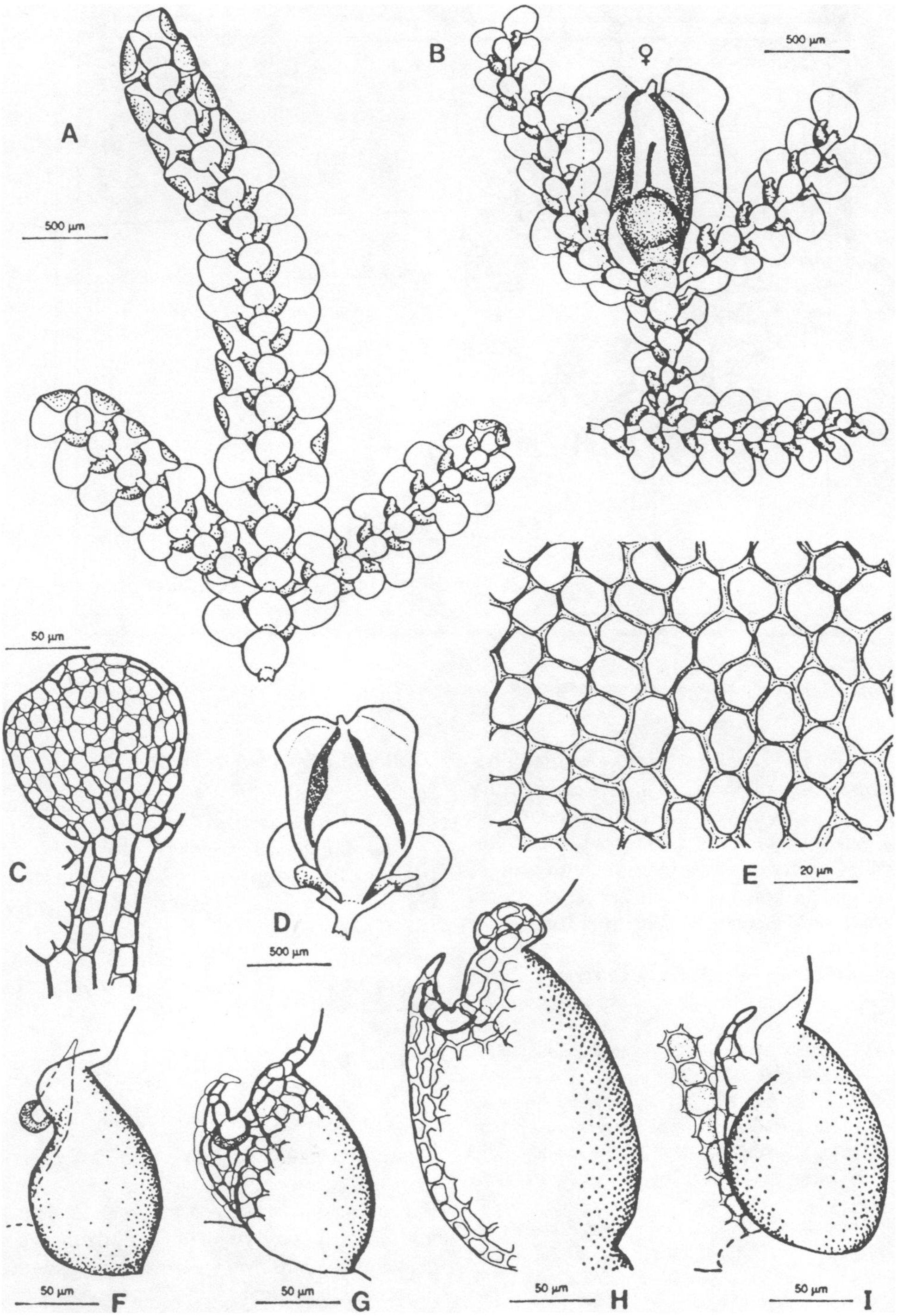

Fig. 39. *Neurolejeunea breutelii* (A, H), *N. sastreana* (B–G) and *N. seminervis* (I). **A.** Habit. **B.** Habit, with gynoecium. **C.** Underleaf. **D.** Gynoecium. **E.** Leaf cells. **F.** Lobule, with papilla-like first tooth. **G.** Ibid., view of inner side. **H.** Lobule. **I.** Lobule and base of leaf lobe with row of ocelli. A, H from Brazil, *Schäfer-Verwimp 8446*. B–G from the type of *N. sastreana*. I from Guyana, *Cornelissen & ter Steege C582*.

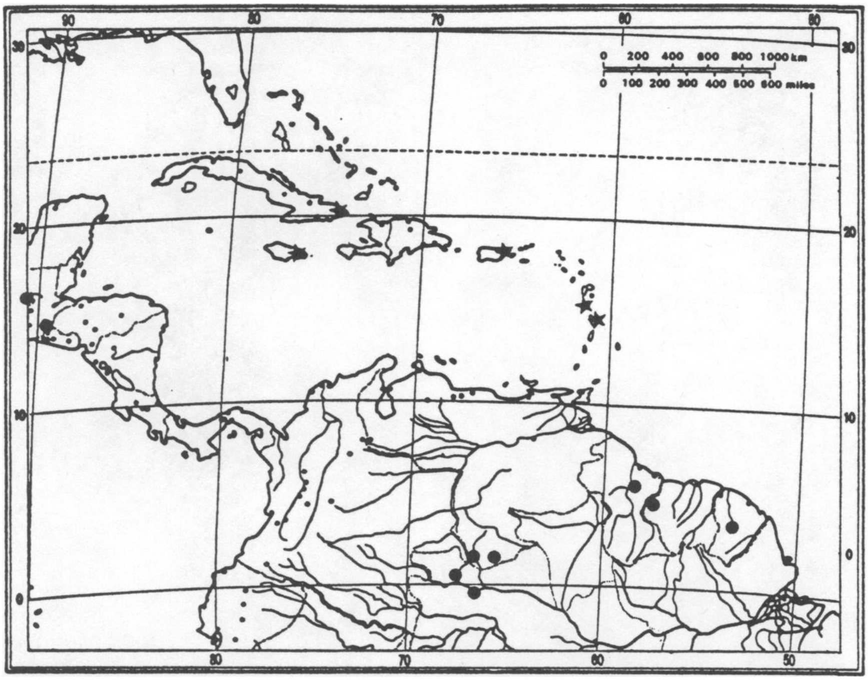

FIG. 40. Distribution of *Neurolejeunea catenulata* (stars) and *N. seminervis* (dots).

stream portion of the Río Negro and the northwestern portion of the Guianas (western Suriname, Guyana). *Neurolejeunea seminervis* grows on bark of trees in the canopy or the understory of dry or moist evergreen rain forest, or in scrub. In the Guianas the species has only been found in the canopy of the high forest.

Specimens examined. **MEXICO.** CHIAPAS: Lacandon forest reserve, near Chajul Biological Station, *Gradstein 7934* (U).

GUATEMALA. Banks of Río Polochic below Panzós, *Maxon & Hay 3095* (US, YU).

VENEZUELA. AMAZONAS: San Carlos del Río Negro, *Spruce s.n.*, *Hepaticae Spruceanae Amazonicae et Andinae 1542* (BM, MANCH, NY, U, YU), *Spruce L69, L397* (MANCH); Cerro Neblina, along Río Mawarinuma, *Halling 4176, 4184, 4186* (NY).

GUYANA. Moraballi Creek, near Bartica, *Richards 502* as "*N. brevinervis*" (BM); Mabura Hill, 180 km SSE of Georgetown, *Cornelissen & ter Steege C582, C666, C711, C866, C886 (U).*

SURINAME. Kabalebo Dam project area, Bekker 1161c (U).

FRENCH GUIANA. Saül, *Montfoort & Ek 466, 1036–38* (U).

BRAZIL. AMAZONAS: upper Rio Negro, São Gabriel, *Spruce* (MANCH, NY, US), Serra Curicuriari, *Schuster 79–15–740, 79–15–757* (NY).

Neurolejeunea seminervis is easily recognized by the characters given in the key. Plants from the Guianas and Central America are rather small (ca. 0.6–0.7 mm wide) and the row of ocelli is maximally 10 cells long. Plants from the Rio Negro are often somewhat larger and may have a row of ocelli up to 22 cells long.

2. **Neurolejeunea** section **Aneurolejeunea** Schuster, Hep. Anth. N. Am. IV: 786. 1980. Type. *Neurolejeunea breutelii* (Gottsche) Evans.

Plants usually blackish when dry; leaf lobes plane or convex, ocelli lacking; lobules inflated throughout, rarely reduced, apical tooth often invisible *in situ*; leaf cells with rather ill-defined, coalescent trigones, the walls often darkish pigmented, especially the primary lamella; dioicous or (rarely) autoicous; gynoecia with (1–)2 sterile innovations; perianth 3-keeled, dorsal keel lacking.

Distribution. Widespread in tropical America, from sea level to 3000 m in the Andes.

Key to the Species of *Neurolejeunea* sect. *Aneurolejeunea*

1. Lobule apex with a conspicuous, 25–30 µm long, papilla-like cell (= 1st tooth), which projects backwards to the stem and has a very thick (10–15 µm) and colorless apical wall; underleaves plane; Venezuela, Puerto Rico. . . . . 4. *N. sastreana*.

1. Papilla-like projecting cell lacking or rudimentary, less than 10 µm long; underleaves concave with upturned margins or plane; widespread neotropical. . . . . 3. *N. breutelii*.

3. Neurolejeunea breutelii (Gottsche) Evans, Bull. Torrey Bot. Club **34:** 13, Pl. 1. 1907; Schuster, Hep. Anth. N. America IV: 786, Fig. 656. 1980; *Lejeunea breutelii* Gottsche, Syn. Hep. 324. 1845; *Symbiezidium breutelii* (Gottsche) Trevisan, Mem. Reale Ist. Lomb., Ser. 3, **4:** 403. 1877; *Ceratolejeunea breutelii* (Gottsche) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 125. 1893. Type. St. Kitts. *Breutel s.n.* (holotype, B, destroyed; isotype, BM, W). Fig. 39.

Lejeunea devexa Lindenberg & Gottsche, Syn. Hep. 750. 1847; *Symbiezidium devexum* (Lindenberg & Gottsche) Trevisan, Mem. Reale Ist. Lomb., Ser. 3, **4:** 403. 1877; *Ceratolejeunea devexa* (Lindenberg & Gottsche) Stephani, Spec. Hep. **5:** 408. 1913; *Neurolejeunea devexa* (Lindenberg & Gottsche) Herzog, Ann. Bryol. **6:** 56. 1933. Type. Mexico. Veracruz: Hacienda de Mirador, *Liebmann s.n.* (holotype, W; isotype, JE).

Ceratolejeunea uleana Stephani, Spec. Hep. **5:** 445. 1913. Type. Brazil. *Ule 87* (holotype, G).

Marchesinia schiffneri S. Arnell *in* Schiffner & Arnell, Oesterr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. **111:** 109. 1964. Type. Brazil. Rio de Janeiro: Mt. Itatiaia, Fazenda Montserrate, ca. 1000 m, *Schiffner 602* (holotype, W, n.v.), *syn. nov.*

Dioicous, rarely autoicous. *Plants* 1–4 cm long × 0.7–1.2(–1.5) mm wide, green brown to black. *Stems* 0.08–0.12(–0.15) mm in diam., in cross section composed of 15–20(–30) epidermal cells surrounding 16–25(–40) medullary cells; ventral merophyte 4(–10) cell rows wide. *Leaves* imbricate or contiguous (shade forms), weakly to strongly convex, diverging from stem at an angle of ca. 90°, falcate, dorsal lobe asymmetrically ovate to oblong, 0.3–0.7(–1.0) × 0.25–0.5(–0.7) mm, apex rounded or obtusely pointed, often broadly recurved, ventral leaf margin straight to arched, forming a sharp to rather broad angle (90°–150°) with the keel; oil bodies 2–4 per cell, ellipsoid to subglobose, 5–9 × 3–4 µm, very finely granulose (Schuster, 1980) or homogeneous with 1–2 small globules (Colombia, *Aguirre 3322). Lobules* flask-shaped, 1/–1/2× leaf length, not flattened, keel arched especially near base, smooth or roughened by weakly mamillose cells, free margin usually involuted, margin cells usually not colorless, apical tooth (= second tooth) large, 3–6 cells long, made up narrowly elongated cells, usually incurved and invisible *in situ* (especially in branch leaves), the sinus sometimes hooked beyond the apical tooth at the position of the first tooth, the first tooth occasionally slightly protuberant, up to 10 µm long. *Underleaves* distant to contiguous, not imbricate, 0.15–0.25(–0.5) mm long, 0.15–0.3(–0.7) mm wide, 1.5–3(–4) × stem width, concave with upturned to recurved margins, rarely plane, insertion line straight or curved. *Androecia* on short or elongated branches, bracts in 3–6 series, underleaves limited to the base of the spike. *Gynoecia* with two sterile innovations, bract lobules narrowly obovate-oblong, hardly elongated beyond the keel, apex of lobules rounded, keel with a 1–2 cells wide wing or without wing; bracteoles obovate-suborbicular, up to 0,6 mm long, apex rounded to truncate, margins plane. *Perianths* emergent, oblong-obovate, ca. 1–1.2 mm long × 0.8–0.9 mm wide, 3-keeled, lateral auricles variable in length, when low (ca. 0.1 mm long) perianth apex shallowly emarginate, when high (ca. 0.3–0.4 mm long) perianth apex deeply retuse, lateral keels sometimes slightly winged, ventral keel well-developed, rounded or with 2–3 folds in the upper half, sometimes horn-like expanded distally, dorsal keel lacking.

Distribution. Throughout tropical America, northwards to southeastern United States, southwards to Rio Grande do Sul, Brazil, from sea level to 3000 m in the northern Andes. *Neurolejeunea breutelii* grows in rather open forest and scrub on bark and rock, or in the canopy of dense rain forests. It sometimes occurs near the sea shore and seems tolerant of salt sprea (e.g. *Vital 6659a* from SE Brazil).

Specimens examined. MEXICO. CHIAPAS: near Tziscao 55 km E of Comitán, *den Held & van Rijn HH57, HH58* (S, U); towards El Triunfo, *Sharp 4518* (TENN); Marques de Comillas region between Lacantun river and Guatemala border, near Boca Chajul village, *Gradstein 8180, 8188, 8190* (MEXU, U). **HIDALGO:** near Apulco, *Sharp 4123a* (TENN). **TAMAULIPAS:** above Gómez Farías, *Iwatsuki & Sharp 4819, 4829, 4831, 4832, 4834, 4835, 4840* (TENN).

GUATEMALA. Alta Verapaz, near Coban, *Türckheim 1957* (NY).

HONDURAS. ATLÁNTIDA: Lancetilla valley, near Tela, *Standley 53385, 55627* (JE). **COMAYAGUA:** Siguatepeque, *Standley 56380* (S). **CORTES:** Lake Yojoa, *Morton 7640* (NY).

UNITED STATES. MISSISSIPPI. JACKSON: Black Creek near Escatawpa, *Schuster 27832* (NY, U); **GEORGE:** Wyatt Hills, *Schuster 27643* (NY). **FLORIDA. LIBERTY:** Apalachicola National Forest, *Breil 2411* (NY).

CUBA. HABANA: I. de Pines, *Bisse 745b* (JE). **SANTIAGO DE CUBA:** Sierra Maestra, Pico Turquino region, *Pócs 9086/A, Bryoph. Neotr. Exsicc. 44* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PAN, QCA, S, SP, U, USJ, XAL); Gran Piedra, *Borhidi & Muniz 5027* (JE), *Pócs & Reyes 9057/A, 9113/C* (G, JE, NY). **GUANTÁNAMO:** near Guantanamo, *Schubert M/166c, M/217b* (JE).

JAMAICA. Portland, *Maxon & Killip 32* (BM, NY, US); Vinegar Hill, *Evans 65, 453* (BM, NY).

DOMINICAN REPUBLIC. La Vega, near biggest waterfalls in Casabito area, *Zanoni & Mejía 12334* (NY).

PUERTO RICO. Río de Maricao, *Britton & Cowell 2677, 4253* (NY); Maricao State Forest, *Thiers 5244* (NY); Toro Negro State Forest, *Griffin s.n.* (U); Luquillo Mts., El Verde, *Reese 14311* (NY).

WINDWARD ISLANDS. ST. KITTS. Type of *N. breutelii*. **GUADELOUPE. BASSE TERRE:** Morne Hirondelle, *Duss 90, 208b* (JE); Bois du Nez, *Duss 5, 54, 160* (NY); Second "Chute du Carbet," *De Sloover 33851 (U); First* "Chute du Carbet," 700-900 m, *Gradstein & Sastre-de Jesús 6617* (U); road St. Claude to La Soufrière, *Gradstein 6575* (U). **DOMINICA.** Morne Diablotin, *Elliott 2163* (BM, JE); Freshwater Lake, *Gradstein 6634* (U), *Schuster 66623* (US); Laudat, *Lloyd 276* (NY). **MARTINIQUE.** Gr. Rivière, *Duss several colls.* (NY).

COLOMBIA. CASANARE: road Socha-Sácama, El Arenal, *vander Hammen & Jaramillo 2507* (COL, U), *Aguirre & Gradstein 3322* (COL, U); Sácama, *Aguirre & Gradstein 3086* (COL, U). **CHOCÓ:** Mun. Nuqui, near Arusi, *Gradstein & Aguirre 8886* (COL, U). **SANTANDER:** Mt. St. Vincente near Charta, *Killip 18978* (JE); Virolín, *Castro et al. 194* (COL).

VENEZUELA. AMAZONAS: Río Negro, Cerro Aracamuni, *Halling 5538* (NY).

FRENCH GUIANA. Comté river, between "bac de Stupan" and bridge "route du Brésil," *Cremers 3868, 3869, 3874 (CAY, U), 3873, 3875* (CAY, JE, U); Itany river, near Touinsky, *Cremers 4797* (CAY, JE, U); Saül, *Bekker 2161-1* (U), *Montfoort & Ek 1031-35* (U).

ECUADOR. LOS RÍOS: Hac. Clementina, Samama, *Harling 2145d* (JE), *2259* (S). **GALÁPAGOS ISLANDS:** Santa Cruz, *Taylor B64149* (CAL, U), *Gradstein H12, H64, H89, H363* (COLO, U), *vanderWerff 2079, 2083* (U).

PERU. SAN MARTÍN: Rioja, *Frahm et al. 1306* (B, U).

BRAZIL. ESPÍRITO SANTO: Pedro Azul, *Schäfer-Verwimp 10105* (hb. Schäfer-Verwimp). **MINAS GERAIS:** St. Barbara, Serra da Caraça, *Hoehne 165* (JE); Sul do Minas, Poços do Caldas, *Schäfer-Verwimp 7069* (JE, U). **RIO GRANDE DO SUL:** Itaimbezinho, *Vianna ICN2522* (U). **SÃO PAULO:** São Bernardo, *Wacker & Decker s.n.* (JE); Jaraguá, *Gehrt 616* (JE); Mun. Cananéia, Is. Cardoso, *Vital 6659a* (JE).

Neurolejeunea breutelii is easily recognized by its black color, the lack of ocelli, and the long, curved apical tooth of the lobule. The lack of a large papilla-like cell protruding from the lobule apex separates the species from the closely related *N. sastreana*. In plants with strongly involuted lobule apices, however, the sinus of the lobule is sometimes notched just beyond the apical tooth. A rounded cell (= the first tooth) may be sticking out from the notch (e.g. Dominica, *Elliott 1202*; Guadeloupe, *Duss*; Peru, *Frahm et al. 1306*) and this condition is somewhat reminiscent of *N. sastreana*. However, in the latter species the protuberant cell has become very conspicuously elongated (25–40 µm long) with a strongly thickened wall. In *N. breutelii* the cell does not exceed 10 µm in length and the wall is thin or slightly thickened only.

Neurolejeunea breutelii shows considerable morphological variation. Cell walls may be very thin or strongly thickened with large confluent trigones. In some populations leaf cells are very conspicuously elongated towards the leaf base, tending to form an obscure vitta. The perianth auricles vary considerably in length but perianths without auricles, as found in *N. catenulata* and *N. seminervis*, have not been observed in *N. breutelii*. Schuster (1980) contends that male plants of *N. breutelii* are somewhat smaller than female plants, but I have not found evidence to support his observation.

Plants from low elevations are usually very small and do not exceed 1 mm in width, whereas mountain plants may be more robust and up to 1.5 mm wide. Unusually robust plants, with a ten cell-rows wide ventral merophyte, leaves up to 0.9 mm long and underleaves up to 0.7 mm wide, have been collected in a cloud forest at about 3000 m in Colombia (*Aguirre & Gradstein 3322*). In shaded habitats, the species may be somewhat etiolated and produce rather distant, elongated leaves and small lobules. Lobules are never reduced in this and other species of *Neurolejeunea*, however.

4. Neurolejeunea sastreana Gradstein, Bryologist **92:** 345, Figs. 7–10. 1989. Type. Puerto Rico. Luquillo Mts., Mt. El Toro (W side), 900 m, Jun 1989, *Gradstein 6537* (holotype, U; isotype, NY). Fig. 39.

Lejeunea breutelii Gottsche var. *regularis* Hampe & Gottsche, Linnaea **25:** 354. 1852. Type. Puerto Rico. *Schwanecke s.n.* (holotype, BM; isotype, G), *syn. nov.*

Dioicous (male and female plants growing mixed). *Plants* 1–2 cm long x 0.6–1 mm wide, blackish brown. *Stems* ca. 0.1 mm in diam., in cross section composed of ca. 16 epidermal cells surrounding 20 medullary cells; ventral merophyte four cell rows wide. *Leaves* contiguous to subimbricate, diverging from the stem at an angle of ca. 90°, falcate, dorsal lobe asymmetrically ovate, 0.45–0.6 x 0.3–0.45 mm, apex rounded, plane, ventral margin curved, forming an angle of 90°–145° with the keel; oil bodies (seen in the type material) 2–4 per cell, globose to bluntly ellipsoid, 5–8 x 4–5 m, colorless, almost homogeneous, the surface smooth or faintly papillose by a few coarse, protruding globules. *Lobules* flask-shaped, up to 1/2x leaf length, rarely reduced, not flattened, keel arched especially near base, forming an angle of 45°–60° with the axis, rounded, smooth or roughened by slightly mamillose cells, free margin involuted, margin cells colorless, apical tooth incurved, *invisible* in optical view, broad triangular, 3 cells long and 3–4 cells wide at base, fragile, in part made up of colorless, thin-walled cells, first tooth large, "papilla-like," protruding from the apex and directing backwards, consisting of an elongated, 25–40 µm long, apically strongly thickened (12–20 µm thick) cell. *Underleaves* distant, ca. 0.2–0.25 mm long, 0.25–0.3 mm wide, 2–3x stem width, insertion line straight. *Androecia* on short-specialized branches, bracts in 3–5 series, underleaves limited to the base of the spike. *Gynoecia* with 1–2 sterile innovations, bract lobules oblong, hardly elongated beyond the keel, apex of lobules rounded, keel without wing; bracteoles obovate-oblong, 0.6 x 0.4 mm, apex rounded, margins plane. *Perianths* as in *Neurolejeunea breutelii*, lateral auricles well-developed (ca. 0,3 mm long), ventral keel with two folds, not horn-like expanded.

Distribution. West Indies, northern Venezuela, 700–1400 m. *Neurolejeunea sastreana* has been collected a few times in submontane rain forest and grows on bark in rather open situations, e.g., at forest margins.

Specimens examined. DOMINICAN REPUBLIC. Without locality, *Eggers 17* (G).

PUERTO RICO. Luquillo Mountains, El Yunque trail, *Griffin s.n.* (JE, U), La Mina USDA Station, *Fulford et al. 207* (NY).

WINDWARD ISLANDS. MARTINIQUE. Without locality, *Duss 589* (G, NY).

VENEZUELA. **ARAGUA:** Parque Nacional H. Pittier, *Onraedt 78.V.6480* (U). **MIRANDA:** Cerros del Bachiller near Cúpira, *Steyermark & Davidse 116821* (MO, U).

Neurolejeunea sastreana has in the past been confused with *N. breutelii*, from which it is immediately recognized by the large, thick-walled, papilla-like cell (= first tooth) protruding from the apex of the lobule. The two species are no doubt closely related as is indicated by the occasional presence of a rudimentary papilla (up to 10 µm long) in *N. breutelii*. The ranges of the two species overlap in the West Indies but *N. sastreana* apparently has a much more restricted distribution. In Puerto Rico, for instance, *N. sastreana* has only been collected in the wet, eastern portion of the island (Luquillo Mts.), whereas *N. breutelii* occurs throughout the island.

Excluded Species

Neurolejeunea lechleri Stephani = *Lopholejeunea nigricans* (Lindenberg) Schiffner

Neurolejeunea portoricensis (Hampe & Gottsche) Stephani = *Physantholejeunea portoricensis* (Hampe & Gottsche) Schuster

BRACHIOLEJEUNINAE

Gradstein subtrib. nov.

Brachiolejeuneae subtribe Brachiolejeuninae Gradstein; Ptychanthoideae tribe Brachiolejeuneae van Slageren & Berendsen *in* Kruijt & Gradstein, Nova Hedwigia **43:** 306. 1986 p.p. Type. *Brachiolejeunea* (Spruce) Schiffn.

Stem epidermis cells colorless, thin-walled or somewhat thickened, distinctly larger than medullary cells; ventral merophyte 2–4(–8) cells wide. Leaf apex rounded or pointed, the margins entire or toothed. Median leaf cells isodiametrical or somewhat elongated, 25–40 µm in diameter, the walls with trigones, oil bodies homogeneous or segmented, usually numerous per cell; ocelli lacking. Underleaf base tristratose, rarely bistratose. Androecia with bracteoles present throughout the spike (limited to the base in *Symbiezidium*). Perianths 2–3(–5)-keeled, frequently toothed-ciliate above, lacking auricles.

Distribution. Mostly neotropical, a few species in the palaeotropics or in southern South America. The subtribe Brachiolejeuninae consists of seven genera (all of which occur in the neotropics): *Acanthocoleus*, *Blepharolejeunea*, *Brachiolejeunea*, *Dicranolejeunea*, *Lindigianthus*, *Odontolejeunea*, *Symbiezidium*.

The enlarged stem epidermis, the large subisodiametrical leaf cells with small trigones and usually many homogeneous or segmented oil bodies, the underleaves with arched insertions and tristratose bases, and the ciliate (more rarely entire) perianths are the main characters of this tribe.

16. **Symbiezidium** Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 402. 1877; Gradstein & van Beek, Beih. Nova Hedwigia **80:** 221. 1985; *Lejeunea* sect. *Phragmicomoideae* Gottsche et al., Syn. Hep. 310. 1845. Lectotype (Evans, 1907a). *Symbiezidium transversale* (Swartz) Trevisan.

Platylejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 130. 1893; *Lejeunea* subgen. *Platylejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 124. 1884 ("*Platy-lejeunea*"). Lectotype (Gradstein & van Beek, 1985). *Lejeunea taeniopsis Spruce* (= *Symbiezidium transversale* var. *hookerianum* (Gottsche) Gradstein & van Beek).

Plants usually large, up to 15 cm long × 2–5 mm wide, green to brown when alive, usually becoming somewhat darker in the dried condition, creeping to pendent. *Branching* sparse to irregularly pinnate, vegetative branches of the Lejeunea type or *Frullania*-type, short sexual branches of the *Lejeunea*-type, flagelliform branches lacking. *Stems* rigid, 0.15–0.3 mm in diam., epidermal cells rectangular, 2–3× broader and 1–1.2× higher than the medullary cells, dorsal epidermal cells as large as or slightly larger than ventral epidermal cells, all cell walls colorless and thickened, the outer epidermal wall ± evenly thickened, the inner cell walls with large, confluent trigones; ventral merophyte 4–8 cell rows wide. *Leaves* widely spreading, convex, little altered when dry, ovate-oblong to ligulate, at opposite sides of the stem often different in length, apex rounded to apiculate, sometimes recurved, margins entire or, rarely, toothed near apex (*Symbiezidium dentatum*), dorsal base usually auriculate, extending ± across the stem and attached to the stem by 2 or 4 (!) U-shaped cells (cross-section), ventral margin straight or concave, the keel very short and curved, making a wide angle with the ventral margin; leaf cells isodiametric-hexagonal, averaging 30–40 m, with triradiate trigones and one intermediate thickening on longer walls; oil bodies *Bazzania*-type; ocelli lacking. *Lobules* small, 1/10–1/4× leaf length, never reduced, hidden behind underleaves, strongly inflated and sac-like, free margin incurved, ± flattened towards apex, apex with a one-celled tooth or notched, hyaline papilla hidden on inner surface of the lobule proximal of the apex. *Underleaves* imbricate, large, (3–)4–10× stem width, apex rounded or truncate, margins entire, bases widely rounded, decurrent and with deeply arched insertion line, tristratose in cross section (insertion line shallowly curved and base bistratose in the African subgenus *Eosymbiezidium*), with 4–8 superior central cells; brown, adhesive rhizoid discs, consisting of coalesced, thick-walled rhizoids, produced in epiphyllous plants. *Androecia* on short-specialized or elongated branches, bracts much smaller than leaves, subequally bilobed, lobule hypostatic, underleaves limited to the base of the male spike; antheridia two per bract. *Gynoecia* on very short *Lejeunea*-type branches, hidden behind stem leaves, usually with one short pycnolejeuneoid innovation, occasionally innovation lacking; bracts in one series, suberect, much smaller than vegetative leaves, subequally bifid, apex of lobe and lobule rounded, keel long, rounded, without wing; bracteoles longer than underleaves, apex rounded or short bifid. *Perianths* small, subcylindrical, usually shorter than vegetative leaves, flattened, the ventral surface usually slightly inflated, with sharp lateral keels and 0–2 small ventral plicae, lateral keels ciliate-laciniate in the upper half, sometimes the keels almost smooth, ventral surface smooth or roughened by ciliae or laciniae, dorsal surface smooth (perianths entirely smooth in *Eosymbiezidium*). *Sporophyte*: seta articulate; spores with a complex ornamentation consisting of clustered verrucae and baculae, and rosettes (van Slageren, 1985: 269); otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution. *Symbiezidium* is an Afro-American genus with three species in the neotropics and one species, *S. madagascariense*, on Madagascar and the Seychelles. The latter species differs considerably from the neotropical species and has been placed in a separate subgenus *Eosymbiezidium* by Gradstein and van Beek (1985). In tropical America, species of *Symbiezidium* are very common epiphytes in virgin or degraded rain forests at rather low elevations. In more mesic areas, such as the Galapagos Islands (Gradstein & Weber, 1982), the genus is usually lacking.

Symbiezidium is a very well defined genus. Recent authors considered it an autonomous genus complex (Gradstein & van Beek, 1985) but in this treatment *Symbiezidium* is classified as the most primitive member of the Brachiolejeuninae. With other members of this subtribe it shares the presence of an enlarged epidermis, the large leaf cells with radiate trigones, the lack of ocelli, the flattened, ciliate perianths and the tristratose underleaf bases. *Symbiezidium* differs from all other genera of the Brachiolejeuninae by its specialized male spikes with reduced underleaves, its abbreviated gynoecial branches and by the innovations which are single and short, sterile or male, or are sometimes lacking. All of these characters are shared with *Stictolejeunea*. It would thus appear that *Symbiezidium* bears some affinity to members of the subtribe Stictolejeuninae and links the Brachiolejeuneae to that subtribe.

The neotropical species of *Symbiezidium* are recognized by their elongated, oblong leaves, the large underleaves (5–10× stem width) with deeply arched insertions, and the small, strongly inflated pouched lobules with incurved free margin, which are hidden behind the underleaves and ± devoid of teeth. In *Marchesinia brachiata*, which resembles *Symbiezidium* when sterile, the lobules are rather flat and distinctly toothed along the free margin (except when reduced). When fertile, *Symbiezidium* stands out by its almost sessile, ciliate-laciniate perianths, inserted on a very short branch and partially or entirely hidden behind the vegetative leaves. In some populations of *S. transversale* var. *transversale*, however, perianth keels may be almost smooth (e.g. Nicaragua, *Proctor et al. 27220*). Except for *S. dentatum*, the neotropical species of *Symbiezidium* are difficult to identify when mature perianths are lacking.

Key to the Species of *Symbiezidium*

1. Leaf apex denticulate; Pacific coast of Colombia and northern Ecuador. . . . . 2. *S. dentatum*.
1. Leaf apex entire (rounded or apiculate); throughout tropical America.
    2. Plants 2–2.5(–3) mm wide; ventral surface of perianth rough due to short spines, cilia or laciniae distributed randomly as well as (sometimes) in 1–2 rows; in rain forests up to 2800 m. . . . . 1. *S. barbiflorum*.
    2. Plants 2.5–5 mm wide; ventral surface of perianth smooth or with laciniae arranged in 1–2 rows (never randomly); in rain forests up to 1700 m. . . . . 3. *S. transversale*.

1. Symbiezidium barbiflorum (Lindenberg & Gottsche) Evans, Bull. Torrey Bot. Club 34: 540, Pl. 31. 1908; Gradstein & van Beek, Beih. Nova Hedwigia 80: 239. 1985; *Lejeunea barbiflora* Lindenberg & Gottsche, Linnaea 24: 630. 1851. Type. Suriname. Paramaribo, "in ramis *Psidii*," *Kegel s.n.* (isotype, BM).

Lejeunea barbiflora Lindenberg & Gottsche var. *depauperata* Lindenberg & Gottsche, Linnaea **24:** 630. 1851. Type. Suriname. Paramaribo, "oude rijweg," *Kegel s.n.* (isotype, GOET).

Lejeunea transversalis (Swartz) Nees var. *fluminensis* Gottsche, Syn. Hep. 311. 1845. Type. Brazil. Rio de Janeiro, *unknown collector* (isotype, S).

Lejeunea hobsoniana var. *confertior* Gottsche et al., Syn. Hep. 748. 1847. Type (Gradstein & van Beek, 1985). Mexico. Veracruz: Hacienda de Mirador, *Liebmann 372b* (lectotype, C).

Lejeunea pogonoptera Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 128. 1884; *Symbiezidium pogonopterum* (Spruce) Stephani, Spec. Hep. **5:** 103. 1912. Type (Gradstein & van Beek, 1985). Brazil. Pará: Caripi, *Spruce L523* (lectotype, MANCH; isolectotype, G).

Lejeunea setosa Stephani, Hedwigia **29:** 14. 1890; *Symbiezidium setosum* (Stephani) Stephani, Spec. Hep. **5:** 104. 1912. Type. Mexico. Hacienda de Jovo, *Liebmann s.n.*

FIG. 41. Distribution of *Symbiezidium barbiflorum* (triangles) and *S. dentatum* (dots).

(holotype, G; isotype, C, W).

Platylejeunea kroneana Stephani, Hedwigia **35:** 117. 1896; *Symbiezidium kroneanum* (Stephani) Stephani, Spec. Hep. **5:** 102. 1912. Type. Brazil. St. Catarina: *Krone s.n.* (holotype, G; isotypes, MANCH, YU).

Monoicous. *Plants* relatively small, 1.5–4 cm long x 2–3 mm wide, green to brown, creeping. *Stems* 0,15–0.2 mm in diam., in cross section with 10–15 epidermal cells surrounding more numerous, smaller medullary cells; ventral merophyte four cell rows wide. *Leaves* ovate to ovate-oblong, up to 1.6 x 1.1 mm, apex rounded or apiculate, margins entire; median cells 30–40 μm in diam., trigones 8–12 μm in diam., intermediate thickenings 0–2 per cell; oil bodies homogeneous or, rarely, with a few septations, *Bazzania*-type, ca. 4–7 per cell, ellipsoid, 10–20 x 4–6 μm. *Lobules* as in the genus, up to 1/5(–1/4)x leaf length. *Underleaves* imbricate, broadly ovate to reniform, 0.5–1 mm long, up to 1.5 mm wide, (3–)4–8x stem width. *Androecia* on short-specialized branches or on innovations, bracts in 4–10 series. *Gynoecia* on a very short branch, with or without one short, vegetative or male innovation, bracts and bracteoles as in the genus. *Perianths* ventral surface weakly or strongly "roughened" by short spines, cilia or laciniae which are distributed randomly and sometimes also in 1–2 rows. *Sporophyte* as in the genus.

Terpenoids: bicyclogermacrene, sesquiterpene-lactone and various sesquiterpene acetates have been detected as major components; the chemical constitution of this species is variable (Gradstein et al., 1985).

Illustration. Evans, Bull. Torrey Bot. Club **34:** 567. 1908. Gradstein and van Beek, Beih. Nova Hedwigia **80:** 232-233, Figs. 2, 3. 1985.

Distribution (Fig. 41). Central America, the West Indies, northern South America, and SE Brazil, from sea level up to 2800 m in the Venezuelan Andes. *Symbiezidium barbiflorum* is the most widely distributed species of the genus and the only one occurring in SE Brazil. It grows in primary and secondary rain forests on trunks, branches, twigs, decaying wood, and occasionally on living leaves.

Selected specimens examined. MEXICO. CHIAPAS: Lagunas de Montebello, *Eggers & Frahm 922447* (U); Lacandon forest reserve, near Chajul Biological Station, *Gradstein 8091* (U).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley 55553* (S), *55337, 55623* (US).

BELIZE. Punta Gorda, *unknown collector* (hb. Fulford).

NICARAGUA. CHONTALES: near La Gateada, on road to Nueva Guinea, *Stevens 2862c* (MO, U).

COSTA RICA. ALAJUELA: Los Angeles de San Ramon, *Tonduz 13613* (NY). San Domingo, *Tonduz s.n.* (G,. NY, YU). Cocos I., *Weber 550c, 561* (COLO), *Gómez 17983, 18022* (MO, U).

PANAMA. PANAMÁ: Barro Colorado I., *Salazar 4375* (PMA, U), *Chung & Aranda 237* (NY).

CUBA. ORIENTE: Baracoa, *Pócs & Reyes 9065* (HAC); Sierra Maestra, *Pócs & Duany 9079* (HAC); El Yunque, *Underwood & Earle 316, 356* (NY, YU). VILLA CLARA: Sierra de Escambray, *Pócs & Borhidi 9004* (HAC).

HAITI. Summit of Haut Piton, *Leonard 15153* (NY); Massif de la Hotte, *Buck 9138* (NY).

JAMAICA. Mt. Diabolo, *Maxon 2223* (US, YU).

PUERTO RICO. Luquillo Mts., *Heller 779, 797* (NY); Maricao, *Pagán 226a* (HAC, NY).

WINDWARD ISLANDS. GUADELOUPE. Vieux Port, *Duss 10, 39, 301* (NY). **MARTINIQUE.** *Hahn s.n.* (NY); Mt. Pelée, *Duss 204, 343, 1060 (NY).*

COLOMBIA. CAUCA: Mun. Mosquera, *Linares 3, 23, 49, 72* (COL). HUILA: San Agustin, *Bischler 609* (COL, PC, U). RISARALDA: Marsella, *Gradstein 3606* (COL, U). MAGDALENA: Parque Nacional de Tayrona, *Diaz 4152* (COL); Río Buritaca, *Winkler 197* (COL).

VENEZUELA. AMAZONAS: Casiquiare, *Mägdefrau 205* (U). FALCÓN: Paraguaná Peninsula, *Griffin & Wingfield PV 1664* (U); Santa Ana, *Steyermark & Braun 94554* (US). ZULIA: Sierra de Perija, *Griffin 40, 54, 187, 271* (FLAS, U).

TRINIDAD. *Fendler s.n.* (NY); Toco Rd., *Britton et al. 1859* (NY, US); Ortoire river, *Britton 2573* (US).

GUYANA. Timehri, *Cornelissen & Gradstein C034* (U); Mabura Hill, *Cornelissen & ter Steege C.595, C.863* (U).

SURINAME. Jodensavanne, *Kegel s.n.* (W); Brownsberg, *Bekker 1063, 1150* (U); Coppename river, Raleighfalls, *Lanjouw 746B* (U); Kabalebo Dam project area, *Bekker 1635, 1672, 1717* (U).

FRENCH GUIANA. Charvein, *Benoist s.n.* (PC, NY); Montsinery, *Gradstein 5784* (U); Kourou, *Bekker 2011, 2014* (U); Saül, *Gradstein 6092, 6151* (U), *Cremers 6279* (CAY, U), *Montfoort & Ek 1550-1154* (U).

ECUADOR. CHIMBORAZO: *Spruce s.n.* (MANCH). ESMERALDAS: near San Lorenzo, *Boom 2573, 2621* (NY). PICHINCHA: Quito, *Jameson s.n.* (NY), NW of San Miguel de los Bancos, *Buck 10524* (NY).

PERU. LORETO: Maynas, between Río Napo and Río Amazonas, *Timme 4875* (NY, US). SAN MARTÍN: Río Huallaga, *Spruce 1531* (MANCH).

BRAZIL. AMAZONAS: Manaus, *Griffin et al. 1–61, 1–69* (FLAS, U); Rio Negro, *Spruce s.n.* (NY), Acanga, *Schuster 79–3–52* (NY), near junction Rio Negro-Rio Branco, *Schuster 79–2–32* (NY); Rio Uatumã, *Buck 3199* (NY). PERNAMBUCO: Rio Formoso, Res. Saltinho, *Cavalcanti Porto s.n.* (PC). RIO DE JANEIRO: *unknown collector* (S). ST.CATARINA: Type of *Symbiezidium kroneanum*. SÃO PAULO: Santos, Rio Branco, *Schiffner 1915, 1967, 2130* (S, W); Icapecirica, *Schiffner 1339, 1428* (W); Cananeia, *Vital 6682* (SP, U); Cardoso I., *Yano 466* (SP, U).

Symbiezidium barbiflorum is closely related to *S. transversale* and the two may be sometimes be difficult to distinguish. Usually, *S. barbiflorum* can be identified without much hesitation by its relatively small size (2–2.5 mm wide) and, in particular, by the perianths with spines, cilia or laciniae covering the ventral surface of the perianth in a random fashion. Perianths in *S. barbiflorum* vary, however, and forms with almost smooth ventral surfaces approach *S. transversale*. Brownish pigmented cells on the ventral perianth surface in these specimens may indicate the location of rudimentary cilia. For identification one should check as many perianths in the collection as possible. Careful searching may often reveal the presence of a few perianths with better developed ventral ornamentation.

Considerable variation is also seen in the size of lobules and underleaves of *Symbiezidium barbiflorum*. Reduced lobules and very narrow underleaves, only 3–4× stem width, were observed in plants growing in the shaded understory of lowland rain forest, e. g., on Barro Colorado I., Panama (*Chung & Aranda 237*) and at Mabura Hill, Guyana (leg. *Cornelissen & ter Steege*).

2. Symbiezidium dentatum Herzog, Feddes Repert. Sp. Nov. Regni Veg. **57:** 175. 1955; *Symbiezidium transversale* (Swartz) Trevisan subsp. *dentatum* (Herzog) Gradstein & van Beek, Beih. Nova Hedwigia **80:** 238. 1985. Type. Colombia. Valle: Dagua valley, Santa Rosa, along Río Caballate, *Killip 11544* (holotype, JE).

Autoicous or dioicous. *Plants* usually robust, 3–6 cm long × 3.5–4.5 mm wide, olive-green to brown, creeping to pendent. *Frullania*-type branches common, long and vegetative. *Stems* 0,2–0,3 mm in diam., in cross section with 20–25 epidermal cells surrounding 50–70 smaller medullary cells; ventral merophyte 6–8 cell rows wide. *Leaves* oblong to ligulate, 2–2.5 × 0.9–1.3 mm, 2–2.5 × longer than wide, apex broadly rounded, denticulate by 4–10 teeth, each tooth 1–3 cells long; median cells 30–45 µm in diam.; oil bodies not observed. *Lobules* globose, very small, 1/10× leaf length. *Underleaves* imbricate, elongate to broadly ovate to reniform, (3–)5–10× stem width, bases long decurrent. *Androecia*: on short or long branches, occasionally on innovations, bracts in 4–25 series. *Gynoecia* on a very short branch, with or without one short, vegetative or male innovation, bracts and bracteoles as in the genus. *Perianths* flat, oblong, narrowed to base, 1.2–1.8 × 0.6–0.7 mm, ca. 2–2.5× longer than wide, lateral keels finely ciliate in the upper half, cilia 5–35 cells long, uniseriate from a two cells wide base, ventral perianth surface smooth. *Sporophyte* not observed.

Illustration. Herzog, Feddes Repert. Sp. Nov. **57:** 173, Fig. 10f–l. 1955.

Distribution (Fig. 41). Pacific coast of Colombia and northern Ecuador, up to 800 m. *Symbiezidium dentatum* is a typical Chocó element and grows in the understory and canopy of wet, ± undisturbed lowland rain forest, on small tree trunks, twigs, lianas, rock, and on living leaves.

Specimens examined. COLOMBIA. CAUCA: Gorgona I., *Killip & Garcia 33144* (US), *Rudas & Aguirre 134* (COL). CHOCÓ: road Quibdo to Tutunendo, *Bischler 191* (COL, PC, U); Río Baudó near Estero de Medio, *Fuchs 22011* (US); road St. Cecilia–Tadó 40 km, *Gradstein 8719* (COL, U); Mun. Nuquí El Amargal 5 km SW of Arusí, *Gradstein s.n., 1992* (COL, U). VALLE: near Buenaventura, *Bischler 323, 472* (COL, PC, U).

ECUADOR. ESMERALDAS: Río San Miguel, *Harling 702, 4670* (S); near San Lorenzo, *Boom 2620* (NY). PICHINCHA: Forest Reserve 18 km NW of San Miguel de los Bancos, *Buck 10476, 10568* (NY, U).

Conservation. Because of its restricted occurrence in undisturbed Chocó rain forests and its very limited range, *Symbiezidium dentatum* is considered a threatened species (Gradstein, 1992c).

Symbiezidium dentatum resembles *S. transversale* var. *transversale* by its smooth perianth surfaces, but is readily recognized by its denticulate leaf apices. As the difference between the two taxa is based on only one morphological character (plus geography), Gradstein and van Beek (1985) treated *Symbiezidium dentatum* as a subspecies of *S. transversale*. In this treatment, however, I have decided to accept *S. dentatum* as a good species, as it is the only neotropical taxon of *Symbiezidium* which can always be identified when sterile.

Symbiezidium dentatum is usually fertile and sex distribution is variable like in the other species of the genus. The majority of the species studied were dioicous and female, one was purely male and one was autoicous. The dioicous male plant had long male spikes whereas in the autoicous plant they were quite small and occurred on short, specialized branches or on short innovations.

3. **Symbiezidium transversale** (Swartz) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877; Gradstein & van Beek, Beih. Nova Hedwigia **80:** 231, Figs. 2-3. 1985.

Symbiezidium transversale is a variable species, which in the past has been described under many different names. Two varieties can be recognized (Gradstein & van Beek, 1985), based on differences in the mature perianths. Material without mature perianths cannot be identified at varietal level, including the following synonyms:

Symbiezidium subrotundum (Kunth) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877; *Jungermannia subrotunda* Kunth, Syn. Pl. Aequin.-Orb., Nov. 5, **1:** 41. 1822; *Lejeunea subrotunda* (Kunth) Hooker ex Gottsche, Lindenberg & Nees, Syn. Hep. 312. 1845. Type. Colombia. "Mt. Quindio, inter Ibagué et Carthago," *Humboldt & Bonpland s.n.* (holotype, BM; isotypes, MANCH, NY, S).

Symbiezidium cordistipulum Stephani, Spec. Hep. **5:** 101. 1912. Type. Costa Rica. Boruca, *Tonduz 15560* (holotype, G). A form with very large and longly decurrent underleaves.

Key to the Varieties of *Symbiezidium transversale*

1. Ventral surface of perianth ± smooth. . . . . 2a. *S. transversale* var. *transversale*.
1. Ventral surface of perianth with 1–2 rows of cilia or lacinia. . . . . . . 2b. *S. transversale* var. *hookerianum*.

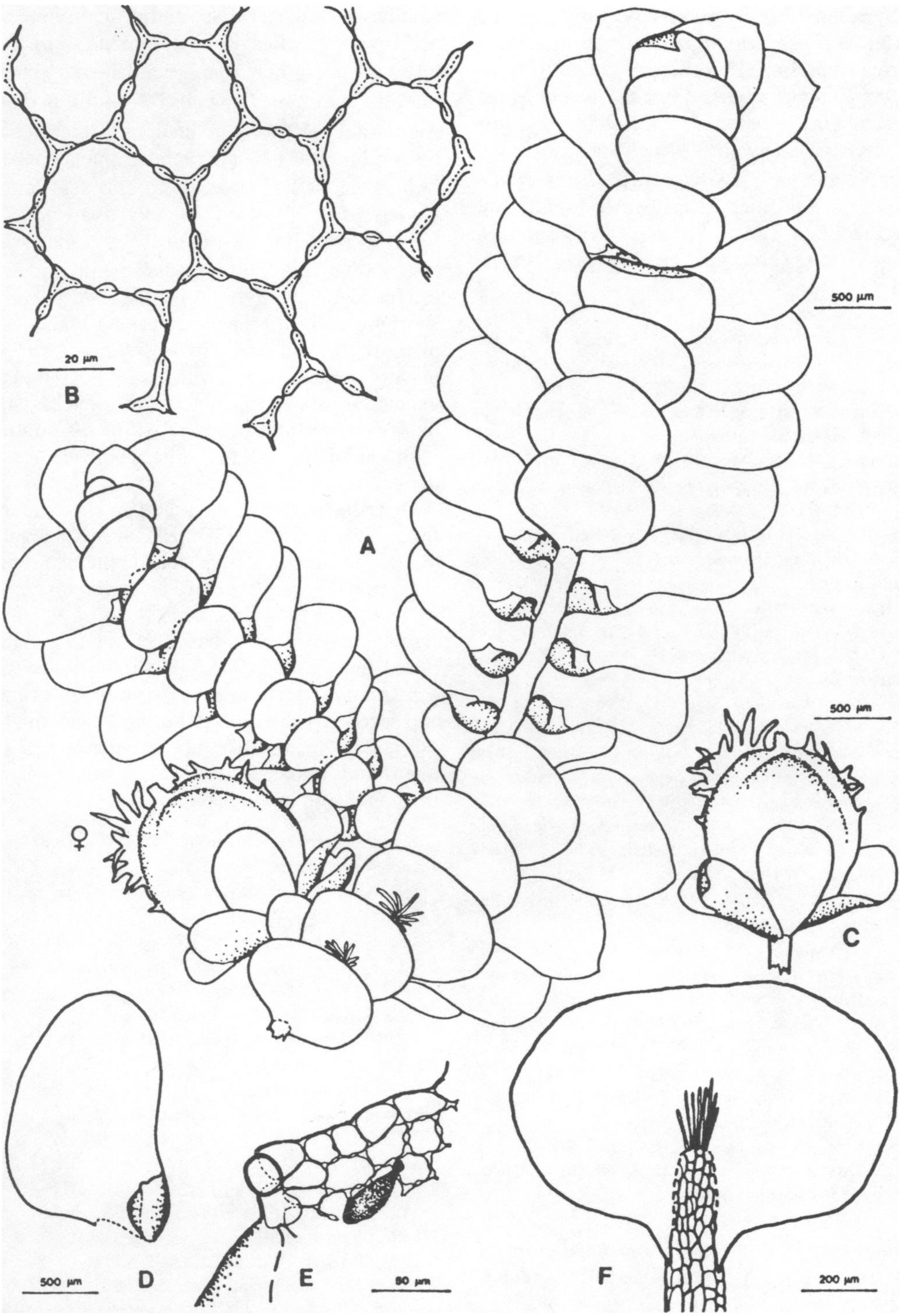

FIG. 42. *Symbiezidium transversale* var. *transversale*. **A.** Habit, with gynoecium. **B.** Leaf cells. **C.** Gynoecium. **D.** Leaf. **E.** Lobule apex. **F.** Underleaf. From Venezuela, *Griffin 54*.

2a. Symbiezidium transversale var. **transversale**; *Jungermannia transversalis* Swartz, Nova Gen. Spec. Pl. Prodr. 144. 1788; *Phragmicoma transversalis* (Swartz) Nees, Naturgesch. Eur. Leberm. **3:** 248. 1838; *Lejeunea transversalis* (Swartz) Nees, Syn. Hep. 310. 1845 “var. α”; *Platylejeunea transversalis* (Swartz) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893. Type. Jamaica. *Swartz s.n.* (holotype, S; isotypes, NY, S, STR). Fig. 42.

Jungermannia granulata Nees *in* Martius, Fl. Bras. **1 (1):** 352. 1833; *Lejeunea granulata* (Nees) Nees ex Mont., Ann. Sci. Nat., Bot. (sér. 2) **3:** 211. 1835; *Phragmicoma granulata* (Nees) Nees, Naturgesch. Eur. Leberm. **3:** 248. 1838; *Symbiezidium granulatum* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877. Type. Brazil. Amazon River, *Sellow s.n.* (holotype, STR; isotypes, BM, W).

Lejeunea hobsoniana Lindenberg, Syn. Hep. 313. 1845; *Symbiezidium hobsonianum* (Lindenberg) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877; *Platylejeunea hobsoniana* (Lindenberg) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893. Type. St. Vincent. Mt. St. Andrews, ex hb. Hooker (holotype, W; isotypes, BM, MANCH, NY, S).

Phragmicoma baccifera Taylor, London J. Bot. **5:** 387. 1846; *Marchesinia baccifera* (Taylor) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3 **(4):** 405. 1877; *Lejeunea baccifera* (Taylor) Stephani, Hedwigia **29:** 140. 1890; *Platylejeunea baccifera* (Taylor) Evans, Trans. Conn. Acad. **10:** 417. 1900; *Symbiezidium bacciferum* (Taylor) Stephani, Spec. Hep. **5:** 107. 1912. Type. “New Holland, Hook. Herb.” (holotype, BM; isotypes, BM, MANCH, NY, S, STR, W). Presumably mislabelled and of neotropical origin.

Lejeunea cryptocarpa Mitten *in* Seeman, Fl. Vitiensis 413. 1871; *Platylejeunea cryptocarpa* (Mitten) Stephani, Bull. Herb. Boissier **5:** 842. 1897; *Symbiezidium cryptocarpum* (Mitten) Stephani, Spec. Hep. **5:** 107. 1912. Type (Gradstein & van Beek 1985). “Hawai. Owyhee, *Menzies, on Leptogium* azureum” (lectotype, NY; isolectotypes, BM, NY, S). Presumably mislabelled and of neotropical origin.

Symbiezidium grandifolium Stephani, Spec. Hep. **5:** 101. 1912. Type (Gradstein & van Beek 1985). Costa Rica. *Tonduz 15671* (lectotype, G).

Monoicous or dioicous. *Plants* usually robust, 2–10 cm long × 2.5–5 mm wide, olive-green to yellow brown to blackish, creeping to pendent. *Stems* 0,15–0,3 mm in diam., in cross section with 12–25 epidermal cells surrounding 20–80 smaller medullary cells; ventral merophyte 4–8 cell rows wide. Leaves ovate-oblong to ligulate, up to 2.5 × 1.4 mm, apex rounded or apiculate, margins entire; median cells 30–46 µm in diam., trigones (7–)10–16 µm in diam., intermediate thickenings 0–3 per cell; oil bodies not observed. *Lobules* as in the genus, up to 1/4× leaf length. *Underleaves* imbricate, broadly ovate to reniform, 0.5–1.5 mm long, up to 1.7 mm wide, 5–10× stem width; brown adhesive rhizoid discs produced in epiphyllous plants. *Androecia* on short-specialized branches, on long branches or on the main stem, bracts in 8–15 series. *Gynoecia* on very short branches, with or without one short, vegetative innovation, bracts and bracteoles as in the genus. *Perianths* ventral surface smooth or with one or two isolated cilia. *Sporophyte* as in the genus.

Distribution. Throughout tropical America (except Mexico and SE Brazil), from sea level up to 1250 m. Records from outside the neotropics, e. g., from Hawaii (type of *Symbiezidium cryptocarpum*) and from Tasmania (type of *S. bacciferum*), are presumably based on erroneous labels (Gradstein & van Beek, 1985). *Symbiezidium transversale* var. *transversale* grows in primary and secondary lowland and submontane rain forests and in old groves (e.g., cacao plantations), on tree trunks, branches, twigs, decaying wood, and ocasionally on living leaves.

Selected specimens examined. BELIZE. Punta Gorda, *unknown collector* (CINC).

NICARAGUA. BLUEFIELDS: Cerro San Isidro, *Proctor 27220* (NY).

COSTA RICA. LIMÓN: Tortuguero, *Steere CR-32, CR-150, CR-173* (NY). Flumen Naranjo, *Tonduz s.n.* (NY). Cocos I., *Weber 549* (COLO), *Howell 222* (CAS).

PANAMA. *Mannee & Gorgone s.n.* (YU).

CUBA. HOLGUIN: *Reyes 968* (HAC). ORIENTE: El Yunque, *Underwood & Earle 1018* (MANCH, NY, YU).

JAMAICA. Dullwood, *Evans 505* (YU). Mansfield, *Maxon 967* (YU). Portland, *Griffin s.n.* (U).

PUERTO RICO. Luquillo Mts., *Heller 784, 1144, 1159, 1161* (NY, YU), El Yunque, *Evans 25, 67, 126* (NY, YU); Maricao, *Pagán 216* (HAC, NY, YU).

WINDWARD ISLANDS. ST. VINCENT. Type of *Symbiezidium hobsonianum*.

COLOMBIA. CHOCÓ: Quibdo, *Bischler 158, 163, 193* (COL, PC, U); Mun. Nuqui, El Amargal 5 km SW of Arusi, *Gradstein 8856* (COL, U). PUTUMAYO: near Puerto Asís, *King & Guevara C-1052* (COL). RISARALDA: Mun. San Antonio de Chami, Geguades, *Gradstein 8846* (COL, U).

COLOMBIA. CHOCÓ: Quibdo, *Bischler 158, 163, 193* (COL, PC, U); Mun. Nuqui, El Amargal 5 km SW of Arusi, *Gradstein 8856* (COL, U). PUTUMAYO: near Puerto Asís, *King & Guevara C-1052* (COL). RISARALDA: Mun. San Antonio de Chami, Geguades, *Gradstein 8846* (COL, U).

VENEZUELA. AMAZONIA: San Carlos del Río Negro, *Spruce s.n.* (MANCH, NY, W, YU). FALCÓN: Mirando, *Sipman 10915* (U).

TRINIDAD. Ortoire river, *Britton 2565a* (NY, YU); Aripo road, *Broadway 5418, 5867* (BM, NY, YU).

SURINAME. *Kegel s.n.* (GOET).

FRENCH GUIANA. *Sagot s.n.* (YU); Mts. de Kaw, *Gradstein 5911* (U); Itany river, Mt. Tortue, *Gradstein 5911* (U).

ECUADOR. Río Bombonasa, *Spruce L109* (MANCH).

PERU. LORETO :San Antonio, *Killip 29319* (NY). Middle Río Blanco, *Tessmann 3* (B, S).

BRAZIL. AMAPÁ: Mun. Macapá 156 NW of Porto Grande, *Mori et al. 17540* (NY). AMAZONAS: road Manaus-Itacoatiara, *Griffin et al. 516, 576, 1006* (FLAS); Rio Negro, Serra Curicuriari, *Schuster 79-15-742* (NY); Rio Uatumã, *Buck 3199* (NY).

BOLIVIA. BENI: Ballívian, Serranía del Pilón Lagas, *Gradstein 7102, 7190* (U).

Smooth perianth surfaces are characteristic of this variety. Occasionally, however, one or two cilia may be produced near the apex of the perianth. Plants with such perianths approach the next variety.

2b. Symbiezidium transversale var. **hookerianum** (Gottsche) Gradstein & van Beek, Beih. Nova Hedwigia **80:** 237, Fig. 2–3. 1985; *Lejeunea transversalis* (Swartz) Nees var. *hookeriana* Gottsche, Syn. Hep. 311. 1845. Lectotype (Gradstein & van Beek, 1985). Guadeloupe. "Hooker misit" (lectotype, STR; isolectotypes, NY, S).

Lejeunea vincentina Gottsche, Syn. Hep. 313. 1845; *Symbiezidium vincentinum* (Gottsche) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat. ser. 3, **4:** 403. 1877; *Platylejeunea vincentina* (Gottsche) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 131. 1893. Type. St. Vincent. Ex hb. *Hooker* (isotypes, G, W).

Lejeunea incrassatum Taylor ex Bescherelle & Spruce, Bull. Soc. Bot. France **36:** 179. 1899. Type. Guadeloupe. *Marie s.n.* (holotype, MANCH).

Lejeunea taeniopsis Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 126. 1884; *Symbiezidium taeniopsis* (Spruce) Fulford, Lloydia **5:** 302. 1942. Type (Gradstein & van Beek, 1985). Brazil. Pará: *Spruce L140* (lectotype, MANCH; isolectotype, YU).

Symbiezidium laceratum Evans, Bull. Torrey Bot. Club **35:** 386. 1908. Type. Haiti. Plaisance to Marmelade, *Nash 654* (holotype, YU; isotype, NY).

Ventral surface of perianth with cilia and/or lacinia in one or two rows.

Terpenoids: various diterpenes are major compounds of this taxon (Gradstein et al., 1985).

Illustration. Gradstein and van Beek, Beih. Nova Hedwigia **80:** 233, Fig. 3. 1985.

Distribution. Throughout tropical America (except Mexico and SE Brazil), from sea level up to 1700 m. *Symbiezidium transversale* var. *hookerianum* grows in similar habitats as var. *transversale*.

Selected specimens examined. BELIZE. Punta Gorda, *unknown collector* (hb. Fulford).

COSTA RICA. Cocos I., *Itow 7* (COLO),

CUBA. Sierra del Rosario, *Pócs & Reyes 9042* (HAC).

JAMAICA. Chopstown, *Bower s.n.* (MANCH).

HAITI. Type of *Symbiezidium laceratum*.

PUERTO RICO. Maricao, *Págan 226a* (HAC, NY); La Mina, *Fulford et al. 282, 291* (hb. Fulford).

WINDWARD ISLANDS. ST. KITT'S. Molyneaux Castle, *Britton & Cowell 689* (NY). **GUADELOUPE.** *Husnot 226* (BM, L, MANCH). **DOMINICA.** *Elliot 2160* (YU). **MARTINIQUE.** *Duss 269, 699* (NY). **ST. VINCENT.** Type of *Symbiezidium vincentinum*.

VENEZUELA. AMAZONAS: Casiquiare, *Mägdefrau 220, 228* (U); Cerro Neblina, Río Mawarinuma, *Halling 4198* (NY).

TRINIDAD. Ortoire river, *Britton 2573* (NY, YU).

GUYANA. Bartica, *Richards 170, 341* (YU); Mabura Hill, *Cornelissen & ter Steege C.677, C.872, C.889, C.919* (U); Upper Mazaruni, Jawalla, *Gradstein 4906* (U).

SURINAME. Grote Zwiebelzwamp, *Lanjouw & Lindeman 819* (U); Brownsberg, *van Slageren H401* (U).

FRENCH GUIANA. Near Cayenne, *Cremers 4259, 3899* (CAY, U).

PERU. SAN MARTÍN: road Tarapoto-Yurimaguas, *Frahm et al. 1394, 1396, 1685, 1731, 1799* (B, U); Rioja, *Frahm et al. 451, 1304* (B, U).

BRAZIL. PARÁ: Reserva Mocambo near Belém, *Lisboa 660, 663* (MG, U). AMAZONAS: road Manaus-Itacoatiara, *Griffin 184, 480, 485, 493, 505, 509* (FLAS, U).

The perianth ornamentation in *Symbiezidium transversale* var. *hookerianum* is somewhat variable. Plants with a single, short row of cilia near the perianth apex approach var. *transversale* and forms with one or two random cilia on the ventral surface, additional to the two rows, approach *S. barbiflorum*. The latter species may usually be separated by its smaller size and more abundant

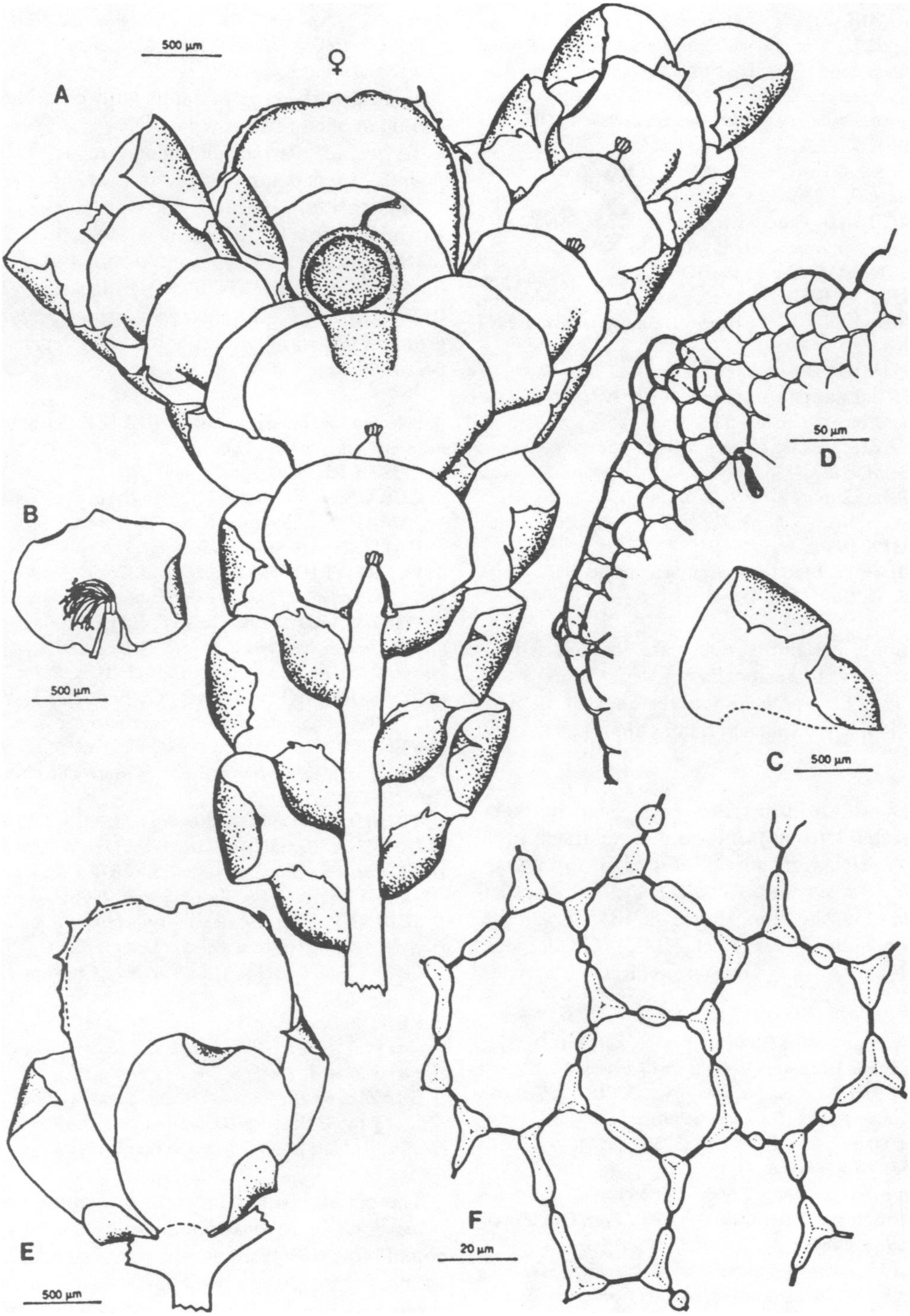

FIG. 43. *Lindigianthus cipaconeus.* **A.** Habit, with gynoecium. **B.** Underleaf. **C.** Leaf. **D.** Lobule free margin. **E.** Gynoecium. **F.** Leaf cells. From Ecuador, *Gradstein et al. 6724.*

production of random spines, cilia and/or lacinia on the ventral surface of the perianth. In case of doubt, several perianths per plant should be examined.

Excluded Species

(see Gradstein & van Beek, 1985: 245–247)

Symbiezidium calyculatum (Taylor) Trevisan = *Leucolejeunea clypeata* (Schweinitz) Evans

Symbiezidium tenuifolium (Taylor) Trevisan = *Omphalanthus filiformis* (Swartz) Nees

17. Lindigianthus Kruijt & Gradstein, Beih. Nova Hedwigia **80:** 165. 1985. Type. *Lindigianthus cipaconeus* (Gottsche) Kruijt & Gradstein. Genus named in honor of Alexander Lindig who made important collections in the Andes of Colombia and was the first to collect material of this genus.

For description see under the species.

Distribution (Fig. 44). *Lindigianthus* is a small, monotypic genus endemic to the Northern Andes (Colombia, Ecuador, N Peru) and Costa Rica.

The genus stands out by its homogeneous, *Massula*-type oil bodies, radiate trigones, robust stems with epidermal cells little higher than medullary cells, winged female bracts, and a flat perianth (like in *Marchesinia*) which lacks ventral or dorsal keels.

1. Lindigianthus cipaconeus (Gottsche) Kruijt & Gradstein, Beih. Nova Hedwigia **80:** 186, Fig. 1. 1985; *Lejeunea cipaconea* Gottsche, Ann. Sci. Nat. Paris, Bot. (sér. 5) **1:** 150. 1864; *Dicranolejeunea cipaconea* (Gottsche) Stephani, Hedwigia **35:** 78. 1896. Type. Colombia ("Nova Granata"). *Lindig s.n.* (lectotype, G). Fig. 43.

Dicranolejeunea circinnata (Spruce) Stephani. Spec. Hep. **5:** 159. 1912; *Lejeunea circinnata* Spruce, Trans. Proc. Bot. Soc. Edinburgh **15:** 141. 1884. Type. Ecuador. Mt. Tunguragua, 2600 m, *Spruce s.n.* (holotype, MANCH).

Dicranolejeunea jelskii (Loitlesberger) Stephani, Spec. Hep. **5:** 159. 1912; *Lejeunea jelskii* Loitlesberger *in* Szyszylowicz, Diss. Cl. Math.-Phys. Acad. Litt. Cracow **29:** 234. 1894. Type. Peru. *Jelski 522* (G, U, W).

Dioicous. *Plants* usually rather robust, to 10 cm long × 1.5–2.5 mm wide, glossy brown, creeping, usually forming mats. *Branching Lejeunea*-type or *Frullania*-type, irregular, flagelliform branches lacking. *Stems* 0.15–0.35 mm in diam., somewhat flattened, in cross section composed of 10–17 slightly thickwalled epidermal cells surrounding 36–66 smaller, ± thinwalled medullary cells, all cell walls colorless; ventral merophyte four cell rows wide. *Leaves* imbricate, when wet widely spreading with broadly recurved apex, when dry leaf apex more strongly recurved-inrolled, enveloping the underleaves, dorsal lobe ovate, 1.2–1.4 × 1 mm, apex acute, margins entire or toothed near apex with 1-4 teeth, ventral margin forming a wide angle of ca. 160° with the keel; median cells subisodiametrical, averaging 25–35 µm in diam., with radiate trigones and an occasional intermediate thickening on longer cell walls; oil bodies small, homogeneous, *Massula*-type, ellipsoid, 10–15(–25) per cell; ocelli lacking. *Lobules* triangular, ca. 1/3× lobe length, rarely reduced, keel arched, free margin with two inflexed teeth, the teeth 2–4 cells long, first tooth longer than second tooth; hyaline papilla located 3–4 cells below the first tooth on the inner surface of the lobule. *Underleaves* strongly imbricate, broadly ovate to reniform, 0.45–0.75 × 0,8–1.3 mm, ca. 4× stem width, apex rounded, margins entire, plane or somewhat recurved, bases broadly rounded, insertion line arched, 0.15–0.2 mm deep; underleaf base at rhizoid disc tri-stratose, in cross section with four superior central cells; rhizoids rarely produced. *Androecia* on an elongated *Lejeunea*-type branch, bracts in ca. 10 series, slightly smaller than leaves, lobule about half the size of the lobe, epistatic, underleaves present throughout; bracteoles present throughout the spike; antheridia two per bract. *Gynoecia* with two pycnolejeuneoid innovations, bracts in one series, narrowly winged along the keel, lobe acute, entire or toothed, lobule large, ca. 1/2–3/4× lobe lenght, acute, lobule and wing partly inserted on the innovation; bracteoles orbicular to elongated, apex rounded, entire or toothed. *Perianths* oblong-lingulate, up to 2.5 mm long, exserted to 1/2, sometimes stalked, flattened, with two sharp lateral keels only, the dorsal and ventral surfaces smooth or slightly furrowed, the lateral keels entire or with a few (up to 3 cells long) obtuse teeth on a wing of one row of cells wide; beak lacking. *Sporophyte*: seta articulate; spores with

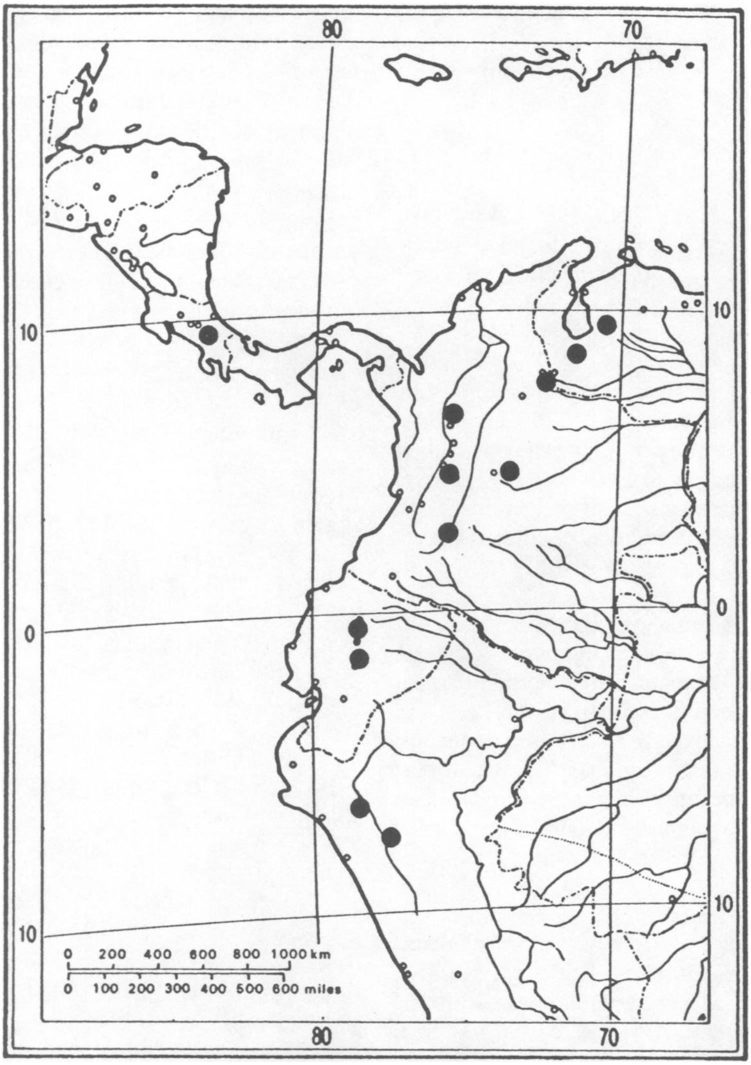

FIG. 44. Distribution of *Lindigianthus cipaconeus*.

rudimentary rosettes; otherwise as in the tribe. *Vegetative reproduction* not observed.

Terpenoids: the species is rich in sesquiterpenoids and diterpenoids; the major components are two unidentified oxygenated sesquiterpenoids and probably a diterpene hydrocarbon (Gradstein et al., 1981).

Distribution (Fig. 44). Costa Rica, Colombia, Ecuador, Peru. *Lindigianthus cipaconeus* occurs in montane and subalpine scrub and lower páramos in the northern Andes, at altitudes of ca. 2000–3500 m. It prefers partially shaded, moist locations and grows on bark, humose soil, and on litter. The author has found *L. cipaconeus* several times at the edges of forests and in bogs, on litter under shrubs and between the rosette leaves of tree fern species of the genus *Blechnum* (*Lomaria*).

Specimens examined. COSTA RICA. Parque Nacional Chirripó, Fila del Cementerio de la Máquina, *Chaverri et al. 1018* (CR, U).

COLOMBIA. ANTIOQUIA: San Pedro, finca Montanita, *Onraedt 83A10307* (hb Onraedt, U). CUNDINAMARCA: Guásca, *Gradstein & Aguirre 3696* (ALTA, B, BC, COL, COLO, FLAS, G, H, MEXU, MICH, NY, PC, PRC, S, TNS, U). HUILA: E slope of Puracé, headwaters of Río Candelaria, *Aguirre & Gradstein 6503* (COL, U). TOLIMA: S slope of Mt. Tolima, *vanderHammen 3383* (COL, U); St. Isabel, Quebrada las Damas above El Orcharál, *Aguirre & Gradstein 1520* (BA, BM, COL, F, G, NY, PC, S, TNS, U).

VENEZUELA. MÉRIDA: Sierra Nevada Nat. Park, Estación La Aguada, *Schäfer-Verwimp 12318* (U). TACHIRA: Distr. Junín, páramo de Tamá, above Villa Páez, *Griffin et al. 826, 828* (FLAS, U). TRUJILLO: Carache, páramo El Jabón, *Griffin & López PV-1269, 1442* (NY).

ECUADOR. PICHINCHA: near Río Cristal W of Lloa, *Gradstein et al. 6795* (U); old road Quito-S. Domingo, W of S. Juan, *Gradstein et al. 6724* (U).

PERU. SAN MARTÍN: road Chachapoyas-Moyabamba km 392, *Frahm et al. 1267* (B, U).

Lindigianthus cipaconeus is a rather robust, glossy brownish plant with strongly convex leaves and broadly recurved, toothed (rarely entire) leaf apices. The underleaves are very large and have deeply arched insertion lines, somewhat auriculate bases and entire margins. The leaf lobules are rather large, at least 1/3 the length of the lobe, and have two small teeth along the free margin. The cell walls of stems and leaves are very thin (except for the radiate trigones and small intermediate thickenings) and are colorless, without any trace of secondary pigmentation. The plants are unmistakable and cannot be confused with any other neotropical species of Lejeuneaceae.

18. Brachiolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 57. 1985; *Lejeunea* subgen. *Brachiolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 129. 1884. Lectotype (Evans, 1908). *Brachiolejeunea laxifolia* (Taylor) Schiffner. Genus named for its arm-like, forked branching.

Plants up to 6 cm long x 1–3 mm wide, green to olive when alive, usually brown when dry, creeping or ascending, often forming mats. *Branching Frullania*- or *Lejeunea*-type, the latter usually less common and short, branching pattern irregular or forked due to paired, floriferous innovations; flagelliform branches lacking. *Stems* with a hyalodermis, epidermal cells larger (at least the dorsal ones) and much thicker-walled than the medullary cells, dorsal epidermal cells larger than the ventral epidermal cells, all cell walls pale colored or the epidermal walls yellowish brown; ventral merophyte 4–6(–8) cell rows wide; dorsal stem surface sometimes with a low ridge ("lamellate paraphyllium"). *Leaves* suberect-convoluted when dry, wide spreading and often squarrose when moist, apex rounded to apiculate-short acuminate, margins entire, ventral margin often incurved; leaf cells elongated, trigones cordate, small to medium-sized, intermediate thickenings scarce or frequent, 0–1 on each longer cell wall, oil bodies homogeneous, *Massula*-type, ocelli lacking. *Lobules* 1/3–1/2x lobe length, never reduced, inflated along the keel, with 2–4(–10) teeth; hyaline papilla positioned on the inner side of the lobule 1–2 cells below the proximal base of the first tooth. *Underleaves* 2–5x stem width, usually orbicular, apex rounded to subtruncate, margins entire, bases decurrent and often folded inwards, insertion line deeply arched; underleaf base at the rhizoid disc tristratose and elongated-stalked, with four superior central cells. *Androecia* in paroicous plants located just below the gynoecia (to be seen on young innovations), in autoicous plants (sect. *Phyllorhizae*) on a short-specialized branch, bracts when paroicous resembling vegetative leaves and inconspicuous, when autoicous much smaller than leaves and strongly inflated with large lobule, lobule epistatic, underleaves present throughout; antheridia 1-2 per bract. *Gynoecia* on main stems or on branches, with 1–2 pycnolejeunoid subfloral innovations, bracts in one series, erect or obliquely spreading, somewhat smaller than leaves, with rounded to apiculate apex and entire or (rarely) toothed margins, the keel with or without wing, the wing not inserted on the associated innovation, lobules ca. 1/3–1/2x lobe length, never reduced; bracteoles longer than underleaves, undivided, margins plane or incurved, entire or slightly toothed. *Perianths* with 3(–4) keels, the keels smooth or dentate-laciniate. *Sporophyte*: seta articulate; spores without or with rudimentary rosettes; otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution. The genus *Brachiolejeunea* has six species, all of which occur in the New World: four in tropical America and two in temperate southern South America. One of the species, *B. phyllorhiza*, has also been reported from tropical Africa. The species grow on bark or rock in rather open situations, at high or low elevations, and are drought-tolerant.

Species of *Brachiolejeunea* are brownish plants with (1) predominantly *Frullania*-type branching, (2) densely imbricate and often squarose leaf lobes, which are strongly suberect-convoluted when dry and have entire margins, (3) lobules which are never reduced and usually bear 2–4 small teeth (up to 10 in *B. conduplicata*), (4) thin-walled, slightly elongated leaf cells with small cordate trigones and *Massula*-type oil bodies, (5) rounded underleaves with a deeply arched insertion line, (6) thick-walled epidermis cells surrounding smaller, thin-walled medullary cells, and (7) a 3-keeled perianth subtended by (1–)2 pycnolejeuneoid innovations and with one pair of small, winged bracts.

Brachiolejeunea was monographed by van Slageren (1985) who recognized four species. A fifth species, *B. phyllorhiza*, was added by Kruijt and Gradstein (1986) and in the present treatment a further species, *B. conduplicata* (Steph.) Gradst., is recognized. The latter two species stand out by their sharp, winged-ciliate perianth keels and short-specialized male branches and are therefore placed in a separate section, sect. *Phyllorhizae* Gradst.

Key to the Sections of *Brachiolejeunea*

1. Lateral perianth keels rounded, smooth; dorsal stem surface with or without a low longitudinal ridge; free margin of lobule plane; paroicous (or dioicous); male bracts inconspicuous, resembling leaves; tropical America (800–3500 m), southern South America. . . . . 1. *B.* sect. *Brachiolejeunea*.
1. Lateral perianth keels sharp, usually winged-ciliate; dorsal stem surface without ridge; free margin of lobule incurved or plane; autoicous; male bracts much smaller than leaves and strongly inflated; tropical America and tropical Africa, below 2000 m. . . . . 2. *B.* sect. *Phyllorhizae*.

1. Brachiolejeunea section Brachiolejeunea

Paroicous (or dioicous); vegetative branches *Frullania*-type, occasionally *Lejeunea*-type; dorsal stem surface with or without lamellate paraphyllium (ridge); leaves rather laxly imbricate, convex to somewhat squarrose when moist, ovate; leaf cells with small trigones and scarce to frequent intermediate thickenings; lobules never reduced, with 2–4 teeth; male bracts inconspicuous, resembling vegetative leaves, present on innovations below immature gynoecium, in 2–4 series; antheridium one per bract; female bracts and bracteoles with entire margins; perianth exserted to 1/3–2/3 of its length, with three keels, lateral keels rounded, smooth, dorsal keel lacking.

Distribution. Mountains of Tropical America (800–3500 m) and temperate portions of Chile and Argentina.

The treatment of sect. *Brachiolejeunea* largely follows van Slageren (1985).

Key to the Species of *Brachiolejeunea* sect. *Brachiolejeunea*

1. Lobule mostly with only two teeth; innovations 1–2; tropical America, 800–2000 m, uncommon. . . . . 3. *B. leiboldiana*.
1. Lobule with 3–4 teeth; innovations paired.
    2. Dorsal stem surface with a 1–4 cells high longitudinal ridge; tropical America, common above 2000 m . . . . 2. *B. laxifolia*.
    2. Ridge lacking; temperate southern South America.
        3. Lobule with four teeth; keel straight; Juan Fernandez Is. . . . . 1. *B. fernandeziana*.
        3. Lobule with three teeth; keel curved; southern Argentina, Chile (Valdivia to Tierra del Fuego). . . . . 4. *B. spruceana*.

1. Brachiolejeunea fernandeziana S. Arnell, Ark. Bot. 4: 18. 1959; van Slageren, Meded. Bot. Mus. Herb. Utrecht 544: 61. 1985. Type. Chile. Juan Fernandez Is.: Masatierra, El Yunque, *Kunkel H298* (holotype, S).

Paroicous. *Plants* up to 3 cm long × 1.3–2 mm wide, green to light brown when dry. *Stems* ca. 0.15 mm in diam., in cross section composed of ca. 15 epidermal cells surrounding ca. 25 medullary cells; ventral merophyte four cell rows wide; dorsal side of the stem without lamellate paraphyllium. *Leaves* laxly imbricate, not squarrose when moist, lobe broadly ovate, not falcate, 1–1.4 × 0.7–1 mm, apex narrowly obtuse-apiculate, ventral margin when spread out forming an angle of 160–180° with the keel; median cells 23–38 × 16–24 μm; oil bodies not observed. *Lobules* ovate, ca. 0.4–0.5 × 0.3 mm, 1/3–2/5× lobe length, apex short truncate, not continuing into the ventral leaf margin, keel straight, free margin plane, curved, with four teeth, teeth 2–3 cells long, upper cell inflexed. *Underleaves* distant to subimbricate, orbicular, 0.3–0.5 mm long, ca.

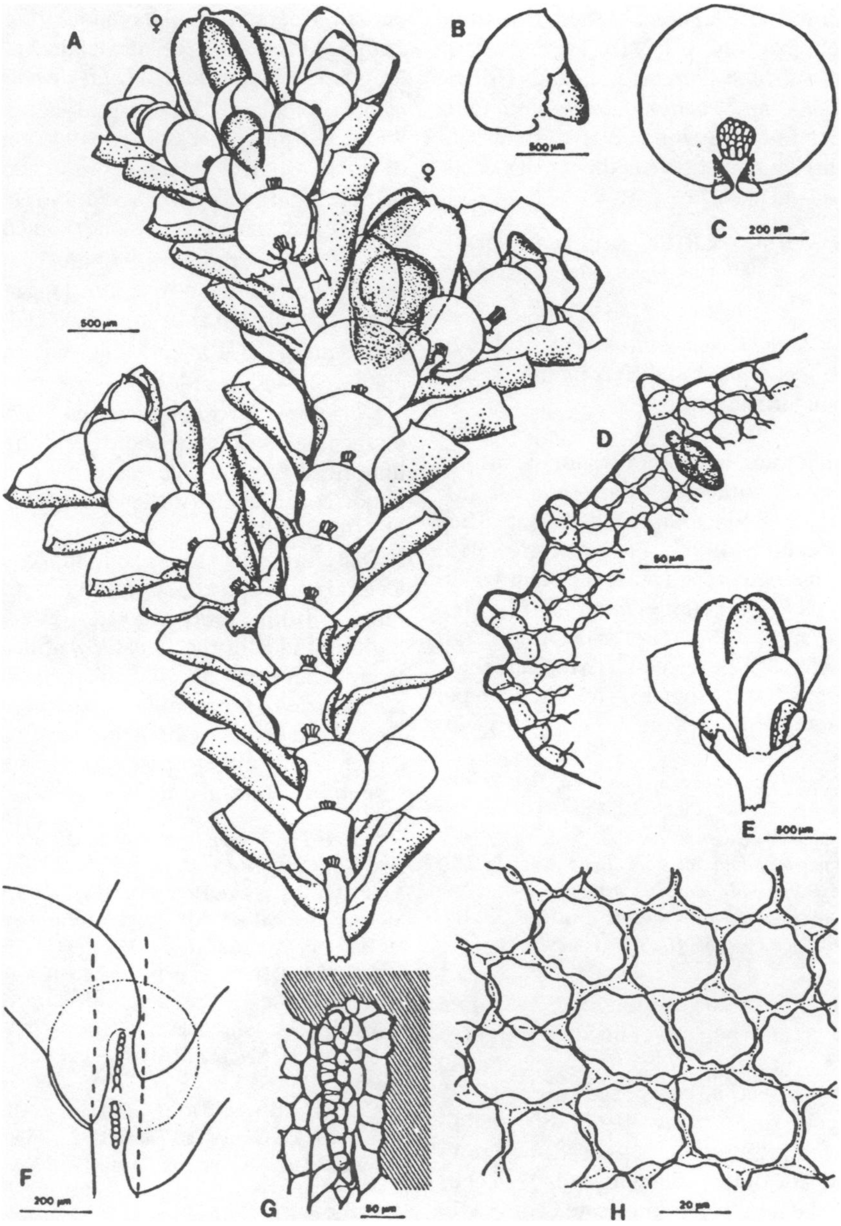

FIG. 45. *Brachiolejeunea laxifolia.* **A.** Habit, with two gynoecia. **B.** Leaf. **C.** Underleaf, showing rhizoid initial cells. **D.** Lobule free margin. **E.** Gynoecium; wing of bracts not shown **F.** Dorsal side of stem, showing two lamellate paraphyllia; positions of dorsal leaf bases indicate that merophytes are interlocking. **G.** Paraphyllium. **H.** Leaf cells. From Colombia, *Bischler 1723.*

2–3× stem width, margins plane, bases slightly folded, insertion line shallowly arched, ca. 0.1 mm deep. *Gynoecia* always with two innovations, bracts narrowly winged along the keel or without wing, lobule ca. 1/3–2/5× lobe length. *Perianths* up to 1.5 mm long, exserted to 1/2–2/3, beak 5–6 cells long. *Sporophyte*: elaters 270–420 µm long.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht 544: Pls. VII, VIII. 1985.

Distribution. Juan Fernandez Islands (Masatierra), 600–900 m. *Brachiolejeunea fernandeziana* has been found growing on fern fronds and bamboo at higher elevations on the moist eastern side of the island.

Specimen examined. **CHILE.** JUAN FERNANDEZ ISLAND: Masatierra, Valle Ingles, high central ridge, *Sparre H254* (S).

Brachiolejeunea fernandeziana is very closely related to *B. spruceana* but differs by the characters mentioned in the key.

2. Brachiolejeunea laxifolia (Taylor) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 63, Pls. VIII–X. 1985; *Phragmicoma laxifolia* Taylor, London J. Bot. **6:** 431. 1847; *Lejeunea laxifolia* (Taylor) Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 130. 1884. Type. Ecuador. Mt. Pichincha, *Jameson s.n.* (holotype, FH-TAYL; isotype, BM). Fig. 45.

Thysananthus mexicanus Taylor, London J. Bot. **7:** 199. 1848. Type. Ecuador. Mt. Pichincha, Feb 1847, *Jameson s.n.* (holotype, FH), *syn. nov.*

Brachiolejeunea mandoni Stephani, Spec. Hep. **5:** 121. 1912. Type. Bolivia. *Mandon 795* (holotype, G).

Brachiolejeunea uleana Stephani, Spec. Hep. **5:** 123. 1912. Type. Brazil. Sierra Itatiaia, *Ule 451* (holotype, G).

Paroicous. *Plants* 2–5 cm long × 1.7–2.5 mm wide, olive green when alive, becoming light to dark brown when dry. *Stems* 0.15–0.2 mm in diam., in cross section composed of ca. 15–25 epidermal cells surrounding 30–60(–80) medullary cells; ventral merophyte 4–6(–8) cell rows wide; dorsal side of the stem with a (1–)2–4 cells high ridge. *Leaves* laxly imbricate, convex to subsquarrose when moist, lobe ovate-falcate, 1–1.4 × 0.6–0.9 mm, apex narrowly obtuse to apiculate, ventral margin when spread out forming an angle of 90–125° with the keel; median cells 25–45 × 17–28 μm; oil bodies homogeneous, ellipsoid-fusiform, 5–7 μm long, 16–27 per cell, in stem cells smaller and more numerous. *Lobules* broadly ovate-triangular, ca. 0.3–0.45 mm long, 1/3–2/5× lobe length, apex oblique, short continuing into the ventral leaf margin, keel curved, free margin plane and straight, usually with 3–4 regularly spatiated teeth, teeth 2–3 cells long, upper cell inflexed. *Underleaves* subimbricate, orbicular, 0.5–0.7 mm long, ca. 3× stem width, margins plane or narrowly recurved, bases distinctly folded, insertion line deeply arched, 0.15–0.2 mm deep. *Gynoecia* with two innovations (exceptionally only one), bracts narrowly winged along the keel, lobule ca. 1/2× lobe length. *Perianths* up to 2 mm long, exserted to 1/2–2/3, beak 5–6 cells long. *Sporophyte*: spores rectangular, 70–105 μm long, without rosettes; elaters 320–470 μm long.

Chemistry: two sesquiterpene alcohols, three oxygenated sesquiterpenoids and the flavonoid luteolin-7-O-glucoside have been detected as major constituents of this species (Gradstein et al., 1981, 1988).

Distribution. Throughout the cordilleras of Central and tropical South America, at elevations ranging from (1500–)2000 to 3500 m; also at high altitudes in the Greater Antilles (Jamaica, Dominican Rep.) and in SE Brazil. *Brachiolejeunea laxifolia* is particularly common in the high Andes and grows on bark and rock, occasionally on leaves, in rather open habitats: forest edges, scrubby vegetations, etc.

Selected specimens examined. **MEXICO.** CHIAPAS: road San Cristobal-Ocosingo km 15–20, *Gradstein 8203, 8310* (U). FEDERAL DISTRICT: *Pringle 15338* (G, U); Morelos, *Schwab 58* (U); Popocatepetl, Amecameca, *den Held & van Rijn HH5* (U).

COSTA RICA. CARTAGO: Aledano, *Chaverri & Lopez 1519* (CR, U).

JAMAICA. Without loc., *Wilson s.n.* (NY).

DOMINICAN REPUBLIC. La Vega, Constanza, *Steere 22623* (NY), *Buck 7823* (NY).

COLOMBIA. ANTIOQUIA: Llanos de Quivá, *Onraedt 83A10461* (U); Boquerón, *Thiers 3823, 3860, 3861* (NY). BOYACÁ: Sierra Nevada de Cocuy, *Grubb & Guymer B3, B475, B379* (BM); road Sogamoso-Pajarita, *Bischler 1732* (COL, PC, U). CASANARE: Sácama, *Aguirre & Gradstein 3095* (COL, U). CAUCA: Volcán Puracé, *Cleef & Fernandez 506 (COL, U); valle de las Papas, Bischler 801* (COL, PC, U). CUNDINAMARCA: La Pena, *Lindig s.n.* (G); páramo de Palacio, *Cleef 3690, 3698, 3750, 3973* (COL, U); páramo de Choachi, *Mägdefrau 1429* (JE, M); páramo El Boquerón, *Troll 2176a, 2180* (JE, NY); páramo de Chisacá, *Bischler 2312, 2331* (COL, PC, U), *Gradstein & Aguirre 3642, 4617* (COL, U). MAGDALENA: Punta de Borrero, *Funck & Schlim 287* (NY). META: páramo de Sumapaz, *Cleef 942, 1170, 7801* (COL, U). NORTE DE SANTANDER: páramo de las Vegas, *Killip & Smith 15743* (JE, S). RISARALDA: St. Rosa de Cabal, *Gradstein & Aguirre 3570, 3589* (COL, U). TOLIMA: Nevada del Tolima, *vanderHammen & Jaramillo 3375* (COL, U).

VENEZUELA. LIBERTADOR: Colonia Tovar, *Steyermark et al. 127850* (MO, U). MÉRIDA: páramo de la Culata, *Griffin & Duarte 856* (FLAS, NY); La Mucuy, *Hertel & Oberwinkler 10245b* (JE); Sierra Nevada, *Onraedt 78V5903* (U). TACHIRA: El Zumbador, *Griffin 208* (FLAS, U). TRUJILLO: páramo El Jabón, *Griffin & Lopez 1463* (FLAS, NY).

ECUADOR. AZUAY: Cuenca, *Harling 2205* (JE, S). CARCHI: páramo El Angel, *Gradstein et al. 3389, 3413, 6666, 6687* (U); *Thiers 4414,4435* (NY). PICHINCHA: Quito, *Jameson several colls.* (BM, FH, G. NY); Mt. Guayrapata, *Spruce s.n.* (BM, G, MANCH, NY, S, W, YU); Pallatanga, *Spruce s.n.* (MANCH). TUNGURAHUA: Abitagua, *Spruce s.n.* (NY); Puela, *Spruce L164* (MANCH).

PERU. AMAZONAS: Leimebamba, *Frahm et al. 974* (B, G, U). CAJAMARCA: Contumazá, *Hegewald 7323* (U). CUZCO: near Paucartambo, *Inoue 34024* (TNS, U). JUNÍN: Huancayo, *Hegewald 9261* (U). SAN MARTÍN: Rioja, *Frahm et al. 657, 796, 1248* (B, G, U).

BRAZIL. MINAS GERAIS: Serra Itatiaia, *Schiffner 2269* (S), *Vital s.n.* (SP, U); Serra da Mantigueira, *Schäfer-Verwimp 12724* (U). RIO GRANDE DO SUL: Serra do Rocinha, *Baptista s.n.* (U). SANTA CATARINA: Serra Geral, *Ule 237* (B, G).

BOLIVIA. COCHABAMBA: Incacorral, *Herzog 4953* (L), *Gradstein 7550* (LPB, U); Coranital, *Herzog 3380, 3398* (JE); Incachaca, *Gradstein 7367, Bryoph. Neotrop. Exsicc. 228* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, XAL). LA PAZ: Unduavi, *Brooke 6842, 6863, 6871* (BM), *Rusby 3087, 3089* (MANCH, NY); Chuspipatta, *Schäfer-Verwimp 11915* (U). TARIJA: road Tarija-Entre Rios, headwaters Río Tambo and Río Posta, *Gradstein 7645, 7649* (LPB, U).

Brachiolejeunea laxifolia is recognized by its 3–4–dentate lobule, the distinct longitudinal ridge or "lamellate paraphyllium" on the dorsal side of the stem (van Slageren & Gradstein, 1981), and the constant presence of two innovations. The species is paroicous but the androecia are easily overlooked as the male bracts are almost identical to vegetative leaves and the antheridia vanish as soon as the gynoecium matures. To observe the antheridia, leaves of young innovations should be examined.

The species is closely related to *B. leiboldiana* and the two may be confused. For differences see under the latter. *Brachiolejeunea laxifolia* may grow together with *Blepharolejeunea securifolia* and *B. incongrua*, which are habitually rather similar but have a very different lobule. *Blepharolejeunea incongrua* also has a very characteristic, short obconical brownish perianth with sharp lateral keels. The perianth of *B. securifolia*, however, is almost identical to that of *B. laxifolia*. Differences between the two species are discussed under *Blepharolejeunea securifolia*.

Brachiolejeunea laxifolia varies somewhat in size and, as in many other liverwort species, plants tend to become bigger with increasing altitude. Innovations are normally paired but single innovations have been observed in material from the Dominican Republic (*Buck 7823*).

3. Brachiolejeunea leiboldiana (Gottsche & Lindenberg) Schiffner, Hedwigia **33:** 182. 1894; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 69. 1985; *Phragmicoma leiboldiana* Gottsche & Lindenberg, Syn. Hep. 296. 1845; *Lejeunea leiboldiana* (Gottsche & Lindenberg) Stephani, Hedwigia **29:** 134. 1890. Type. Mexico. *Leibold s.n.* (holotype, W; isotypes, G, S).

Brachiolejeunea mamillata Stephani, Spec. Hep. **5:** 121. 1912. Type. Mexico. Ex hb. *Nees* (holotype, G).

Brachiolejeunea sulcata Evans ex Stephani, Spec. Hep. **6:** 382. 1923. Type. Jamaica. Cinchona, *Evans 406* (holotype, G).

Paroicous or dioicous(?). *Plants* up to 5 cm long × 1.4–2 mm wide, olive green when alive, becoming light to dark brown when dry. *Stems* 0.15–0.2 mm in diam., in cross section composed of ca. 12–20 epidermal cells surrounding 30–70 medullary cells; ventral merophyte four cell rows wide; dorsal side of the stem with a low, one cell high ridge. *Leaves* imbricate, squarrose when moist, lobe obovate-suborbicular, 1–1.4 × 0.8–1.4 mm, apex usually rounded, occasionally apiculate, ventral margin when spread out forming an angle of ca. 150° with the keel; median cells 30–50 × 20–35 µm; oil bodies homogeneous, ellipsoid-fusiform, 6–8 × 1.5–2.5 µm, 16–30 per cell. *Lobules* broad ovate-subquadrate, ca. 0.4–0.6 mm long, 1/3–1/2× lobe length, apex broad truncate, not continuing into the ventral leaf margin, keel curved, free margin plane and making a sharp angle at the location of the second tooth (as in *Blepharolejeunea*!), with two widely spatiated teeth along the truncate apex, occasionally a smal third tooth present (in a few leaves), teeth (1–)2–3 cells long, upper cell inflexed. *Underleaves* imbricate, ± orbicular, about 0.5–0.7

mm long, 3–4× stem width, margins plane or narrowly recurved, bases distinctly folded, insertion line deeply arched, 0.15–0.2 mm deep. *Gynoecia* with 1–2 innovations, bracts associated with innovation winged along the keel and with a large lobule ca. 1/2– lobe length, bracts not associated with innovation resembling vegetative leaves, without wing and with hardly modified lobule. *Perianths* up to 1.5 mm long, short exserted to 1/3, beak 2–4 cells long. *Sporophyte*: spores rectangular, 60–90 µm long, without rosettes; elaters 220–430 µm long.

Illustration. Van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 69, Pls. X–XII. 1985.

Distribution. Scattered throughout tropical America: Mexico, Jamaica, Colombia, Ecuador, SE Brazil, 800–1650 m. *Brachiolejeunea leiboldiana* grows on bark and rock at forest edges, in scrubby vegetations, in orchards and on roadside trees.

Selected specimens examined. MEXICO. CHIAPAS: near Pueblo Nuevo NE of Tuxtla-Gutiérrez, *Sharp et al. 4070* (TENN). OAXACA: ca. 70 km E of Oaxaca, *Sharp et al. 4633* (TENN).

JAMAICA. Type of *Brachiolejeunea sulcata.*

COLOMBIA. CALDAS: Chinchina, *Gradstein & Aguirre s.n.* (COL, U). CASANARE: *Aguirre & Gradstein 2956, 2995, 3097* (COL, U). RISARALDA: Lembo, *Gradstein & van Zanten 569* (COL, U); near Santa Rosa de Cabal, *Gradstein s.n.* (U).

ECUADOR. TUNGURAHUA: Baños, *Spruce s.n.* (MANCH).

BRAZIL. BAHIA: Serra de Agua de Rega, *Irwin et al. 31124* (U). MINAS GERAIS: Nova Lima, *Vital 8871* (JE, SP). SÃO PAULO: Apiahy, *Puiggari 664* (B, G).

Brachiolejeunea leiboldiana closely resembles *B. laxifolia* but grows at lower altitudes and has a ± truncate lobule with only 2 teeth (rarely 3), a lower ridge on the dorsal stem surface, and normally single instead of paired innovations. By its truncate lobule the species approaches *Blepharolejeunea* which, however, has very different lobule teeth, segmented oil bodies and lacks a paraphyllium.

4. **Brachiolejeunea spruceana** (Massalongo) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 73, Pls. XII, XIII. 1985; *Lejeunea spruceana* Massalongo, Nuovo Giorn. Bot. Ital. **17:** 246. 1885; *Phragmicoma spruceana* (Massalongo) Stephani, Hedwigia **28:** 168. 1889. Type. Argentina. Staten I., *Speggazini 132* (holotype, VER; isotypes, G, MANCH).

Paroicous. *Plants* up to 2.5 cm long × 1–1.8 mm wide, green to brown when dry. *Stems* ca. 0.1–0.18 mm in diam., in cross section composed of 12–17 epidermal cells surrounding 16–33 medullary cells; ventral merophyte four cell rows wide; dorsal side of the stem without lamellate paraphyllium. *Leaves* imbricate, strongly convex to squarrose when moist, lobe ovate-falcate, 0.6–1 × 0.5–0.8 mm, apex rounded, ventral margin when spread out forming an angle of 120–150° with the keel; median cells 22–40 × 13–33 µm; oil bodies not observed. *Lobules* broadly ovate-triangular, ca. 0.25–0.4 × 0.2–0.3 mm, about 1/2× lobe length, apex oblique to subtruncate, not continuing into the ventral leaf margin, keel curved, free margin plane, broadly arched, with three teeth, teeth 2–4 cells long, upper cell inflexed. *Underleaves* distant to subimbricate, suborbicular, 0.3–0.5 mm long, ca. 3× stem width, margins plane, bases slightly folded, insertion line shallowly arched, ca. 0.1 mm deep. *Gynoecia* always with two innovations, bracts without wing or, occasionally, narrowly winged along the keel, lobule ca. 1/2× lobe length. *Perianths* up to 1.2 mm long, exserted to 1/2, beak 5–8 cells long. *Sporophyte*: spores 45–80 µm long, with rudimentary rosettes; elaters 290–380 µm long.

Distribution. Chile (Valdivia to Tierra del Fuego), southern Argentina, at altitudes ranging from sea level to about 400 m (van Slageren, 1985). *Brachiolejeunea spruceana* has been found on bark and shrubs in the wet evergreen *Nothofagus* forest region.

Selected specimens examined. CHILE. AISEN: Playa Negra, *Drehwald P722, P724, P7265* (Hb. Drehwald); between Pto. Aisen and Pto. Chacabuco, *Drehwald P563* (Hb. Drehwald). CHILOE: Petrohue, *Hosseus 524* (JE). LLANQUIHUE: Calbuco, *Schwabe s.n.* (S); Puerto Varas, *Dusén s.n.* (NY). MAGELLANES: Groppler Bay, Douglas s.n. (YU); Lago San Raphael, *Bachman s.n.* (JE); Gray Harbour, *Cunningham s.n.* (NY).

ARGENTINA. Type of *Brachiolejeunea spruceana.*

2. Brachiolejeunea section Phyllorhizae Gradstein *sect. nov.*

A sect. *Brachiolejeunea* differt inflorescentia autoica, bracteis masculinis parvis, perianthiis cristatis. Type. *Brachiolejeunea phyllorhiza* (Nees) Kruijt & Gradstein.

Autoicous; vegetative branches *Frullania*-type only; dorsal stem surface without lamellate paraphyllium (ridge); leaves densely imbricate, squarrose when moist, suborbicular; leaf cells with minute trigones and ± without intermediate thickenings; lobules hidden behind the upcurved surface of the lobe, free margin involuted or plane, with (0–)2–10 teeth; male bracts conspicuous, much smaller and more strongly inflated than vegetative leaves, on short-specialized branches, in 5–10 series; antheridia two (?) per bract; female bracts and bracteoles with entire or slightly toothed margins; perianth immersed or exserted to 1/3 of its length, with 3(–4) keels, lateral keels sharp, dentate-ciliate or almost smooth, ventral keel broadly rounded, smooth, a small dorsal keel sometimes present.

Distribution. Tropical America and tropical Africa, below 2000 m.

Key to the Species of *Brachiolejeunea* sect. *Phyllorhizae*

1. Free margin of the lobule deeply involuted, strongly sinuate-undulate and with 3–10 irregular teeth (visible only after dissection); Guianas, below 300 m. 5. *B. conduplicata.*
1. Free margin of the lobule plane or involuted, not sinuate-undulate, with 0–2(–3) small teeth; throughout tropical America, above 300 m. . . . . . 6. *B. phyllorhiza.*

5. Brachiolejeunea conduplicata (Stephani) Gradstein *comb. nov.*; *Archilejeunea conduplicata* Stephani, Spec. Hep. **4:** 712. 1911. Type. Suriname. Ex hb. Flotow (holotype, G).

Autoicous. *Plants* 1.5–2.5 cm long × 1.5 mm wide, green, becoming olive brown when dry. *Stems* about 0.2 mm in diam., in cross section composed of 15–20 thick-walled epidermal cells with yellowish brown walls surrounding 4—50 colorless medullary cells. *Leaves* densely imbricate, deeply concave and squarrose when moist, lobe suborbicular, 1–1.5 mm long, apex broadly rounded, margins entire, ventral margin broadly upcurved, when spread out forming a wide angle with the keel and soon curving towards towards apex; median cells 35–50 × 25–30 µm; oil bodies not observed. *Lobules* broadly ovate, ca. 0.4–0.6 mm long, about 2/5x lobe length, never reduced, strongly inflated, apex oblique, continuing into the ventral margin of the lobe, keel ± curved, free margin deeply involuted in the upper half, the outline waving and undulate, irregularly toothed, with 3–4 conspicuous teeth (2–3 cells long) separated by lunulate sinuses and 3–6 additional 1-celled teeth (visible only upon dissection), the larger teeth variously pointing upwards or downwards. *Underleaves* imbricate, broadly ovate, ca. 0.4 × 0.7 mm, 3–4x stem width, margins narrowly recurved, bases not folded, insertion line arched. *Androecia* as in the section. *Gynoecia* with 1–2 innovations, bract lobe asymmetrically obovate-lanceolate, ca. 0.6 mm long, apex obtuse, margins entire and irregularly undulate, lobule ca. 1/4–1/3x lobe length, keel with a 2–5 cells wide wing in the lower half; bracteole margins entire, incurved and ± enveloping the ventral surface of the perianth. *Perianths* obovate, ca. 1 mm long, exserted to 1/3 or immersed, 3–4-keeled, dorsal surface deeply concave, without or with a low, sharp keel, lateral keels winged above and with 5–6 ciliate teeth up to 5 cells long, ventral keel broadly rounded, smooth or with an occasional tooth near apex; beak 3–4 cells long. *Sporophyte* not observed.

Illustration. Kruijt & Gradstein, Nova Hedwigia **43:** 303, Fig. 1s. 1986 (as *Brachiolejeunea phyllorhiza*).

Distribution. *Brachiolejeunea conduplicata* is a rare species, known only from lowland areas in the Guianas where it has been found in the canopy of mixed lowland rain forest and in orchards, together with *Archilejeunea auberiana*, *Frullanoides tristis* and *Lopholejeunea subfusca*.

Specimens examined. SURINAME. Without loc., *Curie s.n.* (BM, G, MANCH).

FRENCH GUIANA. Saül, *Gradstein 6188a* (U), *Montfoort s.n.*, 2 colls. (U).

Habitually, *Brachiolejeunea conduplicata* is similar to *B. phyllorhiza* and Kruijt and Gradstein (1986) considered the two conspecific. The deeply involute and undulate free lobule margin with numerous irregular teeth clearly separate *B. conduplicata* from *B. phyllorhiza*, however. There are 3–4 principal teeth, which are separated from each other by a lunulate sinus. Each principal tooth is associated with 1–3 accessory, small, one-celled teeth. The waving outline of the free margin is visible in surface view but the peculiar dentation can be observed only after dissection of the lobule.

6. Brachiolejeunea phyllorhiza (Nees) Kruijt & Gradstein, Nova Hedwigia **43:** 299. 1986; *Jungermannia phyllorhiza* Nees *in* Martius, Fl. Bras. **1 (1):** 348. 1833; *Lejeunea phyllorhiza* (Nees) Nees, Syn. Hep. 312. 1845; *Symbiezidium phyllorhizum* (Nees) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 402. 1877; *Dicranolejeunea phyllorhiza* (Nees) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893. Type. Brazil. "Flumen Amazonum," *Martius s.n.* (holotype, STR; isotypes, B, G, S, W).

Phragmicoma subcristata Lindenberg & Gottsche, Syn. Hep. 744. 1847; *Marchesinia subcristata* (Lindenberg & Gottsche) Kuntze, Revis. Gen. Pl. **2:** 837. 1891; Type. Mexico. Veracruz: Hacienda de Mirador, *Liebmann s.n.* (syntype, W-hb. Lindenberg 5970; isosyntypes, BM, S); Dos Puentes, *Liebmann s.n.* (syntype, W-hb. Lindenberg 5971).

Lejeunea glaziovii Bescherelle & Spruce, Bull. Soc. Bot. France **36:** 197. 1889. Type. Brazil. Rio de Janeiro, *Glaziou 7404* (holotype, MANCH; isotypes, BM, G, JE, NY, U).

Autoicous. *Plants* 1.5–4 cm long x 1–2.5 mm wide, green, yellow brown to brown when dry. *Stems* about 0.1–0.2 mm in diam., in cross section composed of 9–25 epidermal cells surrounding 25–70 medullary cells. *Leaves* normally densely imbricate, deeply concave and squarrose when moist with the lobe subvertical in position and somewhat clasping the stem, lobe suborbicular, 0.8–2 mm long, apex broadly rounded, sometimes short apiculate, margins entire or ± crenulate, ventral margin broadly upcurved, when spread out forming an angle of ca. 140–180° with the keel; median cells 35–50 x 25–32 μm; oil bodies homogeneous, ellipsoid-fusiform, 15–25 per cell. *Lobules* narrow oblong to broad obovate-triangular, 0.3–0.6 x 0.2–0.35 mm, about 1/3x lobe length, never reduced, inflated, apex oblique to truncate, not continuing into the ventral margin of the lobe, keel ± straight, free margin plane or incurved, sometimes waving, never undulate, in broad lobules making a sharp angle at the location of the second tooth (as in *B. leiboldiana*!), with 2(–3) widely spatiated teeth, teeth 1–3 cells long, ± inflexed, sometimes reduced. *Underleaves* imbricate, orbicular to broadly ovate, 0.3–0.6 x 0.4–0.8 mm, 3–5x stem width, apex rounded to truncate, margins narrowly recurved, rarely plane, bases decurrent and hardly folded, insertion line arched. *Gynoecia* with 1–2 innovations, bracts associated with innovations erect, obovate, shorter than perianth, apex acute or rounded, margins entire or weakly toothed, winged along the keel and with a large lobule ca. 1/3–1/2x lobe length, bracts not associated with innovation resembling vegetative leaves, without wing; bracteole margins plane or incurved, entire or slightly toothed. *Perianths* obovate, up to 1.2 mm long, short exserted to 1/3 or immersed, 3-keeled, dorsal surface concave or plane, the lateral keels usually winged and with 1–5 teeth or lacinia up to 15 cells long, rarely smooth, the broad ventral keel rounded or with two sharp, diverging, smooth or denticulate ridges; beak about four cells long. *Spores* rectangular, 50–110 μm long, with about eight rudimentary rosettes; elaters 220–430 μm long.

Flavonoids: 6-hydroxyluteolin-7-O-glucoside, luteolin-7-O-glucoside and luteolin as free aglycone (Gradstein et al., 1988).

Illustration. Kruijt & Gradstein, Nova Hedwigia **43:** 303, Fig. 1. 1986.

Distribution. Scattered throughout the dryer portions of tropical America: Central America, Greater Antilles, northern South America and southeastern Brazil. The species has not yet been recorded with certainty from the southeastern portion of the tropical Andes (Peru, Bolivia); material from that region identified as *Brachiolejeunea phyllorhiza* by Kruijt and Gradstein (1985) belongs to *Acanthocoleus*. The species has also been recorded from Africa by Kruijt and Gradstein but some of these specimens have also been misidentified. The type of *Dicranolejeunea lilleana* Pears. (East Africa), for example, is a species of *Acanthocoleus* and does not belong to *B. phyllorhiza*.

Brachiolejeunea phyllorhiza occurs at submontane and lower montane elevations, ranging from 300 to 2500 m, and grows on bark or rock in rather dry, open forests and plantations or on road-side trees. The species seems to be mostly lacking in rain forest areas.

Selected specimens examined. MEXICO. CHIAPAS: road San Cristobal–Ocosingo km 15, 2500 m., *Gradstein 8318* (U). **VERACRUZ:** Huatusco, *Liebmann s.n.* (G, S); Orizaba, *Düll 4/A52b* (JE).

GUATEMALA. RETALHULAE: vic. of San Felipe, *Maxon & Hay 3537, 3547, 3556* (US).

COSTA RICA. SAN JOSÉ: near Santa Maria de Dota, *Standley & Valerio 43411, 43436* (US); Alajuelita, *Tonduz 15556bis* (G); S. Vincente, *Tonduz 6238* (G).

CUBA. *Unknown collector* (G).

JAMAICA. *Ex hb Mitten* (BM, NY); St. Thomas, Farm Hill, *Orcutt 3451* (US).

HAITI. Dessalines, *Leonard 7869* (JE).

COLOMBIA. CUNDINAMARCA: Sasaima, *Onraedt 78A6432* (U). **TOLIMA:** Mariquita, *Linares & Gradstein 1419* (COL, U).

VENEZUELA. ARAGUA: Maracay, *Onraedt 78V4537* (JE, U). **LARA:** Río Clara, *Griffin et al. 278* (FLAS, U). **MÉRIDA:** *Moritz s.n.* (B, BM, G, L); Colegio La Salle, *Onraedt 78V: 4782, 4784, 4788, 4793, 5756* (U).

ECUADOR. PICHINCHA: Quito, *Jameson s.n.* (NY).

PERU. AMAZONAS: Prov. Chachapoyas, Molinopampa, *Wurdack 1518b* (US).

BRAZIL. BAHIA: Ilheùs, *Vital 8735* (SP, U). **MINAS GERAIS:** Caldas, *Mosén s.n.* (G, S, U). **RIO DE JANEIRO:** Glaziou 7404, 7406 (G). **SÃO PAULO:** Apiahy, *Puiggari 706, 1105* (G); Cerqueira Cesar, *Hoehne 427* (JE, S); Taipas, *Schiffner 1030* (W); Luis Antonio, *Vital 2745* (SP, U); Caraguatatuba, *Vital 8780* (SP, U).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Brachiolejeunea phyllorhiza is easily recognized by the densely imbricate and usually squarrose, suborbicular leaves with broadly rounded apex and with a very broad, somewhat truncate lobule with 2 widely spatiated, small teeth, by the large, rounded underleaves with recurved margins, by the 3-keeled perianths with winged-cilate keels, and by the short-specialized male branches which are usually present somewhat lower down on the female shoots. The species has long been associated with the genus *Dicranolejeunea* but Kruijt and Gradstein (1986) have pointed out that the species belongs in *Brachiolejeunea* because of its homogeneous oil bodies, winged female bracts with well-developed lobules, broad ventral merophyte and anatomical characteristics of the underleaf base. Moreover, the densely imbricate leaves of *B. phyllorhiza,* which are deeply concave and squarrose when moist, and the lack of any tendency for the lobules to become reduced, are unusual in *Dicranolejeunea* and are characteristic of *Brachiolejeunea* species. The species is also similar to *Brachiolejeunea* in chemical respects and elaborates the same kinds of luteolin-type flavonoids as *B. laxifolia* (Gradstein et al., 1987).

Brachiolejeunea phyllorhiza is habitually very similar to *B. conduplicata* and the two were considered conspecific by Kruijt and Gradstein (1986); differences are discussed under the latter. *Brachiolejeunea phyllorhiza* has also been confused with *Acanthocoleus aberrans* (e.g., Kruijt and Gradstein, 1986). The latter species is readily distinguished from *B. phyllorhiza* by (1) its narrower, two cells wide ventral merophyte, (2) much more spatiated, flat leaves (never squarrose) with usually apiculate or short acuminate apex, (3) smaller, less inflated lobules which are often reduced (never reduced in *Brachiolejeunea*!), (4) smaller underleaves with plane (never recurved) margins, and (5) female bracts without wings and with lobules reduced to a minute fold. Moreover, the oil bodies in *Acanthocoleus* are not homogeneous but finely segmented when fresh. The following binomina placed in synonymy of *Brachiolejeunea phyllorhiza* by Kruijt and Gradstein (1986) belong to *Acanthocoleus*:

Archilejeunea argentinica Herz. = *A. trigonus*
Archilejeunea trigona (Nees & Mont.) Steph. = *A. trigonus*
Dicranolejeunea lilleana Pears. = *A.* sp.
Dicranolejeunea pulchella Herz. = *A. aberrans* var. *aberrans*
Dicranolejeunea renauldii Steph. = *A. aberrans* var. *laevis*
Dicranolejeunea rotundata Evans = *A. aberrans* var. *laevis*
Dicranolejeunea setacea St. = *A. aberrans* var. *laevis*

Excluded Species

(see van Slageren, 1985: 118–126)

Brachiolejeunea acuta Winkler, Rev. Bryol. Lichénol. **35:** 316. 1968. Type. El Salvador. Santa Ana: Cerro Miramundo, *Winkler B/6/c/8* (hb. Winkler, n.v.) = ? The material has not been made available. Judging from the original description this species should be excluded from *Brachiolejeunea* (van Slageren, 1985: 124).

Brachiolejeunea cordistipula Stephani = *Hygrolejeunea catinulifera* (Spruce) Stephani

Brachiolejeunea paramicola Herzog = *Aureolejeunea paramicola* (Herzog) Schuster (*Omphalanthus paramicola* (Herzog) Gradstein)

19. Blepharolejeunea S. Arnell, Svensk Bot. Tidskr. **56:** 335. 1962; van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 113. 1985. Type. *Blepharolejeunea harlingii* S. Arnell (= *B. saccata* (Stephani) van Slageren & Kruijt). Genus named for the leaf margin cilia, resembling eye-lashes, of the type species.

Plants up to 3(–6) cm long x 0.8–2 mm wide, glossy green to brown to blackish, creeping, rarely ascending, forming small mats. *Branching Frullania- or Lejeunea*-type, branching pattern irregular or forked due to paired, floriferous innovations; flagelliform branches lacking. *Stems* with ± symmetric epidermis, epidermal cells slightly larger and usually somewhat thicker-walled than the medullary cells, all cell walls pale colored, without brownish pigmentation; ventral merophyte (2–)4 cell rows wide. *Leaves* convoluted and suberect to spreading when dry, wide spreading and convex when moist, not squarrose, lobe ovate-suborbicular, apex rounded, sometimes apiculate, margins entire or toothed; cells isodiametrical to slightly elongated, trigones simple triangular or cordate, intermediate thickenings scarce or frequent, 0–1 on each longer cell wall, oil bodies finely segmented, *Jungermannia*-type, soon becoming homogeneous and smooth upon degeneration; ocelli lacking. *Lobules* ovate-subrectanglar, ca. 1/2x lobe length, never reduced, inflated along the keel, flattened towards the free margin, apex truncate and with two dissimilar teeth, the second tooth usually more conspicuous than the first tooth: first tooth situated in the sinus, incurved and blunt, second tooth situated at lobule angle, sharp, pointing outwards; hyaline papilla positioned on the inner side of the lobule 1–2 cells below the proximal base of the first tooth. *Underleaves* ca. 3–6x stem width, suborbicular, plane, apex rounded, margins entire, bases cuneate or rounded, insertion line arched or almost straight; underleaf base at the rhizoid disc bistratose and short or tristratose and elongated-stalked, with four superior central cells. *Androecia* located below the gynoecia, bracts resembling vegetative leaves but slightly smaller, the lobule more strongly inflated, epistatic, underleaves present throughout; antheridia one per bract. *Gynoecia* on main stems or on branches, with two pycnolejeuneoid subfloral innovations, bracts in one series, slightly larger than leaves, with rounded to apiculate apex and entire or toothed margins, the keel with or without a small wing, the wing free or inserted on the associated innovation, lobule small or large, up to 2/3x lobe length, bracteoles longer than underleaves, undivided, entire. *Perianths* with three or five keels, the keels smooth or ciliate above. *Sporophyte*: seta articulate; spores with or without rosettes; otherwise as in the tribe. *Vegetative reproduction* not observed.

Distribution. The genus *Blepharolejeunea* is restricted to the New World and contains five species (van Slageren & Kruijt, 1985). Four species grow at montane elevations, above 1200 m, in tropical South and Central America; one species, *B. fuegiana*, occurs in southern Patagonia and Tierra del Fuego. The species grow on bark or rock in very moist environments: forest, scrub and páramos.

The species of *Blepharolejeunea* were originally placed in *Brachiolejeunea*, *Dicranolejeunea* or *Archilejeunea* and it is only recently that *Blepharolejeunea* was recognized as a natural genus. The distinctive character of the genus is the truncate apex of the lobule which bears two heteromorphic teeth, the first tooth blunt and usually incurved and inconspicuous, the second one sharp and clearly visible.

As the type species differs considerably from the other species of the genus, *Blepharolejeunea* is divided here in two subgenera following Schuster (1980). The treatment of the species largely follows van Slageren and Kruijt (1985).

Key to the Subgenera of *Blepharolejeunea*

1. Leaves falcate; leaf margin dentate to ciliate; ventral merophyte two cell rows wide; oil bodies homogeneous when fresh; in wet lower montane rain forests (1200–1850 m) . . . . 1. *B.* subgen. *Blepharolejeunea*.
1. Leaves spreading, not falcate; leaf margin entire; ventral merophyte four cells wide; oil bodies finely segmented when fresh (becoming homogeneous on age!); in tropical America usually above 2000 m. . . . . 2. *B.* subgen. *Oreolejeunea*.

1. Blepharolejeunea subgenus Blepharolejeunea

For description see under *B. saccata*.

Distribution. Tropical America. *Blepharolejeunea* subgen. *Blepharolejeunea* contains only one species, *B. saccata*.

1. **Blepharolejeunea saccata** (Stephani) van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 138. 1985; *Dicranolejeunea saccata* Stephani, Hedwigia **35:** 78. 1896. Type. Cuba. *Wright 1074* (holotype, G).

Blepharolejeunea harlingii S. Arnell, Svensk Bot. Tidskr. **56:** 335. 1962. Type. Ecuador. Napo-Pastaza: Mera, *Harling 3364* (holotype, S).

Dioicous ? (androecia not seen). *Plants* up to 2.5 cm long x 0.8–1.3 mm wide, green to brown when dry, creeping. *Branching Lejeunea-* or *Frullania*-type. *Stems* 0.1–0.13 mm in diam., in cross section composed of about 9–12 epidermal cells surrounding 15–20 slightly smaller medullary cells, all cells walls thin or slightly thickened; ventral merophyte two cell rows wide. *Leaves* laxly imbricate, obliquely spreading and strongly falcate, dorsal lobe obovate-falcate, 0.7–1 × 0.4–0.7 mm, sometimes squarrose, apex apiculate, plane or slightly recurved, dorsal margin dentate to ciliate, rarely subentire, with 1–7 teeth, the teeth 1–5 cells long, ventral margin entire or with one tooth, plane, forming a sharp angle of 90° with the keel; median cells 30–45 × 20–25 μm, trigones small, cordate to simple-triangular, oil bodies (B.M. Thiers, cited on specimen label) 10–20 per cell, elliptical, very small (less than 0.1× cell length), homogeneous. *Lobules* strongly inflated, ovate-subrectangular, 0.4–0.5 mm long, first tooth inflexed, 2–3 cells long, second tooth straight, 1–2 cells long, the teeth separated by 3–5 free margin cells, margin cells not larger than the inner cells of the lobule. *Underleaves* distant, ± orbicular, 0.2–0.35 mm long, 2.5× stem width, line of insertion almost straight. *Androecia* not observed. *Gynoecia*: bract lobes obovate, up to 0.8 mm long, weakly convex, apex rounded, upper margins dentate-ciliate with up to 8 teeth, lobule short, less than 1/3× lobe length, lobule apex truncate and with a small tooth, keel sharp, winged, the wing inserted on the innovation; bracteole obovate, shorter than bracts, 0.8 mm long, convex, apex truncate, margins plane. *Perianths* exserted to 1/5, obconical, with three keels: two sharp lateral keels and one broadly rounded ventral keel, the ventral keel smooth, the lateral keels winged and dentate-ciliate above; beak four cells long. *Sporophyte* not observed.

Illustration. van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 139, Fig. 9. 1985; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 232, Pl. IV. 1985.

Distribution. A rare species, known from a few localities in the Greater Antilles (Cuba, Dominica), Costa Rica, Colombia, Venezuela (Guayana) and Ecuador, at elevations between 1200–1850 m. *Blepharolejeunea saccata* grows on bark in very moist lower montane rain forest and scrub.

Specimens examined. COSTA RICA. San José: *Standley 57842* (JE).

CUBA. HOLGUIN : *Reyes 967* (HAC, U). Santiago de Cuba : Sierra Maestra, *Bisse & Leopold 19065/a2* (JE).

DOMINICA. *Elliot s.n.* (JE).

COLOMBIA. Antioquia: Mun. Guatapé, Vereda Santa Rita, *Thiers 4067 (NY).*

VENEZUELA. Bolivar: Cerro Guaiquinima, *Sipman 27171* (B, U).

ECUADOR. Type of *B. harlingii.*

Conservation. *Blepharolejeunea saccata* has a rather wide neotropical distribution but is rare throughout its range. There are only four recent records: from eastern Cuba (two collections), Colombia, and Venezuela. The species grows in undisturbed, wet montane rain forest and its continued existence may be threatened due to the rapid destruction of these forests in the neotropics. The species has been classified as "at risk" by Gradstein (1992c).

Blepharolejeunea saccata is the smallest species of the genus and very different from the species of the subgenus *Oreolejeunea* by its falcate-subsquarrose leaves with sharply dentate to ciliate margins, its very strongly inflated lobules, and by the ventral merophyte which is only two cell rows wide. The degree of dentation of the leaves varies considerably. The ventral margin of the leaf lobe stands at a sharp angle (ca. 90°) with

FIG. 46. Distribution of *Blepharolejeunea chimantaensis* (star) and *B. incongrua* (dots).

the keel; in the species of the subgen. *Oreolejeunea* the angle is usually much wider. Moreover, *B. saccata* has homogeneous oil bodies whereas in subgen. *Oreolejeunea* they are finely segmented in fresh material. As the segmented oil bodies in this genus degenerate rapidly and soon become homogeneous by fusion of the small droplets, oil bodies have to be checked within one or two days of collecting.

2. **Blepharolejeunea** subgenus **Oreolejeunea** Schuster, Phytologia **5:** 424. 1980; *Oreolejeunea* (Schuster) Schuster, Hep. Anth. N. America **4:** 762. 1980. Type. *Blepharolejeunea securifolia* (Stephani) Schuster (= *Oreolejeunea securifolia* (Stephani) Schuster). Subgenus named for its occurrence at high altitudes.

Stem with a four cell rows wide ventral merophyte; leaves obliquely to widely spreading, not falcate; leaf margins entire; ventral leaf margin usually forming a rather wide angle of 130-180° with the keel; oil bodies finely segmented, *Jungermannia*-type, becoming homogeneous upon degeneration; lobules narrowly inflated along the keel.

Distribution. Tropical America (1800–4500 m), southern Chile (below 500 m). In the neotropics *Blepharolejeunea* subgen. *Oreolejeunea* is restricted to rather open, cool, moist montane environments: edges of montane cloud forest and scrub, and alpine vegetations.

1. Keel ± straight; apical tooth of lobule (= second tooth) 6-10 cells long; perianth with two sharp ventral keels; southern Chile. . . . . .3. *B. fuegiana*.

Key to the Species of *Blepharolejeunea* subgen. *Oreolejeunea*

1. Keel arched; apical tooth shorter; perianth with one broadly rounded ventral keel; tropical America.
    2. First tooth of lobule consisting of one enlarged margin cell; female bracteole as long as the bracts, strongly concave; leaves strongly concave, the apex broadly rounded. Guayana Highlands of eastern

Venezuela. . . . . 2. *B. chimantaensis.*

2. First tooth of lobule 2–3 cells long, often incurved (when incurved, sometimes seemingly consisting of only one cell!); female bracteole shorter than the bracts, plane or concave above; leaves plane or concave, the apex narrowly rounded, obtuse or apiculate; Andes, Central America, SE Brazil.
    3. Lobule margin cells enlarged, the teeth separated from each other by 3–4 margin cells; perianth up to 1 mm long, obcuneate, lateral keels sharp, entire or winged-ciliate above; lobule of female bract less than 1/3× lobe length. . . . . 4. *B. incongrua.*
    3. Lobule margin cells not enlarged, the teeth separated from each other by 4–7 margin cells; perianth over 1 mm long, oblong, lateral keels rounded, entire; lobule of female bract 1/2–2/3× lobe length . . . . .5. *B. securifolia.*

2. Blepharolejeunea chimantaensis van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 126. 1985. Type. Venezuela. *Bolivar:* Macizo del Chimantá, W sector of Acopán-tepui, *Steyermark et al. 128593* (holotype, U; isotypes, FLAS, VEN).

Dioicous? (androecia not seen). *Plants* up to 2.5 cm long × 1,2 mm wide, glossy dark green to brown when dry, creeping. *Branching* mainly Frullania-type, occasionally *Lejeunea*-type. *Stems* ca. 0.15 mm in diam., in cross section composed of 12–13 thick-walled epidermal cells surrounding 17–20 somewhat smaller, thick-walled medullary cells; ventral merophyte (2–)4 cell rows wide. *Leaves* laxly imbricate, obliquely spreading, strongly convex, dorsal lobe suborbicular, 0.7–0.8 × 0.7 mm, apex rounded, hollow but not recurved, margins entire, ventral margin upcurved, when spread out forming an angle of 135–180° with the keel; median cells 30–45 × 25–35 μm, trigones well-developed, simple-triangular to slightly radiate, oil bodies not observed. *Lobules* broadly ovate-subrectangular, ca. 0.4 mm long, first and second teeth consisting of only cell, cell of first tooth large, rounded, second tooth cell small, the teeth separated by 3–4 free margin cells, margin cells not larger than the inner cells of the lobule. *Underleaves* subimbricate, orbicular, ca. 0.5 mm long, 5× stem width, line of insertion arched. *Androecia* not observed. *Gynoecia*: bract lobes obovate, up to 1.2 mm long, convex, apex rounded, margins entire, lobule small, 1/6–1/4× lobe length, with broadly rounded apex, keel rounded, without wing; bracteole suborbicular, almost as long as the bracts, strongly convex, apex rounded, margins not incurved. *Perianths* immature, resembling B. incongrua. *Sporophyte* not observed.

Illustration. van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 127, Figs. 4, 5. 1985; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 226, Pl. I. 1985.

Distribution (Fig. 46). Endemic to the eastern portion of the Guayana Highland (Macizo Chimantá). *Blepharolejeunea chimantaensis* was found at an altitude of 1850 m on wet, shaded banks of gullies in table mountain summit forest.

Specimens examined. Only known from the type.

Blepharolejeunea chimantaensis is closely related to *B. incongrua* from which it differs by its shorter first lobule tooth, consisting of only one cell, and the larger, strongly concave female bracteoles.

3. Blepharolejeunea fuegiana (Bescherelle & Massalongo) Gradstein, Beih. Nova Hedwigia **80:** 108. 1985; van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 130. 1985; *Lejeunea fuegiana* Bescherelle & Massalongo, Bull. Mens. Soc. Linn. Paris **79:** 638. 1886; *Archilejeunea fuegiana* (Bescherelle & Massalongo) Stephani, Spec. Hep. **4:** 714. 1911. Type. Chile. Tierra del Fuego: Cape Horn, *J.D. Hooker s.n.* (lectotype, VER; isolectotype, MANCH).

Archilejeunea magellanica Stephani, Spec. Hep. **4:** 716. 1911. Type. Chile. Tierra de Fuego: Borja Bay, *Vanadis expedition s.n.* (holotype, G).

Paroicous. *Plants* to 1.5 cm long × 1.1–1.7 mm wide, green to light brown when dry, creeping. *Branching Frullania*-type and *Lejeunea*-type. *Stems* 0.1–0.15 mm in diam., in cross section composed of about 10–12 thick-walled epidermal cells surrounding ca. 15 somewhat smaller, more or less thick-walled medullary cells; ventral merophyte (2–)4 cell rows wide. *Leaves* laxly imbricate, obliquely to widely spreading, dorsal lobe obovate-subfalcate, 0.7–1 × 0.6–0.8 mm, apex narrowly rounded, plane or recurved, margins entire, ventral margin forming a straight line or wide angle of 160–180° with the keel; median cells 15–30 × 10–20 µm, trigones well-developed, simple-triangular, occasionally confluent, oil bodies not observed. *Lobules* short rectangular, ca. 0.4 mm long, first tooth inflexed, 3–4 cells long, second tooth not incurved, (3–)5–6 cells long, the teeth separated by 3–5 free margin cells, margin cell not larger than the inner cells of the lobule. *Underleaves* not or barely imbricated, orbicular, 0.4–0.5 mm long, ca. 4× stem width, line of insertion shallowly curved. *Androecia* located below the gynoecium after 1–2 series of vegetative leaves, bracts in 1–3 series. *Gynoecia*: bract lobes olong-spathulate, up to 1.2 mm long, convex above, apex narrowly rounded, margins entire, lobule small, ca. 1/6× lobe length, apex rounded and usually with one short tooth, keel sharp, without or with a narrow wing; bracteole obovate-oblong, shorter than the bracts, up to 0.7 mm long, convex, apex truncate, margins plane. *Perianths* normally emergent to 1/4, sometimes stalked and more longly exserted, obovoid-oblong, with five sharp, equal-sized keels in the upper half: two lateral, two ventral, one dorsal; beak 4–5 cells long. *Sporophyte* not observed.

Illustration. van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 129–131, Figs. 5, 6. 1985; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 228, Pl. II. 1985.

Distribution. Southern Chile. *Blepharolejeunea fuegiana* is only known from the southern tip of Tierra del Fuego and from the southern Patagonian Channels, occurring at altitudes below 500 m. The species usually grows on bark, in Nothofagus forest or moorland; it has also been found growing on fronds of Hymenophyllaceae.

Specimens examined. CHILE. Magellan area, *unknown collector* (NY). Hermite I., *Hariot 77* (G, PC). Cape Horn, *unknown collector* (NY). Puerto Arturo, Olgytta, *Roivainen 933* (NY).

Blepharolejeunea fuegiana stands out by its rectangular leaf lobule with a very long apical tooth and its sharply 5-keeled perianth (2 lateral, 2 ventral, 1 dorsal). The two ventral keels develop on the sides of a broad swelling which corresponds with the ventral keel of the other species of the genus.

4. Blepharolejeunea incongrua (Lindenberg & Gottsche) van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 133, Figs. 7, 8, 10. 1985; *Lejeunea incongrua* Lindenberg & Gottsche, Syn. Hep. 750. 1847; *Symbiezidium incongruum* (Lindenberg & Gottsche) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Dicranolejeunea incongrua* (Lindenberg & Gottsche) Stephani, Hedwigia **35:** 79. 1896. Type. Mexico. Sempoaltepec, *Liebmann 170b* (holotype, W; isotypes, C, G, S).

Phragmicoma nitidiuscula Gottsche, Ann. Sci. Nat., Bot. (sér. 5) **1:** 145. 1864; *Brachiolejeunea nitidiuscula* (Gottsche) Schiffner, Hedwigia **33:** 186. 1894. Type (van Slageren & Kruijt, 1985). Colombia. Cundinamarca: Choachi, *Lindig 1739* (lectotype, G; isolectotypes, BM, MANCH, PC, S).

Paroicous. *Plants* to 3 cm long × 1.1–1.7 mm wide, green to glossy dark or reddish brown when dry, creeping, forming small mats on bark. *Branching* mainly *Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.1–0.15 mm in diam., in cross section composed of about 11–15 thick-walled epidermal cells surrounding 15–20 somewhat smaller, ± thin-walled medullary cells, dorsal epidermal cells slightly larger than the ventral epidermal cells; ventral merophyte (2–)4 cell rows wide. *Leaves* laxly to densely imbricate, rather widely spreading, dorsal lobe ovate-falcate, 0.7–1 × 0.6–0.8 mm, apex rounded to apiculate, recurved, margins entire, ventral margin forming an angle of 120–150° with the keel; median cells 20–35 × 15–25 µm, trigones well-developed, cordate to simple-triangular, oil bodies 15–30 per cell, small, ellipsoid to subglobose, finely segmented, *Jungermannia*-type, each oil body made up of 3–8 very small granules, becoming homogeneous on age. *Lobules* broadly ovate-subrectangular, ca. 0.4 mm long, first tooth inflexed, 2 cells long, second tooth not inflexted, 2–3 cells long, the teeth separated by 3–4 free margin cells, margin cells larger than the other lobule cells. *Underleaves* barely imbricate, orbicular, 0.4–0.5 mm long, ca. 4× stem width, line of insertion arched. *Androecia* located below the gynoecium after 1–2 series of vegetative leaves, bracts in 2–6 series. *Gynoecia*: bract lobes obovate-falcate, up to 1.2 mm long, convex above, apex rounded to apiculate, margins entire, lobule small, less than 1/3× lobe length, apex with one distinct tooth, keel sharp, without or with a narrow wing; bracteole broadly obovate, distinctly shorter than bracts, ca. 0.7 mm long, convex, apex rounded, margins plane or slightly recurved. *Perianths* normally immersed, exserted to 1/3 when stalked, obconical, usually brown, with three keels: two sharp lateral keels and one broad rounded ventral keel, the ventral keel smooth, the lateral keels smooth or irregularly ciliate above; beak 4–5 cells long. *Sporophyte*: spores rectangular, 55–90 μm long, with rosettes; elaters 300–360 μm long.

Terpenoids: various unidentified diterpenoids are the main constituents of this species (Gradstein et al., 1985).

Illustration. van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 134–137, Figs. 7, 8. 1985; van Slageren, Meded. Bot. Mus. Herb. Utrecht **544:** 230, Pl. III. 1985.

Distribution (Fig. 46). Mexico, Costa Rica, Andes of Venezuela to Bolivia, and SE Brazil (Mt. Itatiaia), ca. 2000–4000 m. *Blepharolejeunea incongrua* grows on bark of trees and shrubs in rather open, humid, high-montane environments: at forest edges, in shrubby vegetations, in páramos, etc.

Selected specimens examined. MEXICO. OAXACA: road N of Llano de Las Flores, *Iwatsuki & Sharp 5352d* (TENN).

COSTA RICA. SAN JOSÉ: Macizo Buenavista, Cerro Asunción, *Chaverri et al. 1436* (USJ, U); 97 km S of Cartago, *Griffin et al. 435, 560* (FLAS, U).

COLOMBIA. ANTIOQUIA: Llanos de Quivá, *Onraedt 83A10466* (hb. Onraedt). ARAUCA: Sierra Nevada de Cocuy, *Cleef 10047a* (COL, U). BOYACÁ: páramo El Boquerón, *Troll 2180* (NY, S); páramo al NW de Bel°n, *Cleef 1889* (COL, U). CASANARE: Alto El Poleo, above Sácama, *Aguirre & Gradstein 2880a* (COL, U). CUNDINAMARCA: Choachi, *Lindig s.n.* (BM, G, MANCH, S); páramo de Guasca, *Aguirre et al. s.n.* (COL, U); páramo de Chingaza, *Gradstein 4236* (COL, U). META: páramo de Sumapaz, *Cleef 1204a* (COL, U). RISARALDA: above St. Rosa de Cabal, *Aguirre & Gradstein 1282, 1326* (COL, U), *Gradstein 3570* (B, BA, BM, COL, F, FLAS, MEXU, NY, PC, S, SP, TNS, U, USJ). TOLIMA: above St. Isabel, *Aguirre & Gradstein 1503, 1595, 1650* (COL, U).

VENEZUELA. MÉRIDA: páramo El Batallón, *Griffin & Dugarte PV-1110* (NY); Sierra Nevada, towards Pico Espejo, *Schäfer-Verwimp 12324* (U). TACHIRA: páramo El Rosal, *Griffin et al. 680a* (FLAS, U). TRUJILLO: Boconó, páramo de Guaramacal, *Griffin et al. 1054, 1055* (FLAS, U).

ECUADOR. CARCHI: páramo El Angel, *Gradstein et al. 68945* (U). COTOPAXI: Mt. Cotopaxi, *Gradstein et al. 75, Bryoph. Neotrop. Exsicc. 135* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, XAL). PICHINCHA: Otavalo, *Gradstein et al. 3372* (U).

PERU. AMAZONAS: road Chachapoyas–Cajamarca, *Hegewald 6958* (U), *6960b* (JE), *Frahm et al. 1145* (B, BA, COL, F, FLAS, G, H, MEXU, NY, PRC, S, SP, U, VBI). SAN MARTÍN: road Chachapoyas–Moyabamba, above Rioja, *Frahm et al. 808* (B, U).

BRAZIL. Serra de Itatiaia, *Schäfer-Verwimp 7573, 9565, 11155* (U).

BOLIVIA. COCHABAMBA: *Herzog s.n.* (G, U, YU); Incachaca, *Gradstein 7395* (LPB, U). LA PAZ: road La Paz-Coroico, ca. 3000 m, *Gradstein 7066, 7067* (LPB, U).

Blepharolejeunea incongrua usually grows in dense, glossy reddish brown mats on bark. The species is easily recognized by the obconical, brownish perianths with sharp lateral keels and a broad, rounded ventral keel. The lateral keels may be smooth or with a few cilia above. When perianths are lacking, characters of the lobule serve to distinguish the species (see Key).

5. Blepharolejeunea securifolia (Stephani) Schuster, Phytologia **45:** 424. 1980; van Slageren & Kruijt, Beih. Nova Hedwigia **80:** 142, Figs. 1-3. 1985; *Lejeunea securifolia* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 131. 1884, nom. illeg.; *Brachiolejeunea securifolia* Stephani, Spec. Hep. **5:** 128. 1912; *Oreolejeunea securifolia* (Stephani) Schuster, Hep. Anth. N. America **4:** 762. 1980. Type. Ecuador. Pichincha: Quito, *Jameson s.n.* (isotypes, NY, YU). Fig. 47.

Brachiolejeunea hans-meyeri Stephani, Spec. Hep. **5:** 118. 1912. Type (van Slageren & Kruijt 1985). Ecuador. Chimborazo: páramo el Altar, *Meyer 4220* (lectotype, G; isolectotype, JE).

Brachiolejeunea schwabei Herzog, Rev. Bryol. Lichénol. **23:** 60. 1954. Type. Chile. Fray Jorge, *Schwabe 194* (holotype, JE, n.v.), syn. fide van Slageren and Kruijt (1985).

Brachiolejeunea asplundii Herzog, Svensk Bot. Tidskr. **51:** 190. 1957. Type. Ecuador. Pichincha: páramo Guamani, *Asplund s.n.* (holotype, JE).

Paroicous. *Plants* 1.5–3(–6) cm long × 1.5–2 mm wide, green to light brown to dark brown when dry, creeping or ascending, forming small mats on bark or rock. *Branching* mainly *Frullania*-type, occasionally *Lejeunea*-type. *Stems* 0.1–0.15 mm in diam., in cross section composed

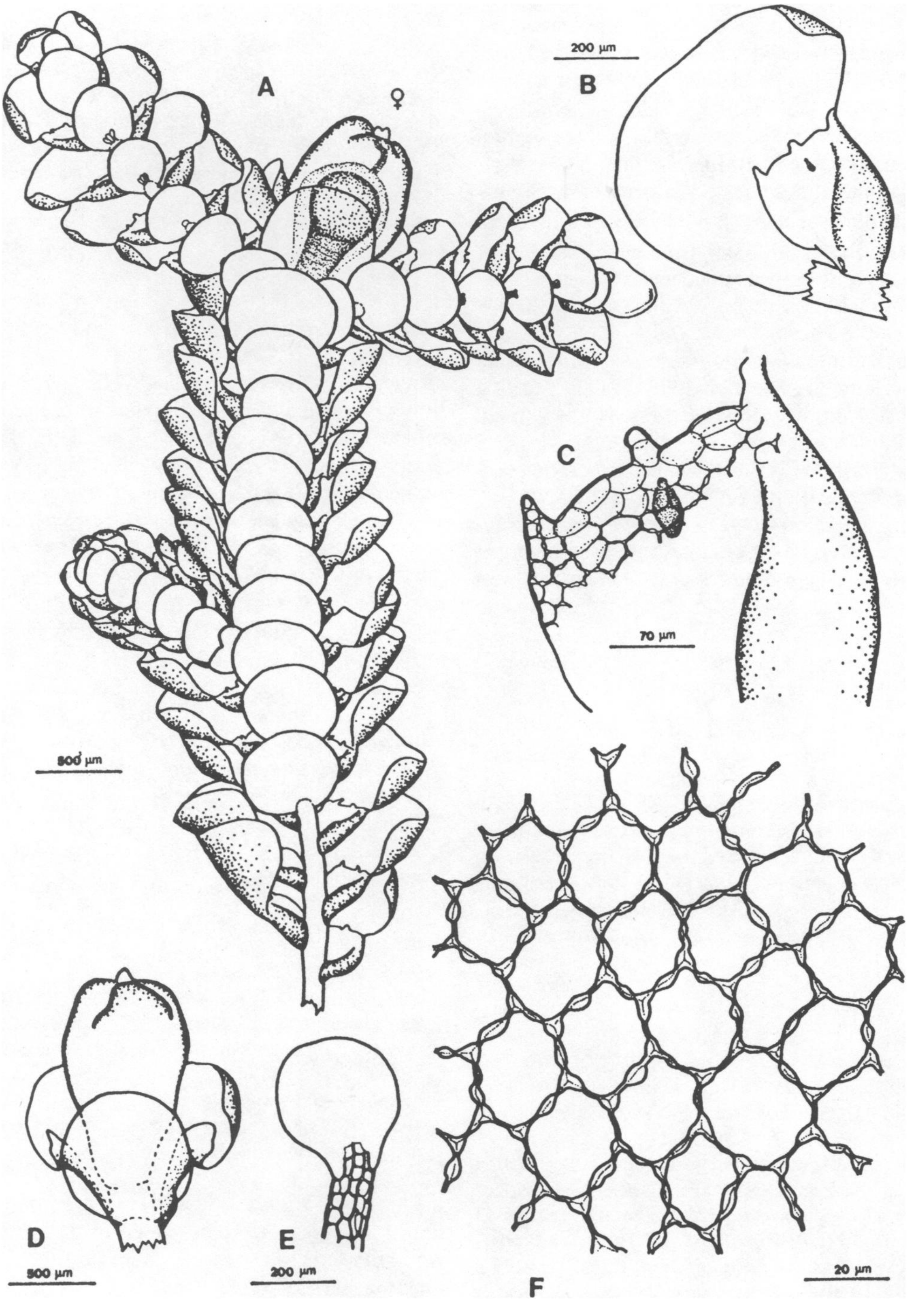

FIG. 47. *Blepharolejeunea securifolia.* **A.** Habit, with gynoecium. **B.** Leaf. **C.** Truncate lobule apex; note dissimilar teeth. **D.** Gynoecium. **E.** Underleaf. **F.** Leaf cells. From Colombia, *Aguirre & Gradstein 4616.*

of about 11–15 thick-walled epidermal cells surrounding 20–30 somewhat smaller, almost thin-walled medullary cells, dorsal epidermal cells slightly larger than the ventral epidermal cells; ventral merophyte four cell rows wide. *Leaves* laxly to densely imbricate, widely spreading, dorsal lobe ovate-falcate, 0.9–1.4 × 0.7–1.1 mm, apex rounded to apiculate, recurved, margins entire, ventral margin forming an angle of 120–150° with the keel; median cells 25–40 × 15–30 µm, trigones small, cordate to simple-triangular, oil bodies 15–30 per cell, small, ellipsoid to subglobose, finely segmented, *Jungermannia*-type, each oil body made up of 4–10 very small granules, becoming homogeneous on age. *Lobules* broadly ovate-subrectangular, ca. 0.4–0.6 mm long, first tooth inflexed, (1–)2–3 cells long, second tooth not inflexed, 2–5 cells long, the teeth separated by 4–7 free margin cells, margin cells not larger than the inner cells of the lobule. *Underleaves* subimbricate, ± orbicular, 0.5–0.8 mm long, 4–6× stem width, line of insertion arched. *Androecia* located below the gynoecium after 1–4 series of vegetative leaves, bracts in 1–5 series. *Gynoecia*: bract lobes ovate-falcate, up to 1.2 mm long, convex above, apex rounded, margins entire, lobule 1/2–2/3× lobe length, with obtuse apex, keel rounded, without or with a narrow wing; bracteole broadly obovate, 0.8–1 mm long, convex, apex rounded-truncate, margins incurved. *Perianths* normally exserted to 1/3–1/2, sometimes stalked and fully exserted, obovoid-oblong, usually with three smooth, rounded keels in the upper 1/3-2/3: two lateral, one ventral, the ventral keel sometimes sulcate above; beak 4–5 cells long. *Sporophyte*: spores rectangular, 60–95 µm long, without rosettes; elaters 320–370 µm long.

Terpenoids: bicyclogermacrene, pinguisone and various unidentified sesquiterpenoids are the main components of this species; pinguisone is the chemical marker (Gradstein et al., 1981).

Distribution. Andes of Venezuela to N Chile, and SE Brazil (Mt. Itatiaia); in the Andes occurring only above 3000 m., on Mt. Itatiaia collected in the summit area above 2000 m. *Blepharolejeunea securifolia* grows on bark, humus and on rock in humid high montane environments, e. g., in low forests and on twigs in scrubby vegetations, usually near rivulets.

Selected specimens examined. MEXICO. DISTRICT FEDERAL: Amecameca, *Eggers & Frahm 792219* (U).

COSTA RICA. SAN JOSÉ: Macizo Buenavista, *Chaverri et al. 1577* (USJ, U).

COLOMBIA. BOYACÁ: Sierra Nevada de Cucuy, *Bischler 2795, 2898* (COL, PC), *Grubb & Guymer B44, B46, B 102, B416* (BM); páramo N de Belén, *Cleef 1990, 2291* (COL, U); páramo de Pisva, *Cleef & Florschütz 5970a* (COL, U). **CASANARE:** above Sácama, *Aguirre & Gradstein 2856* (COL, U). **CUNDINAMARCA:** above Bogotá, *Troll 2181a* (NY); páramo de Palacio, *Cleef 6723a* (COL, U); páramo de Cruz Verde, *Cleef 2795* (COL, U); páramo de Chisacá, *Gradstein & Aguirre 3642* (COL, U). **MAGDALENA:** Sierra Nevada de Santa Marta, *Winkler C326* (U). **META:** páramo de Sumapaz, *Cleef 942a, 7880b, 8178a* (COL, U). **RISARALDA:** above St. Rosa de Cabal, *Gradstein & Aguirre s.n.* (COL, U).

VENEZUELA. MÉRIDA: Sierra Nevada, teleferico Aguada-La Montaña, *Griffin et al. 247* (FLAS, U); páramo de los Conejos, *Griffin & López* PV586 (FLAS, U); road Valera-Pico Aquila, *Schäfer-Verwimp 12116* (U); páramo de la Culata, *Griffin & Dugarte PV-865* (NY).

ECUADOR. CARCHI: páramo El Angel, *Gradstein et al. 3457* (U), *Thiers 4435 p.p.* (NY). **CHIMBORAZO:** type of *Brachiolejeunea hans-meyeri*. **PICHINCHA:** páramo de Guamani, *Asplund s.n.* (JE, S).

PERU. ANCASH: Huaraz, *Philippi P-253* (B, U).

BRAZIL. Mt. Itatiaia, *Vital s.n.* (SP, U).

CHILE. Type of *Brachiolejeunea schwabei.*

Blepharolejeunea securifolia has an oblong perianth with three rounded keels in the upper half, somewhat like *Brachiolejeunea laxifolia* with which it may grow in the field. The truncate lobule with only two teeth and the lack of a dorsal paraphyllium on the stem in *B. securifolia* clearly separate it from *B. laxifolia*. Moreover, the leaf bases in *Brachiolejeunea laxifolia* are somewhat sheathing, with the lobules suberect and rather close to the stem, the ventral leaf margins in that species are incurved and the leaf apex is more or less plane. In *Blepharolejeunea securifolia* the leaf bases and lobules are rather widely spreading, the ventral leaf margins are plane and the leaf apex is distinctly recurved. Finally, the underleaf apex is recurved in *B. laxifolia* whereas in *B. securifolia* it is plane.

Blepharolejeunea securifolia may also grow together with *B. incongrua*. The two species are readily distinguished by the characters given in the Key.

20. Dicranolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; Kruijt, Bryophyt. Biblioth. **36:** 47. 1988; *Lejeunea* subgen. *Dicranolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 138. 1884. Lectotype (Evans 1914). *Dicranolejeunea axillaris* (Nees & Montagne) Schiffner. Genus named for its paired innovations.

For description see under the species.

Distribution (Fig. 49). The genus *Dicranolejeunea*, as circumscribed by Kruijt (1988), is restricted to the neotropics and contains only one species, *D. axillaris*, which is common at montane elevations, especially in the Andes.

Dicranolejeunea is closely related to *Acanthocoleus*. Differences are discussed under the latter. The present treatment follows Kruijt (1988).

1. Dicranolejeunea axillaris (Nees & Montagne) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; Kruijt, Bryoph. Biblioth. **36:** 47, Pls. 3-5. 1988; *Lejeunea axillaris* Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **5:** 59. 1836; *Symbiezidium axillare* (Nees & Montagne) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877. Type. Peru. *d'Orbigny s.n.* (holotype, STR; isotypes, BM, S). Fig. 48.

Lejeunea dubiosa Lindenberg & Gottsche, Syn. Hep. 752. 1847; *Dicranolejeunea dubiosa* (Lindenberg & Gottsche) Stephani, Spec. Hep. **5:** 157. 1912. Type. Mexico. Sempoaltepec, Liebmann 6/1842 (holotype, W; isotype, C).

Lejeunea ciliatiflora Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 140. 1884; *Dicranolejeunea ciliatiflora* (Spruce) Stephani, Spec. Hep. **5:** 157. 1912. Type. Ecuador. Mt. Tunguragua, *Spruce s.n.* (holotype, MANCH; isotype, G).

Lejeunea hypoacantha Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 140. 1884; *Dicranolejeunea hypoacantha* (Spruce) Stephani, Spec. Hep. **5:** 157. 1912. Type. Ecuador. Pallatanga, *Spruce s.n.* (holotype, MANCH; isotype, G).

Peltolejeunea galapagona Stephani, Hedwigia **35:** 123. 1896. Type. Ecuador. Galápagos Islands and Floreana ("Charles"), *Andersson s.n.* (holotype, G; isotype, S).

Dicranolejeunea longissima Stephani, Spec. Hep. **5:** 161. 1912. Type. Costa Rica. Cartago, *Werckle s.n.* (holotype, G).

Dicranolejeunea pulcherrima Stephani, Biblioth. Bot. **87:** 255. 1916. Type (Bonner 1965). Bolivia. Corani valley, *Herzog 4743* (lectotype, G; isolectotypes, B, S).

Paroicous; *plants* to 7 cm long × 1–2 mm wide, glossy light green to brown green when alive, green to yellow brown to rather dark brown in the dried condition, loosely creeping, ascending or pendent. *Branching Frullania*-type or, rarely, *Lejeunea*-type, irregular or forked due to repeatedly fertile paired innovations, flagelliform branches lacking. *Stems* 0.1–0.25 mm in diam., not flattened, with a distinct hyaloderm, in cross section composed of 9–13 large, thinwalled, strongly outwardly bulging epidermal cells surrounding 25–60 much smaller medullary cells, the outer medullary cells usually thick-walled and forming a distinct subepidermis, the inner medullary cells thin-walled or slightly thickened; ventral merophyte only two cell rows wide. *Leaves* subimbricate, when wet obliquely spreading, when dry suberect-convoluted, dorsal lobe ovate, 0.7–1.5 × 0.5–1.1 mm, apex short acuminate or acute, margins usually toothed near apex with 1–7 teeth, sometimes entire, the teeth consisting of 1–12 cells, ventral margin forming an angle of ca. 100–150° with the keel; median cells slightly elongate, averaging 30–40 µm in largest diam., with cordate to bulging-rounded trigones and one intermediate thickening on longer cell walls; oil bodies small, 12–15(–20) per cell, finely segmented, *Jungermannia*-type, ellipsoid to subglobose, ca. 3–5 × 2–2.5 µm; ocelli lacking. *Lobules* ovate to short rectangular, ca. 1/4–1/3× lobe length, rarely reduced, somewhat inflated along the keel, keel arched, free margin with two inflexed teeth, the first tooth (1)2–4 cells long, second tooth smaller, 1–2 cells long; hyaline papilla positioned 1 cell below the proximal base of the first tooth on the inner surface of the lobule. *Underleaves* distant to contiguous, orbicular to broadly ovate, 0.3–0.5 × 0,3–0.8 mm, 2–3.5× stem width, apex rounded, margins entire, usually narrowly recurved, bases cuneate, insertion line arched, 0.1–0.2 mm deep; underleaf base at rhizoid disc tri-stratose and short stalked, in cross section with two superior central cells; rhizoids rarely produced, secondary rhizoid disc lacking. *Androecia* just below the gynoecium (to be seen on young innovations), bracts few, ± similar to vegetative leaves, lobule epistatic, underleaves present throughout; antheridia one per bract. *Gynoecia* with (1–)2 pycnolejeuneoid, repeatedly fertile innovations, bracts in one series, slightly smaller than vegetative leaves, un-

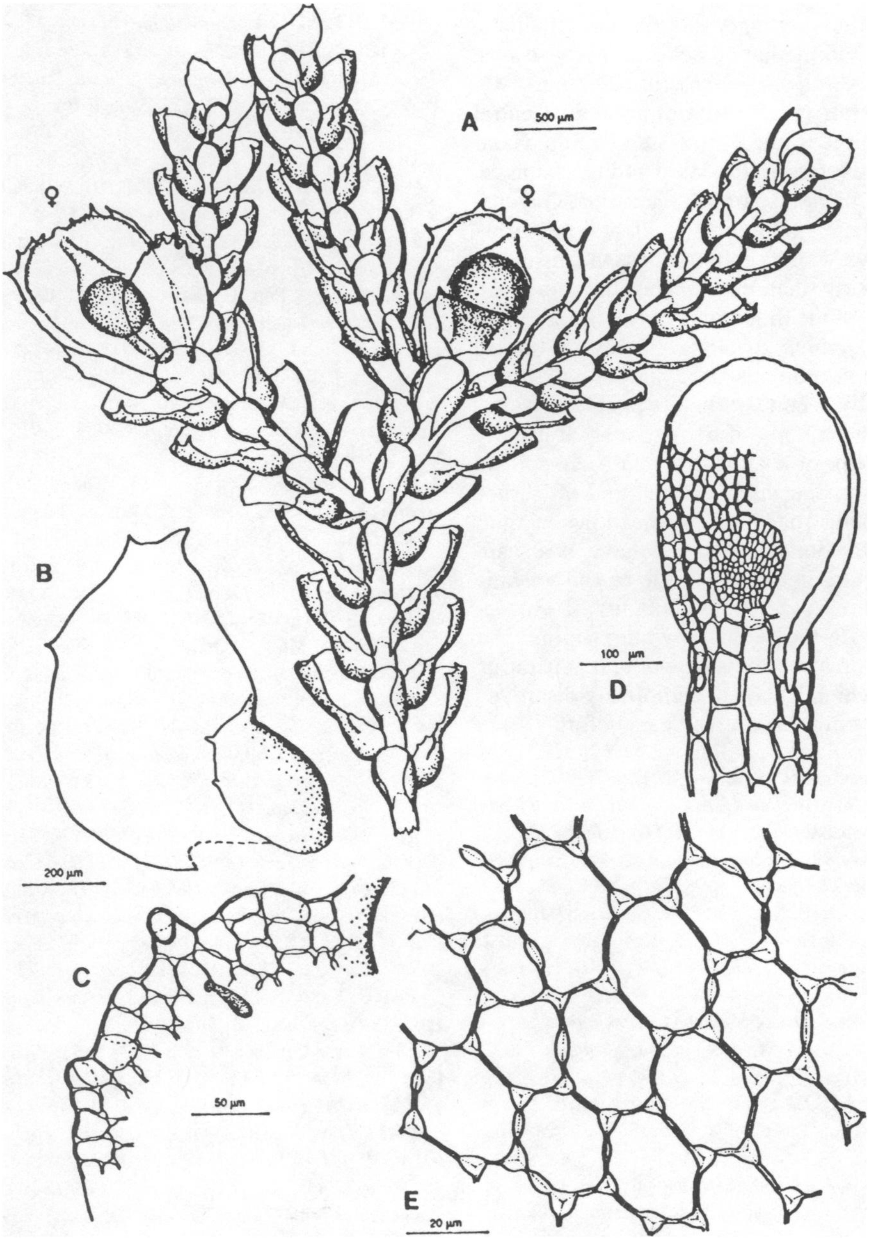

FIG. 48. *Dicranolejeunea axillaris*. **A.** Habit, with two gynoecia. **B.** Leaf. **C.** Lobule apex. **D.** Underleaf; note two cells wide ventral merophyte. **E.** Leaf cells. From Guadeloupe, *Gradstein 6599*.

winged, lobe acute to obtuse, usually toothed with 5–15 teeth or laciniae, lobule very small, ca. 1/7× lobe lenght; bracteoles orbicular to elongated, about as long as the bracts, apex rounded, toothed with up to 20 teeth (rarely ± entire). *Perianths* obovoid-pyriform, averaging 1.5 mm long, exserted to 1/2, with two sharp, winged, ciliate or laciniate lateral keels, dorsal surface smooth, ventral surface with one broad, rounded keel with 0–2 ridges, the ridges sometimes with a few short laciniae near apex, apex emarginate, beak 4–6 cells long. *Sporophyte*: seta articulate, spores with rudimentary rosettes; otherwise as in the tribe. *Vegetative reproduction* lacking.

Distribution (Fig. 49). Common in Central America, in the tropical Andes and on the Galapagos Islands; rare in the West Indies (Jamaica, French Antilles); also on Mt. Roraima, Guyana; at submontane and montane elevations, 500–3200 m. In view of its commonness in the Andes, it is surprising that the species has not been recorded from the mountains of SE Brazil.

Dicranolejeunea axillaris grows in humid montane environments as a pioneer in rather open, scrubby secondary habitats, at forest margins or in the canopy of dense forest. It usually occurs on bark or rock, occasionally on soil. In the Andes the species is often found on shrubs and rock along roads and in meadows at mid-montane elevations, and may behave as a roadside weed. On the summit cone of the volcano "La Soufrière" (ca. 1000–1400 m) of Guadeloupe, in 1988, the author saw huge amounts of *D. axillaris* on low shrubs in young, regenerating woodland which had been completely destroyed by volcanic eruption twelve years before.

Selected specimens examined. MEXICO. Chiapas: Tziscao S of Comitán, *den Held & van Rijn HH65* (U); road San Cristobal-Ocosingo 15 km, *Gradstein 8301* (U). **Hidalgo:** near Jacala, *Robinson s.n.* (US); Palo Semita NE of Jacala, *Weber & Charette B-9851, Crypt. exsicc. Mus. Hist. Nat. Vindob.* (B, BM, NY, S, U, US, UPS). **District Federal:** Valle de Bravo, *Düll A21, A22* (U). **Veracruz:** road Orizaba-Teheacan, *Frahm 792749* (B, U); Huatusco, *Liebmann s.n.* (B).

GUATEMALA. Alto Verapaz: *Türkheim 1344* (B, BM, G, NY, YU); road Tactic-Tamahu, *Standley 71077, 71126* (NY, US).

EL SALVADOR. San Salvador, *Mabille s.n.* (MANCH); laguna Las Ninfas, Feb 1969, *Brinson s.n.* (FLAS, U).

COSTA RICA. Cartago: Tapanti Forest Reserve, *Griffin & Eakin 247* (FLAS, U); La Estrella, *Standley 39379* (US); La Verbena, near Alajuelita, *Tonduz 15631* (B, NY); **Puntarenas:** near San Vito, *Sipman 11822, 11935* (U); Coliblanco, *Maxon 347* (NY, YU).

PANAMA. Chiriqui: David, *Hélion 119, 434* (G); Cerro Punta, *Salazar 5253* (PMA, U).

JAMAICA. Cinchona, *Cummings 12* (BM, NY, YU), *Underwood s.n.* (NY); Morce's Gap, *Evans 84* (B, BM, NY, US, YU); Flamstead, *Jaegerholm s.n.* (S, YU).

WINDWARD ISLANDS. GUADELOUPE. Champflore, Roche river, *Duss 612* (NY); summit area of volcano La Soufrière, *Gradstein & Sastre-de Jesus 6599* (U). **MARTINIQUE.** *Duss 1033* (NY).

COLOMBIA. Antioquia: San Pedro, *Onraedt 83A10356* (U); Río Negro, *Onraedt 83A9914* (U). **Boyaca:** Sierra Nevada de Cocuy, near Bocotá, *Grubb & Guymer B369, B378, B382* (BM); Pajarito, *Bischler 1796* (COL, U). **Caldas:** Manizales, *Bischler 282* (COL, U). **Cauca:** Tambito, *Bischler 282* (COL, U). **Cundinamarca:** NW of Facatativá, *King et al. C-846* (US); Río Checua, *Schaeck 72Am32* (JE). **Huila:** Salamina, *Wallis s.n.* (B, BM, G). **Magdalena:** Sierra Nevada de Santa Marta, *Winkler C266* (U). **Risaralda:** St. Rosa de Cabal, Termales, *Gradstein 3516, Bryoph. Neotr. Exsicc. 35* (B, BA, BM, COL, FLAS, G, H, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, W, XAL). **Santander:** between Piedecuesta and Las Vegas, *Killip & Smith 15496* (JE, NY). **Tolima:** W of Fresno, *King et al. C-925, C-937* (US); St. Isabel, *Gradstein 3267* (U).

VENEZUELA. Lara: Parque Nacional Yacamba, *Griffin & Lopez 253* (NY). **Mérida:** Mucuy, *Onraedt 78V5533* (JE, U); **Portuguesa:** 67 km NO of Guanare, *Steyermark et al. 126724* (MO, U, VEN). **Tachira:** Páramo de Tama, *Griffin et al. 82* (U). **Trujillo:** Boconó, St. Rita, *Griffin et al. 1212* (U).

GUYANA. Mt. Roraima, *Gradstein 5260* (U).

ECUADOR. Azuay: páramo de Matango, Allioni s.n. (G). Chimborazo, Mt. Altar, Spruce s.n. (MANCH). **Pastaza:** *Spruce s.n.* (MANCH). **Pichincha:** Quito, *Jameson s.n.* (NY); Mt. Pichincha, *Wallis s.n.* (B, S), *Gradstein et al. 6729* (U), *Thiers 4373* (NY). **Tunguragua:** Rio Verde, *Spruce s.n.* (MANCH). **Galápagos Islands:** Floreana, *Gradstein & Weber H159* (BM, NY, U); Isabela, Alcedo, *VanderWerff 1469, 2020* (U); Pinta, *Gradstein et al. H526, H527* (U); San Cristobal, El Progreso, *Balasz 12/F* (U); Santa Cruz, near Puntudo, *Gradstein & Weber H23, H69* (COLO, U); behind Schiess Farm, *VanderWerff 2083,2222, 2224, 2226, 2228* (U).

PERU. Cuzco: Macchu Picchu, *Hegewald 8676* (U). **Huanuco:** Sinchono, *Aguilar 837b* (US). **La Libertad:** Trujillo, Cerro Campana, *Ayala 7104* (US). **Pasco:** Villa Rica, *Jacobson 102* (NY); Oxapampa, *Hegewald 8450* (U). **San Martín:** above Rioja, *Frahm et al. 546* (B, G, U).

BOLIVIA. Cochabamba: Incacorral, *Herzog 5894* (G, L, YU), *Gradstein 7557* (U); Tablas Monte, *Herzog 4539, 4632* (B, G, YU), *Gradstein 7432* (U); road Cochabamba-Villa Tunari km 112, *Gradstein 7504, 7515* (LPB, U). **La Paz:** Yungas, *Rusby 5050a* (YU); near Sacramento Alto, *Mishida et al. B-22-1* (U). **Santa Cruz:** Prov. Florida, near Yerba Buena, *Nee & Vargas 38285B* (NY).

In addition, there are three poorly documented specimens from temperate portions of Chile, far south of the range of *Dicranolejeunea axillaris*: Arique, *Suchler s.n.* (NY); Valdivia, *Sumthil s.n.* (NY); S Chile, *without collector* (NY). Pending the discovery of good material of *Dicranolejeunea axillaris* from these areas, I think these disjunct records should be excluded.

FIG. 49. Distribution of *Dicranolejeunea axillaris*.

Dicranolejeunea axillaris is easily recognized by (1) its very laxly dichotomous habit, (2) light brownish green color, (3) obliquely spreading, somewhat dentate leaves (sometimes entire!) with small lobules, (4) widely spatiated, orbicular underleaves, (5) two cells wide ventral merophyte, (6) the flattened, ciliate-laciniate perianth with two long, repeatedly fertile innovations and (7) dentate female bracteole. The latter character immediately separates the species from *Acanthocoleus aberrans*. When growing on bark, *D. axillaris* is usually pendent, as opposed to the species of *Acanthocoleus* (formerly placed in *Dicranolejeunea*) which grow appressed to the substrate.

Excluded Species

(see Kruijt, 1988: 111–117)

Dicranolejeunea affixa (Taylor) Stephani = *Cyclolejeunea accedens* (Gottsche) Evans

21. Acanthocoleus Schuster, Bull. Torrey Bot. Club **97:** 339. 1970; Kruijt, Bryophyt. Biblioth. **36:** 59. 1988; *Dicranolejeunea* subgen. *Acanthocoleus* (Schuster) Kruijt, Beih. Nova Hedwigia **80:** 158. 1985. Type. *Acanthocoleus fulvus* Schuster (= *Acanthocoleus aberrans* (Lindenberg & Gott.) Kruijt). Genus named for the ciliate-laciniate perianth.

Plants rather tiny, 1–4 cm long × 0.8–2 mm wide, dull green to brown green when alive, usually becoming brown when dry, creeping. *Branching Lejeunea*-type or, in robust vegetative shoots, *Frullania*-type, irregularly pinnate, flagelliform branches lacking. *Stems* fragile, epidermal cells smooth, fewer and much larger (1.2–3×) than the medullary cells, dorsal epidermal cells as large as ventral epidermal cells or slightly smaller, walls of the epidermis thickened, those of the medulla thin except for the walls bordering the epidermis, all cell walls colorless; ventral merophyte 2(–4) cell rows wide. *Leaves* subconvoluted and suberect when dry, wide spreading when moist, lobe apex rounded to acuminate, margins entire or toothed with 1–8 teeth; median cells slightly elongate, trigones cordate (simple triangular in some palaeotropical species), intermediate thickenings rare, occasionally one present on longer cell walls; oil bodies finely segmented, *Jungermannia*-type, soon degenerating and becoming homogeneous on age (there are doubtful reports of homogeneous oil bodies in palaeotropical species which need confirmation), small, rather numerous per cell; ocelli lacking. *Lobules* ovate-rectangular, ca. 1/4–2/3× lobe length, often reduced, inflated along the keel, flattened towards the free margin, with (1–)2 teeth, the first tooth always larger than the second tooth; hyaline papilla positioned on the inner side of the lobule 1–3 cells the proximal base of the first tooth. *Underleaves* ± orbicular, 2–4× stem width, apex rounded, margins entire, plane bases cuneate, insertion line arched; underleaf base at the rhizoid disc tristratose and short stalked, with (2–)4 superior central cells; secondary rhizoid disc not produced. *Androecia* below the gynoecium (paroicous) or on separate, short-specialized *Lejeunea*-type branches (autoicous), bracts similar to vegetative leaves in paroicous plants or modified, smaller and with strongly inflated lobules in autoicous plants, lobules epistatic, bracteoles present throughout, similar to underleaves in paroicous plants, smaller in autoicous plants; antheridia 1–2 per bract. *Gynoecia* on main stems or on branches, with 1–2 pycnolejeuneoid innovations (lejeuneoid in *Acanthocoleus javanicus*), bracts in one series, largely inserted on the innovation, suberect, about as large as vegetative leaves but the inner bract narrower, lobule small or obsolete, keel without wing; bracteoles much shorter than the perianth, orbicular to obovate, apex widely rounded, margins plane or slightly recurved, entire. *Perianths* exserted to 1/4–1/2, obovate-obpyriform, with 3–5 keels or terete-eplicate, lateral keels when present usually winged and dentate-ciliate, sometimes smooth, ventral keel usually low, rounded and smooth, sometimes split into two sharp, winged-dentate accessory keels, dorsal keel lacking or small; beak short, sometimes recessed. *Sporophyte*: seta articulate, made up of 14–16 outer rows of cells and 4–5 inner rows; spores finely verrucose, without or with rudimentary rosettes; otherwise as in the tribe. *Vegetative reproduction* lacking.

Distribution. The pantropical genus *Acanthocoleus* was monographed by Kruijt (1988) who recognized seven species, including two in the neotropics. In the present treatment, three species and a new variety are recognized in tropical America. The species grow on bark or rock (rarely on soil) in rather dry, semi-deciduous forests and scrub, or in the outer canopy of humid evergreen rain forests, at submontane and lower montane elevations from about 150 to 2600 m.

Acanthocoleus has been segregated from *Dicranolejeunea* and is obviously closely related to the latter. Similarities are particularly striking between *D. axillaris* and *A. aberrans* var. *laevis.* The two genera differ in growth form, stem structure and female involucre. *Dicranolejeunea*'s are rather robust plants, with stems ascending from the substrate and often freely pendent; their branches are always of the *Frullania*-type. In contrast, species of *Acanthocoleus* are much smaller plants with creeping stems which closely adhere to the surface. *Lejeunea*-type branches are more common in this genus than *Frullania*-type branches.

Correlated with growth form is a significant difference in the anatomy of the stem of the two groups. In *Dicranolejeunea* the epidermal cells of the stems are very large and strongly bulging outwards, and the walls of the outer medullary cells are conspicuously thickened, forming a rather distinct subepidermis; the walls of the inner cells are thin. In *Acanthocoleus* the epidermal cells are smaller and never bulging outwards, and the outer medullary cells are scarcely thicker-walled than the inner medullary cells. The distinctly toothed female bracts and bracteoles of *Dicranolejeunea* also separate the genus from *Acanthocoleus*, which has a completely entire involucre or, occasionally, a few small teeth on the upper bract margins only.

In spite of these differences, *Acanthocoleus* and *Dicranolejeunea* are very similar in their general morphology and one might consider treating them as subgenera rather than genera. It should be realized, however, that the differences between the two are not weaker than those separating some other genera of *Lejeuneaceae*, e. g., *Mastigolejeunea* and *Thysananthus*. I have therefore, reluctantly, decided to accept *Acanthocoleus* and *Dicranolejeunea* as genera, following Kruijt (1988).

Key to the Species of *Acanthocoleus*

1. Lobule large, 1/2–2/3× lobe length, rarely reduced, first tooth of the lobule 3–6 cells long; leaves orbicular; paroicous; Greater Antilles, Mexico, ca. 800–2500 m. . . . . 2. *A. juddii.*
1. Lobule smaller, 1/4–2/5× lobe length, often reduced, first tooth 0–2 cells long; leaves ovate; autoicous or paroicous.
    2. Paroicous; perianth entirely smooth, terete or weakly 3-keeled with broadly rounded lateral keels; leaf apex rounded, entire; S Brazil, Peru, Bolivia, northern Argentina, ca. 1000–2600 m . . . . . . 3. *A. trigonus.*
    2. Autoicous; perianth ciliate, distinctly keeled with sharp lateral keels; leaf apex pointed, rarely rounded, toothed or entire; throughout the neotropics, 150–2600 m . . . . 1. *A. aberrans.*

1. Acanthocoleus aberrans (Lindenberg & Gottsche) Kruijt, Bryophyt. Biblioth. **36:** 62, Pl. 6. 1988.

Acanthocoleus aberrans was treated by Kruijt (1988) as a broadly defined, variable species, occurring in the neotropics and in Africa. In this study, I have been able to recognize two distinct varieties in the neotropics, based on their very different perianths and some additional features.

Key to the Varieties of *Acanthocoleus aberrans*

1. Ventral surface of perianth with two sharp, dentate-ciliate keels; Central America and West Indies, uncommon. . . . . 1a. *A. aberrans* var. *aberrans.*
1. Ventral surface of perianth smooth or with a few cilia, sharp ventral keels lacking; widespread in tropical America. . . . . 1b. *A. aberrans* var. *laevis.*

1a. Acanthocoleus aberrans var. **aberrans;** *Lejeunea aberrans* Lindenberg & Gottsche, Syn. Hep. 751. 1847; *Symbiezidium aberrans* (Lindenberg & Gottsche) Trevisan, Mem. Reale Ist. Lomb. Sci. Mat. Nat., ser. 3, **4:** 403. 1877; *Dicranolejeunea aberrans* (Lindenberg & Gottsche) Stephani, Spec. Hep. **5:** 156. 1912. Type. Mexico. Veracruz: Huatusco, *Liebmann 395* (holotype, W; isotypes, C, G). Fig. 50.

Phragmicoma acuminata Lindenberg & Gottsche, Syn. Hep. 745. 1847; *Marchesinia acuminata* (Lindenberg & Gottsche) Kuntze, Revis. Gen. Pl. **2:** 836. 1891; *Dicranolejeunea acuminata* (Lindenberg & Gottsche) Stephani, Spec. Hep. **5:** 157. 1912; *Lejeunea aberrans* Lindenberg & Gottsche var. *conferta* Gottsche, Mex. Leverm. 284. 1863. Type. Mexico. Veracruz: Huatusco, *Liebmann 347* (holotype, W; isotype, G).

Dicranolejeunea neesiana Stephani, Spec. Hep. **5:** 162. 1912. Type. Mexico. *Ex hb. Nees* (holotype, G).

Dicranolejeunea pulchella Herzog, Rev. Bryol. Lichénol. **20:** 139. 1951. Type. Costa Rica. San José: St. Maria de Dota, *Standley & Valerio 43153* (holotype, JE).

Acanthocoleus fulvus Schuster, Bull. Torrey Bot. Club **97:** 339, Fig. 2. 1970. Type. Dominica. Morne Diablotins, *Schuster 66602a* (hb. Schuster, n.v.). The type specimen has not been made available on loan but the original description and illustration of this taxon leave no doubt as to its identity.

Autoicous. *Plants* 1–2 cm long × 0.6–1.5 mm wide, brownish. *Stems* ca. 0.15 mm in diam., in cross section composed of 11–12 epidermal cells surrounding numerous medullary cells, dorsal epidermal cells about as large as the ventral epidermal cells; ventral merophyte two cells wide. *Leaves* contiguous to imbricate, dorsal lobe ovate, 0.7–0.9 × 0.5–0.7 mm, apex apiculate to short acuminate, never rounded, margins entire to slightly toothed near apex, ventral margin forming a rather sharp angle of ca. 90–140° with the keel; median cells ca. 30–40 × 25 μm, with very small, cordate trigones; oil bodies (Schuster, 1970) small, 10–15(–25) per cell, finely segmented, *Jungermannia*-type, ellipsoid to subglobose, ca. 3–8 × 2–2.5 μm. *Lobules* ovate, up to 0.3 mm long, 1/4–2/5× lobe length, never (?) reduced, keel arched, free margin with 1–2 teeth separated from each other by 3–7 margin cells, first tooth (1)2–3 cells long, inflexed, second tooth smaller, 1–2 cells long. *Underleaves* subimbricate, ca. 0.4 mm, 3× stem width, margins plane, insertion line arched. *Androecia on short Lejeunea*-type branches, spicate or capitate, bracts in 2–6 series, modified, about half the size of the leaves, lobule strongly inflated, about 1/3–2/3× bract lobe, bracteoles smaller than underleaves; (1–)2 antheridia per bract. *Gynoecia* with

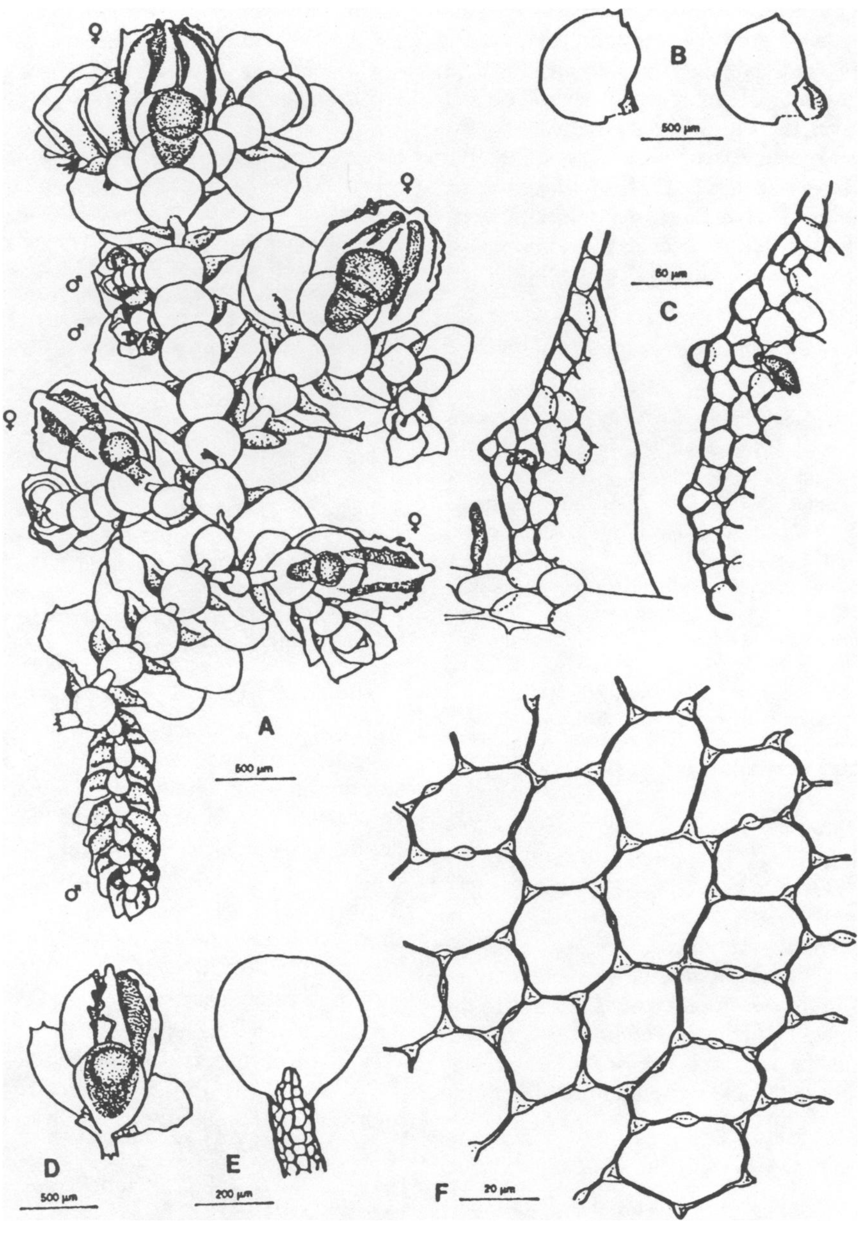

FIG. 50. *Acanthocoleus aberrans* var. *aberrans*. **A.** Habit with gynoecia and androecia. **B.** Leaves. **C.** Free margin of well developed (right) and reduced lobule. **D.** Gynoecium. **E.** Underleaf. **F.** Leaf cells. From Jamaica, *Griffin s.n.*

1(–2) innovations, the innovation normally sterile, bract lobes ovate-oblong, up to 0.7 mm long, apex apiculate to short acuminate, margins entire or toothed near apex with 1–5 teeth, lobule very small, sometimes reduced, keel smooth; bracteoles 0.5–0.6 mm long, margins plane. *Perianths* subcylindrical, up to 1 mm long × 0.5–0.6 mm wide, emergent to 1/3–1/2, with 4–5(–6) sharp keels: 2 lateral, 2(-3) ventral and 0–1 dorsal keel, the keels dentate-ciliate above, the lateral keels sometimes winged; beak 2–4 cells long.

Distribution (Fig. 51). Mexico, Costa Rica, Jamaica, French Guiana, at altitudes of 150–1500 m. *Acanthocoleus aberrans* var. *aberrans* is a rather rare neotropical taxon, which has been gathered only a few times. It grows on bark or rock in rather open woodlands and scrub and on isolated trees. In French Guiana it has been collected in the outer canopy of virgin rain forest. It lacks in the more humid, shaded portions of the rain forest.

Specimens examined. **MEXICO.** CHIAPAS: Lagunas de Montebello, *Eggers & Frahm MX32* (U); road San Cristobal-Ocosingo km 65, Gradstein s.n., 1992 (U). HIDALGO: near Chapulhuacan, *Sharp 1577a, 2803* (hb. Fulford); S of Tamazundia, *Robinson s.n.* (US).

GUATEMALA. ALTO VERAPAZ: Finca Mocca, *Johnson 170s* (US).

COSTA RICA. Type of *Dicranolejeunea pulchella*.

JAMAICA. Cinchona, *Evans 139, 251* (B, BM, NY, US, W, YU), *Maxon 1366, 1368, 1369, 1189, 1191* (US), *Underwood 489, 1113, 2330* (NY, YU).

DOMINICA. Type of *Acanthocoleus fulvus*.

FRENCH GUIANA. Saül, *Montfoort & Ek 12* (U).

The perianths in *Acanthocoleus aberrans* var. *aberrans* are normally 5-keeled with two sharp, dentate-ciliate ventral keels and a low dorsal keel. A third ventral keel was observed in material from Jamaica (Fig. 50A). In material from Mexico described as *Phragmicoma acuminata* Gott., the dorsal keel is lacking and one of the ventral keels is only weakly developed. These plants approach var. *laevis*.

1b. Acanthocoleus aberrans var. **laevis** Gradstein *var. nov.* A var. *aberrans* different perianthiis facie ventrali laevibus. Type. Brazil. Rio de Janeiro: Serra de Itatiaia, Visconde de Maua, Maromba, 1450 m, 17 April 1987, *Schäfer-Verwimp 8330*, (holotype, U; isotypes, G, SP, hb. Schäfer-Verwimp).

? *Lejeunea loxensis* Gottsche, Syn. Hep. 335. 1845, nom. dubium (Kruijt, 1988); *Dicranolejeunea loxensis* (Gottsche) Stephani, Spec. Hep. **5:** 161. 1912. Type. Peru (?). "In cortice *Chinae Loxae*," *Häcker s.n.* (holotype destroyed in B).

? *Lejeunea caldana* Ångström, Öfvers. Förh. Kongl. Svenska Vetensk-Akad. **33:** 84. 1876; *Lophocolea caldana* (Aongström) S. Arnell, Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. **111:** 108., nom. inval. [error for *Lopholejeunea caldana*]; *Lopholejeunea caldana* (Ångström) auct., nom. herb. Type. Brazil. *Widgren & Henschen s.n.* (n.v.). The type has not been located. Other collections of this species (hb S, W) belong to *Acanthocoleus aberrans*.

Dicranolejeunea setacea Stephani, Hedwigia **35:** 78. 1896. Type. Brazil. *Ule 258* (holotype, G).

Dicranolejeunea renauldii Stephani, Hedwigia **35:** 78. 1896. Type. Ecuador. Ex hb. Renauld (holotype, G).

Homalolejeunea corcovadensis Stephani, Hedwigia **35:** 98. 1896; *Marchesinia corcovadensis* (Stephani) Stephani, Spec. Hep. **5:** 143, 148. 1912. Type. Brazil. Rio de Janeiro: Mt. Corcovado, *Ule 92* (holotype, G), *syn. nov.*

Odontolejeunea paulina Stephani, Hedwigia **35:** 116. 1896; *Cyclolejeunea paulina* (Stephani) Stephani, Spec. Hep. **5:** 186. 1913. Type. Brazil. São Paulo: Apiahy, *Puiggari s.n.* (holotype, G, n.v.), syn. fide Grolle (1989).

Dicranolejeunea paulina Gottsche ex Stephani, Spec. Hep. **5:** 167. 1912. Type (Kruijt, 1988). Brazil. São Paulo: Apiahy, *Puiggari 278* (lectotype, G).

Dicranolejeunea rotundata Evans, Trans. Conn. Acad. Arts. Sci. **18:** 323. 1914. Type. Peru. St. Ana, *Foote s.n.* (holotype, YU).

Thysananthus schiffneri S. Arnell *in* Schiffner & Arnell, Oesterr. Akad. Wiss. Math.-Naturwiss. Kl., Denkschr. **111:** 119. 1964 "*schiffnerii*" Type. Brazil. Paraná: Rio Paranapanema, Salto Grande, on trees, ca. 500 m, *Schiffner 2097* (holotype, W; isotype, S), *syn. nov.*

Autoicous. *Plants* 1–2 cm long x 0.6–1.5 mm wide, yellowish green to brown. *Stems* 0.1–0.15 mm in diam., in cross section composed of 9–12 epidermal cells surrounding 17–40 medullary cells, dorsal epidermal cells about as large as the ventral epidermal cells; ventral merophyte two cells wide. *Leaves* contiguous to imbricate, dorsal lobe ovate, 0.5–0.9 x 0.4–0.7 mm, apex apiculate to short acuminate, rarely rounded, margins entire to toothed near apex with 1–5 teeth, the teeth consisting of 1–6 cells, ventral margin forming an angle of ca. 90–170° with the keel; median cells ca. 30–40 x 25 µm, with very small, cordate trigones; oil bodies small, 10–15(–25) per cell, finely segmented, *Jungermannia*-type, ellipsoid to subglobose, ca. 2–6 x 2–2.5 µm. *Lobules* ovate, up to 0.3 mm long, 1/4–1/3x lobe length, often reduced, keel arched, free margin with 1–2 teeth separated from each other by 3–7 margin cells, first tooth (1)2–4 cells long, inflexed, second tooth smaller, 1–2 cells long, sometimes obsolete. *Underleaves* subimbricate, 0,2–0.4 mm, 2–3x stem width, margins plane or slightly recurved, insertion line arched. *Androecia* as in var. *aberrans*. *Gynoecia* with (1–)2 innovations, innovations often fertile, bract lobes ovate-oblong, up to 0.7 mm long, apex apiculate

FIG. 51. Distribution of *Acanthocoleus aberrans* var. *aberrans* (stars) and var. *laevis* (dots).

to short acuminate, margins entire or toothed near apex with 1–5 teeth, lobule small, up to 1/5× lobe lenght, sometimes reduced, keel smooth; bracteoles 0.5–0.6 mm long, margins plane or narrowly recurved. *Perianths* obcuneate, up to 1 mm long × 0.6–0.7 mm wide, emergent to 1/3–1/2, rather flattened, with 2 sharp lateral keels and one swollen, rounded, broad or narrow ventral keel, the lateral keels usually winged over 1/2 or more of perianth length and dentate to ciliate above, cilia up to 10 cells long and 1–3 cells wide, occasionally wings and cilia reduced, the ventral keel smooth or with a few ciliae; beak 2–4 cells long. *Sporophyte* as in the genus; seta with 16 outer rows of cells throughout its length.

Distribution (Fig. 51). Scattered throughout tropical America, at altitudes of 250–2600 m; towards the southern limits of its range occurring below 1500 m. The variety has also been recorded from tropical Africa (Kruijt, 1988, as Acanthocoleus aberrans). *Acanthocoleus aberrans* var. *laevis* grows on bark or rock in rather open, mesic woodlands and scrub, and on isolated trees. It mostly lacks in the humid, evergreen forest regions.

Selected specimens examined. MEXICO. DISTRICT FEDERAL: Desierto de los Leones, *Sharp 1682* (TENN), *Horton 7536* (JE); Tlaxpehualco, *Antipovich 70* (US); E of Lerma along Route 15, *Hermann & Crum 20858* (US). OAXACA: road Llano de las Flores to Tuxtepec, *Iwatsuki & Sharp 2770* (TENN); above Tamazulapam, *Sharp et al. 2540, 2809* (TENN). TAMAULIPAS: above Gomez Farias, *Sharp 8714d* (TENN).

CUBA. GRANMA: Sierra Maestra, Pico Boyamesa, *Pócs 9066/BQ* (EGR, HAC, U). GUANTÁNAMO: Meseta de Guasco, *Pócs et al. 9190/H* (EGR, HAC, U). SANTIAGO DE CUBA: Gran Piedra, *Reyes 209, 1400* (HAC, U); Manguita, *Lippold 16692* (JE). VILLA CLARA: Sierra del Escambray, Pico Portrerillo, *Pócs & Borhidi 9011/AY* (U).

JAMAICA. Hardware Gap, *Griffin s.n.* (U).

HAITI. Near St. Michel de l'Atalaye, *Leonard 7577* (US).

WINDWARD ISLANDS. GUADELOUPE. Morne

Graine-Verte, *Duss 440* (NY, U).

COLOMBIA. BOYACÁ: road Arcabuco-Villa de Leiva, *vanderHammen et al. 2480* (U). **CUNDINAMARCA:** Sasaimira, *King C-849* (U). **MAGDALENA:** Sierra Nevada de Santa Marta, San Lorenzo, *Winkler 223* (U). **TOLIMA:** Ibagué, *Micholitz s.n.* (G NY, U).

VENEZUELA. LARA: Sierra de Portuguesa, *Griffin & Lopez 363a* (FLAS, U). **MERÍDA:** Mucuy, *Onraedt 78V5508, 78V6519* (U); *Fendler s.n.* (B, G).

ECUADOR. Popayan, Spruce s.n. (MANCH). **GALÁPAGOSISLANDS:** Santa Cruz, Mt. Crocker, *Gradstein & Weber H47, H76* (U).

PERU. SANMARTÍN: above Rioja, *Frahm et al. 797* (B, U).

BRAZIL. DISTRICTFEDERAL: Planalto, near Cia, *Irwin et al. 31688, 31691, 31696, 31700* (NY, U). **MINAS GERAIS:** Rio dos Vieiras, *Vital 6219* (SP, U). **PARANÁ:** Rio Paranapanema, Salto Grande, *Schiffner 2111* (S, W); Morretes, *Dusén 12077* (S). **RIO GRANDE DO SUL:** Baje, *Vital 9194* (JE). **SANTACATARINA:** Serra Geral, *Ule 239* (B, G); Ipema, Lajes, *Reitz & Klein 15653* (US). **SÃO PAULO:** Apiahy, *Puiggari s.n.* (G); Alto de Serra, *Schiffner 395* (UPS); Rio Branco, Santo, *Schiffner 2129* (UPS); near Raiz da Sierra, *Schiffner 924* (W); Mt. Jaraguá, near Taipas, *Schiffner 1032* (S); Barra do Turvo, *Vital 6219* (SP, U); Pirassununga, *Vital 2734b* (SP, U).

BOLIVIA. COCHABAMBA: Incacorral, *Herzog 5024* (B, G, L). **TARIJA:** along Río Bermejo 6 km SE of La Marmore, *Gradstein 7690, 7698, 7699, 7700, 7701, 7704* (LPB, U).

ARGENTINA. CATAMARCA: Belén, Quebrada del Río Blanco, *Sleumer 2155* (S).

PARAGUAY. ALTO PARANÁ: 35 km N of Hernandarías, *Geissler 14542, 14545, 14645* (G). **GUAIRÁ:** Cordillera del Ybytyruzú S of Colonia Independencia, *Geissler 15095* (G). **PARAGUARÍ:** Ybicuí, Colonia Boquerón, *Geissler 14505* (G).

URUGUAY. Tacuarembó, Arroyo Yaguary, *Zorrón 2866* (US).

Acanthocoleus aberrans var. *laevis* is the most common and widespread taxon in the genus. All records from the South American mainland, except those from French Guiana, are referable to this taxon. In addition, African records of *A. aberrans* may also belong to this variety. In Central America and the West Indies, both var. *laevis* and the typical variety of *A. aberrans* occur.

Acanthocoleus aberrans var. *laevis* stands out by its perianth with a smooth ventral surface, lacking sharp keels (as in *Dicranolejeunea axillaris*). Occasionally a few ciliae are produced at the lateral edges of the swollen ventral perianth surface (e.g. Guadeloupe, *Duss 440*) but sharp ventral keels are never produced. In var. *aberrans*, on the other hand, the ventral surface of the perianth has (1–)2 sharp, ciliate ventral keels. Besides their different perianths, the two varieties tend to differ in a few other morphological traits, none of these being constant, however. In var. *laevis* innovations are always paired and frequently fertile, leaf lobules are frequently reduced, and leaf apices are sometimes rounded instead of pointed. In the typical variety of *A. aberrans*, innovations are mostly single (sometimes paired) and usually sterile, the lobules are never (?) reduced, and the leaf apex is always pointed, never rounded.

The cilia of the perianth vary considerably in length and may become reduced. Forms with subentire perianths, only bearing a few scattered teeth near apex, occur frequently near the southern limits of the range (e.g. collections from Paraguay, leg. Geissler).

Some collections of *Acanthocoleus aberrans* var. *laevis*, including the types of *Dicranolejeunea rotundata* Evans, *D. renauldii* Steph. and *D. setacea* Steph., have been misidentified as *Brachiolejeunea phyllorhiza* by Kruijt and Gradstein (1986). For differences with that species see under the latter. *Acanthocoleus aberrans* var. *laevis* is also very similar to *Dicranolejeunea axillaris*; differences have been discussed above under the genus. Sterile specimens with rounded leaf apices cannot be distinguished from *A. trigonus*.

2. Acanthocoleus juddii Kruijt, Bryophyt. Bibl. **36:** 93. 1988. Type. Haiti. Massif de la Selle, La Visite National Park, ravine of Rivière Blanche, near where crossed by road from Seguin to Furcy, *Judd 4338* (holotype, U).

Paroicous. *Plants* up to 2 cm long x 2 mm wide, green to brown. *Stems* ca. 0.15 mm in diam., in cross section composed of 10–12 epidermal cells surrounding 25–40 medullary cells, dorsal epidermal cells slightly larger than ventral epidermal cells; ventral merophyte 2 cells wide. *Leaves* imbricate, dorsal lobe orbicular, 0.6–0.9 mm, apex apiculate, occasionally rounded, margins entire, ventral margin forming a straight line or wide angle (150–180°) with the keel; median cells 30–40 x 25 m long, oil bodies not observed. *Lobules* (sub)rectangular, 0.4–0.6 x 0.2–0.4 mm, 1/2–2/3× lobe length, occasionally reduced, keel straight, free margin with 1–2 teeth separated from each other by 3–6 margin cells, first tooth large, triangular, 3–6 cells long and 2–4 cells wide at base, the tip inflexed, second tooth small, 1–2 cells long, sometimes obsolete. *Underleaves* distant to subimbricate, 0,2–0.4 mm, 2–3× stem width, insertion line arched. *Androecia* located on main stem or branches directly below the gynoecium, bracts in 2–4 series, almost similar to leaves, lobules somewhat more inflated, bracteoles not smaller than underleaves; one antheridium per bract. *Gynoecia* with two innovations, bract lobes narrow oblong, up to 0.8 mm long, apex acute-apiculate, margins entire, lobule up to 1/3× lobe length, sometimes reduced; bracteoles ca. 0.7 mm long, plane. *Perianths* up to 1 mm long, emergent to 1/2, with three keels: 2 sharp lateral keels and one broad rounded keel, the lateral keels winged in the upper 1/3 and with 2–6 teeth, the ventral keel smooth; beak 3–4 cells long.

Illustration. Kruijt, Bryophyt. Bibl. **36:** 95, Pl. 12. 1988.

Distribution (Fig. 53). A rare species, known from Mexico, Cuba and Haiti, at elevations of 800–1800 m in the Greater Antilles and ca. 2500 m in Mexico. *Acanthocoleus juddii* always grows on rock.

Specimens examined. MEXICO. Valley of Mexico, Cañada, *Pringle 10690* (YU).

CUBA. SANTIAGO DE CUBA: Laguna Victoria II, *Reyes 1380* (U). VILLA CLARA: Sierra de Escambray, *Pócs & Borhidi 9011/BH, 9011/AY* (U).

HAITI. Type of *Acanthocoleus juddii.*

Acanthocoleus juddii is a well-defined species, separated from its congeners by its large, rectangular lobules with very conspicous teeth, and by the broad, orbicular leaf lobes.

3. Acanthocoleus trigonus (Nees & Montagne) Gradstein, Contr. Bot. Univ. Michigan Herb. **18:** 101. 1992; *Lejeunea trigona* Nees & Montagne, Ann. Sci. Nat., Bot. (sér. 2) **5:** 61. 1836; *Archilejeunea trigona* (Nees & Montagne) Stephani, Spec. Hep. **4:** 721. 1911. Type. Peru. Laguna: Santa Cruz, "in *Parmelia speciosa,*" *d'Orbigny s.n.* (holotype, STR; isotype, PC-MONT). Fig. 52.

Archilejeunea argentinica Herzog, Feddes Repert. Spec. Nov. Regni Veg. **55:** 12. 1952. Type. Argentina. Cordoba: Ongamira, *Hosseus s.n.* (Bauer 533) (holotype, JE), *syn. nov.*

Paroicous. *Plants* 1–2 cm long × 1.5–2 mm wide, dull green to brown. *Stems* ca. 0.2 mm in diam., in cross section composed of 11–16 epidermal cells surrounding 25–40 medullary cells; ventral merophyte 2(–4) cells wide. *Leaves* (sub)imbricate, dorsal lobe ovate, 0.8–1.1 × 0.6–0.9 mm, apex rounded to obtuse to apiculate (apiculate especially on female shoots), margins entire, ventral margin forming a straight line or wide angle (150–180°) with the keel; median cells 33–40 × 25–30 m long, with minute, cordate trigones; oil bodies not observed. *Lobules* triangular to ovate, ca. 1/4–2/5× lobe length, often reduced, keel curved, free margin with 0–2 small teeth (large lobules have 2, small lobules 0–1 teeth), 1–2 cells long. *Underleaves* distant, 0,3–0.5 mm, 1.5–3× stem width, insertion line curved. *Androecia* located on main stem or branches directly below the gynoecium, bracts in 3–6 series, lobes similar to leaves but lobules larger, ca. 1/2× leaf length, distinctly inflated and with incurved free margin; bracteoles not smaller than underleaves; one antheridium per bract. *Gynoecia* with 1–2 innovations, bract lobes ovate to oblong, up to 0.8 mm long, apex apiculate, margins entire or with a few 1-celled teeth, lobule minute; bracteoles ca. 0.5 mm long, sometimes gibbose, margins plane. *Perianths* up to 1 mm long, emergent to 1/2, usually entirely inflated and terete, sometimes bluntly trigonous above, smooth; beak 2–3 cells long. *Sporophyte* seta made up of 14–16 outer rows of cells and 4–5 inner rows.

Distribution (Fig. 53). *Acanthocoleus trigonus* has a restricted, subtropical distribution. It occurs along the southern edge of the neotropics, mainly in southern Bolivia (1600–2600 m), southern Brazil (1100 m) and northern Argentina. The type is from central Peru. The species has apparently been overlooked because except for the type all collections are of recent date. It grows on rocks along streams in semi-deciduous, riparian woodlands or scrub, in areas with a prolonged dry season.

Specimens examined. PERU. Type of *Acanthocoleus trigonus.*

BRAZIL. SANTA CATARINA: Serra do Corvo Branco, road Urubici-Crao Pará, just below the pass, Dec 1990,

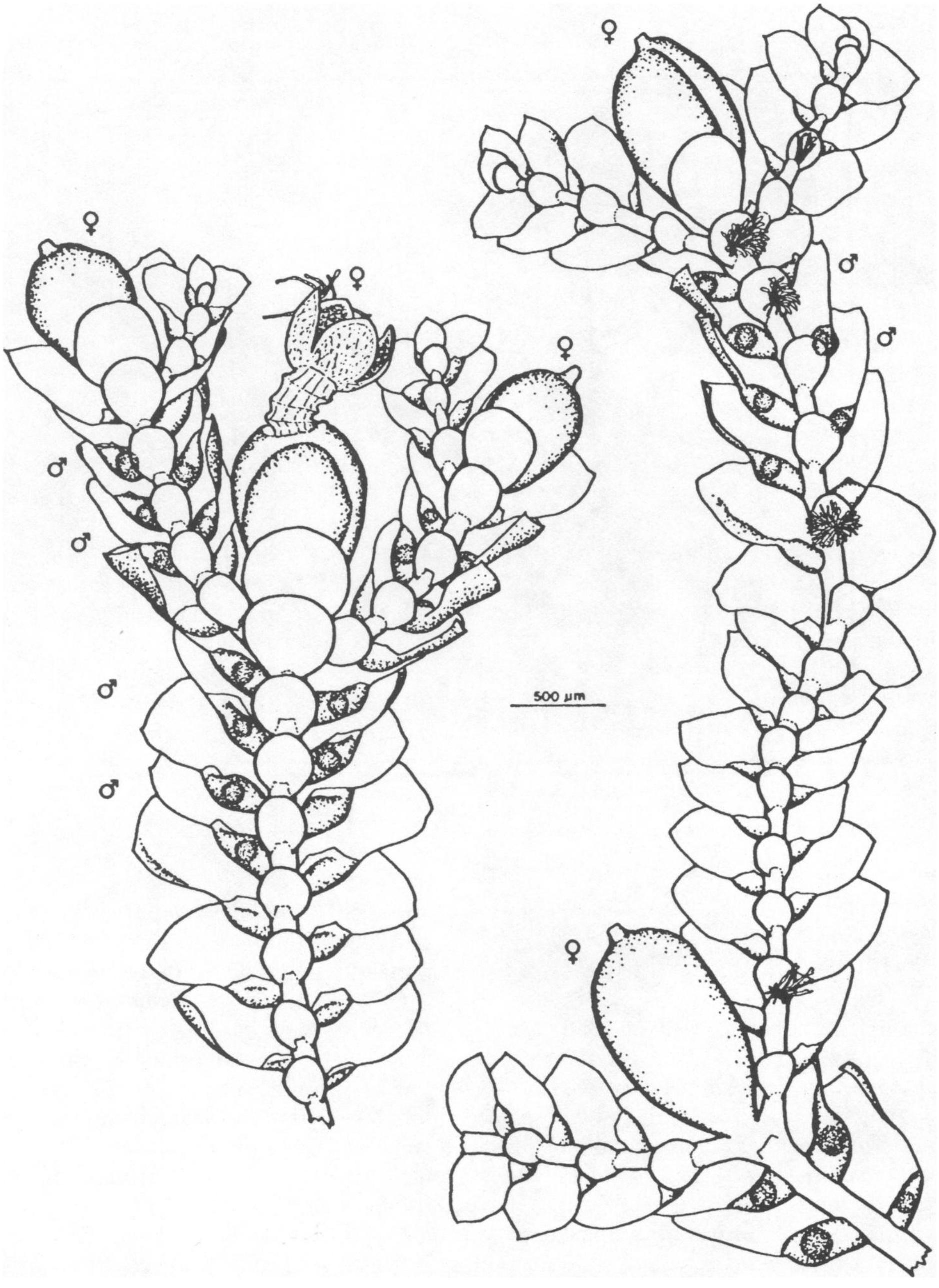

FIG. 52. *Acanthocoleus trigonus*. Habit of two fertile plants, showing paroicous sex distribution, fertile innovations and sporophyte with articulate seta. From Bolivia, *Gradstein 7607* (left) and *7721*.

Schäfer-Verwimp 13496 (hb. Schäfer-Verwimp, U).

BOLIVIA. CHUQUISACA: Río Jatum Mayu 14 km NW of Zudañez, *Lewis 84-0489* (LPB, U). TARIJA: along road Tarija-Bermejo, ca. 10 km N of La Marmora, *Gradstein 7720, 7721* (LPB, U); headwaters of Río Los Pinos 20 km NW of Padcaya, *Lewis 84-2910* (LPB); headwaters Río Posta along road Tarija-Entre Rios 1950 m, *Gradstein 7648* (LPB, U); headwaters Río Huayco along road Narvaez-San Josecito, *Gradstein 7687* (LPB, U); along Río Tambo ca. 5 km S of Narvaez, *Lewis 84-2631, 84-2675* (LPB), *Gradstein 7651* (LPB, U); Cerro Sarzo 4 km NW of Canaletas, *Lewis 84-2510* (LPB).

FIG. 53. Distribution of *Acanthocoleus juddii* (diamonds), *A. trigonus* (stars) and *Odontolejeunea rhomalea* (dots).

ARGENTINA. CORDOBA: Dept. Ischilín, Ongamira, *Hosseus 1514, 1515*, ster., topotypes of *Archilejeunea argentinica* Herz. (NY).

Although described as early as 1836, as *Lejeunea trigona* Nees & Mont., *Acanthocoleus trigonus* has long been known only from the very scanty type specimen. Stephani (1909-12) placed it in *Archilejeunea*, and Kruijt and Gradstein (1985) associated it with *Brachiolejeunea phyllorhiza*. Recently (Gradstein, 1992a), I have shown that the species has been misunderstood and belongs in *Acanthocoleus*.

During fieldwork in southern Bolivia (Dept. Tarija) in 1989, I discovered large populations of *Acanthocoleus trigonus* on boulders along streams in humid gallery forests. The species was easily recognized in the field by its fully inflated, terete perianths without keels. Terete perianths are rather common in the *Lejeuneoideae* (*Omphalanthus*, *Taxilejeunea*, *Sphaerolejeunea*, etc.) but in the *Brachiolejeuneae* they were unknown. In addition to the terete ones, bluntly trigonous perianths are produced in *A. trigonus*.

Other characteristic features of *Acanthocoleus trigonus* are its paroicous sexuality and its leaf apex, which is usually rounded instead of apiculate as in other species of *Acanthocoleus*. The lobules in the Bolivian materials are usually small and often reduced (except for those of the male bracts), but in a rather robust specimen from southern Brazil (*Schäfer-Verwimp 13496*), they are well-developed and have two distinct teeth. A very unusual feature of *Acanthocoleus trigonus* is the seta which consists in part of only 14 outer rows of cells.

Acanthocoleus trigonus is closely related to *A. chrysophyllus* (Lehm.) Kruijt from Africa, with which it shares the paroicous sexuality, ovate leaves, and rather small lobules. However, in the African species the leaves are acute or short acuminate, the perianths are always three-keeled and the lateral keels are rather sharp and frequently winged-toothed.

When sterile, *Acanthocoleus trigonus* cannot be distinguished with certainty from *A. aberrans* var. *laevis* even though rounded leaves, characteristic of *A. laevis*, are rare in *A. aberrans*.

22. Odontolejeunea (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 127. 1893; Teeuwen, Nova Hedwigia **48:** 1. 1989; *Lejeunea* subgen. *Odontolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 142. 1884. Lectotype (Evans, 1904). *Odontolejeunea lunulata* (Weber) Schiffner. Genus named for its toothed leaves.

Plants up to 4 cm long × 0.8–3.5 mm wide, glossy green to brown green when alive, usually becoming brown when dry, creeping. *Branching Lejeunea*-type, rarely *Frullania*-type, irregularly pinnate, flagelliform branches lacking. Stems with a distinct hyalodermis, epidermal cells smooth or slightly convex, thickwalled, fewer and much larger (2–5×) than the medullary cells, dorsal epidermal cells as large as ventral epidermal cells or slightly smaller, walls of the inner medullary cells thin, those of the outer medullary cells often somewhat thickened, all cell walls colorless or the ventral epidermal walls somewhat brownish; ventral merophyte only two cell rows wide. *Leaves* variously convoluted, crisped or revoluted when dry, wide spreading when moist, lobe apex rounded, margins sharply toothed; median cells (sub)isodiametric, trigones cordate or simple triangular, intermediate thickenings frequent; oil bodies homogeneous or segmented, *Massula*-type or *Calypogeia*-type; ocelli lacking. *Lobules* 1/5–2/5× lobe length, sometimes reduced, inflated along the keel, flattened towards the free margin, with 1–6 teeth; hyaline papilla positioned on the inner side of the lobule below the proximal base of the first tooth. *Underleaves* 2–5× stem width, apex rounded, margins toothed or entire, bases short decurrent and often folded, seemingly auriculate, insertion line deeply arched; underleaf base at the rhizoid disc tristratose and elongated-stalked, with two superior central cells; rhizoids often coalesced and forming an adhesive disc. *Androecia* on short or long branches, bracts smaller than leaves, lobules strongly inflated, epistatic, underleaves present throughout; antheridia two per bract. *Gynoecia* on main stems or on branches, with 1(–2) pycnolejeunoid subfloral innovations, rarely without innovation, bracts in one series, resembling leaves but lobules reduced to small, narrow folds, keel very short, without wing; bracteoles longer than underleaves, undivided, the margins plane or slightly recurved, toothed or entire. *Perianths* exserted to 1/2, obpyriform, with three keels, the lateral keels winged and dentate-ciliate, the ventral keel smooth and unwinged or slightly winged-dentate; beak short, sometimes recessed. *Sporophyte*: seta articulate; spores with rudimentary rosettes; otherwise as in the tribe. *Vegetative reproduction* by means of short, caducous branchlets with somewhat modified leaves ("cladia").

Distribution. The genus *Odontolejeunea* contains three species (Teeuwen, 1989), all of which occur in the neotropics. One species, *O. lunulata*, is also distributed in tropical Africa. The species are found in lowland and montane forests, from sealevel to 3200 m, and are usually epiphyllous but may also grow on bark.

Odontolejeunea differs from all other genera of Ptychanthoideae by its ability to produce short, caducous branchlets or "cladia." Teeuwen (1989) has demonstrated that the shape of the basal leaves of the cladia is different in each species of *Odontolejeunea*. Cladia may not always be present, however. Further characteristic features of *Odontolejeunea* include the toothed leaves, the very conspicuous hyaloderm made up of epidermal cells 2–5× larger than the medullary cells, the two cells wide ventral merophyte, the dentate-ciliate perianth, and the predominant growth of the plants on living leaves and twigs. *Odontolejeunea* frequently produces adhesive rhizoids discs or "secondary rhizoid discs" (Gradstein, 1975), which are characteristic of epiphyllous Lejeuneaceae and are an adaptation to growth on leaves. A remarkable feature of *Odontolejeunea* is the occurrence within the genus of two types of oil bodies: homogeneous (*O. lunulata*) and segmented (*O. decemdentata*). The present treatment largely follows Teeuwen (1989).

Key to the Species of *Odontolejeunea*

1. Underleaf margins toothed.
    2. Lobule with 2–4 teeth; leaves convoluted or irregularly crisped when dry; leaf cells oriented in length

rows (as usual in Lejeuneaceae); throughout the neotropics, 0–3000 m, very common. 2. *O. lunulata.*

2. Lobule with 4–6 teeth; leaves plane or with margins curved upwards (dorsad) when dry; leaf cells oriented in transverse rows extending from the dorsal to the ventral leaf margin; South and Central America, 0–3200 m, uncommon. . . . . . 3. *O. rhomalea.*

1. Underleaf margins entire.
   3. Lobule with 2–4 teeth; underleaf bases auriculate; throughout the neotropics, 0–3000 m, very common. . . . . 2. *O. lunulata.*
   3. Lobule with 0–1(–2) teeth; underleaf bases cuneate, auricles lacking; throughout the neotropics, 0–1800 m, uncommon. . . . . 1. *O. decemdentata.*

1. Odontolejeunea decemdentata (Spruce) Stephani, Spec. Hep. **5:** 171. 1912; Teeuwen, Nova Hedwigia **48:** 10. 1989; *Lejeunea decemdentata* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 148. 1884. Type. Ecuador. Río Bombonasa, *Spruce L215* (holotype, MANCH; isotype, G).

Lejeunea hapalochroa Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 149. 1884; *Cyclolejeunea hapalochroa* (Spruce) Stephani, Spec. Hep. **5:** 188. 1913. Type. Peru. San Martín: Mt. Guayrapurina, *Spruce s.n.* (MANCH, n.v.), syn. fide Grolle (1989).

Odontolejeunea tocoriensis Stephani, Hedwigia **35:** 117. 1896. Type. Costa Rica. Quebrada de Tocori, *Tonduz 3077b* (holotype, G; isotype, BM).

Odontolejeunea longispica Evans, Bull. Torey Bot. Club **35:** 380. 1908. Type. Jamaica. *Harris 11119* (holotype, YU; isotype, NY).

Dioicous. *Plants* to 2 cm long × 0.8–1.8 mm wide, glossy greenish to pale brown when dry. *Branching Lejeunea*-type, rarely *Frullania*-type. *Stems* 0.08–0.13 mm in diam., in cross section composed of ca. 10–12 epidermal cells surrounding 10–25 much smaller medullary cells. *Leaves* distant to subimbricate, crisped when dry, dorsal lobe ovate, 0.5–1.0 × 0.3–0.7 mm, apex obtuse, margins plane, distally with 7–12 teeth, ventral margin sometimes untoothed, forming a more or less straight line with the keel; median cells ca. 20–40 μm, with small cordate or simple triangular trigones and 1(–2) intermediate thickenings on longer cell walls; oil bodies (fide A. Schäfer-Verwimp, pers. comm.) 7–15 per cell, fewer in leaf margin cells, finely segmented, 3–4 × 3–11 μm, ellipsoid to subglobose. *Lobules* ovate-triangular or almost rounded, small, sometimes reduced, 1/5–1/3× lobe length, keel curved, free margin with 1(-2) erect or incurved teeth, first teeth 1–2 cells long, second tooth one-celled or lacking. *Underleaves* distant, orbicular to transversely obovate, 0.15–0.3 mm in diam., 1.5–3× stem width, margins plane or slightly recurved, entire or bluntly crenulate, bases cuneate, short decurrent, neither folded nor auriculate, insertion line arched to 0.12 mm deep. *Androecia* as in the genus. *Gynoecia*: bract lobes slightly larger than leaves, margins with 4–12 teeth; bracteoles obovate, up to 0.5 mm long, margins entire or crenulate. *Perianths* with two dentate-ciliate lateral keels and one smooth ventral keel; beak 2–3 cells long, not recessed. *Sporophyte* as in the genus. *Vegetative reproduction*: cladia frequent, basal leaves acuminate, their margins with numerous small teeth.

Illustration. Teeuwen, Nova Hedwigia **48:** 13, Pl. 1. 1989.

Distribution. Costa Rica, West Indies (Jamaica, Saba), French Guiana, along the Andes from Venezuela to Bolivia, and in SE Brazil, from sea level to 1800 m. *Odontolejeunea decemdentata* is the rarest species of the genus and grows in humid virgin rain forest on living leaves, occasionally on twigs.

Specimens examined. COSTA RICA. ALAJUELA: Cordillera Central, *Eggers CR1,36* (U); **GUANACASTE:** El Arenal, *Standley & Valerio 45161a* (JE, S, US). San Marcos, *Tonduz 15576* (G).

JAMAICA. Portland, Seamen's Valley, *Maxon & Killip 8* (NY, S).

WINDWARD ISLANDS. SABA. *Suringar s.n.* (L)

COLOMBIA. CUNDINAMARCA: Bogotá, La Vega, *Apollinaire s.n.* (G, NY). **VALLE:** between Cali and Buenaventura, *Bischler 489* (COL, U).

VENEZUELA. ARAGUA: Maracay, *Onraedt 78 V 5645a* (JE). **ZULIA:** Sierra de Perija, San José de Altos, *Griffin 188* (NY, U).

FRENCH GUIANA. Saül, Mt. Galbao, *Bekker 2322* (U).

ECUADOR. AZUAY: Gualaquiza, *Allioni 6484, 6591* (G, S). **CHIMBORAZO:** *Spruce s.n.* (MANCH). **LOS RIOS:** Hacienda Clementina, *Harling 296, 519, 520, 2145, 5538* (JE, S). **NAPO-PASTAZA:** Mera, *Harling 3170, 3183* (S, UPS). **SANTIAGO-ZAMORA:** Méndez, *Harling 969* (JE, S, UPS).

PERU. Type of *Lejeunea hapalochroa.*

BRAZIL. RIO DE JANEIRO: Parque National Itatiaia, Mata atlantica, Veu de Noiva, *Schäfer-Verwimp 14687* (U). Also recorded from Sao Paulo State, by Grolle (1989).

BOLIVIA. COCHABAMBA: road Cochabamba-Villa Tunari km 112, *Gradstein & Lewis 7519, Bryoph. Neotrop.*

Exsicc. 227 (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MEXU, MG, MO, NY, PMA, QCA, S, SP, U, USJ, XAL).

Odontolejeunea decemdentata is the smallest species of the genus and stands out by its pale color, segmented oil bodies, entire underleaves without auricles, and by its few (1–2) lobule teeth.

2. **Odontolejeunea lunulata** (Weber) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 128. 1893; Teeuwen, Nova Hedwigia **48:** 14. 1989; *Jungermannia lunulata* Weber, Hist. Musc. Hep. Prodr. 33. 1815; *Lejeunea lunulata* (Weber) Nees, Syn. Hep. 326. 1845. Type. "E regionibus tropicis in foliis Musae," *Sprengel s.n. (BM, S).* Fig. 54.

Jungermannia tortuosa Lehmann & Lindenberg *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. **4:** 50. 1832; *Lejeunea tortuosa* (Lehmann & Lindenberg) Lehmann & Lindenberg, Syn. Hep. 327. 1845; *Odontolejeunea tortuosa* (Lehmann & Lindenberg) Stephani, Spec. Hep. **5:** 171. 1912. Type. Africa. "Oware" (holotype, S; isotypes, G, MANCH, W).

Phragmicoma calcarata Montagne, Ann. Sci. Nat., Bot. (sér. 2) **19:** 259. 1843; *Lejeunea lunulata* (Weber) Nees fo. *calcarata* (Montagne) Gottsche et al., Syn. Hep. 326. 1845; *Odontolejeunea calcarata* (Montagne) Stephani, Spec. Hep. **5:** 171. 1912. Type. Suriname. *Splitgerber 1206* (holotype, PC-MONT; isotypes, BM, G, L).

Lejeunea martinicensis Lindenberg, Syn. Hep. 328. 1845; *Odontolejeunea martinicensis* (Lindenberg) Stephani, Spec. Hep. **5:** 171. 1912. Type. Martinique. *Sieber s.n.* (holotype, W; isotypes, G, S).

Lejeunea sieberiana Gottsche, Syn. Hep. 328. 1845; *Odontolejeunea sieberiana* (Gottsche) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 127. 1893. Type. Africa. Mauritius. *Sieber s.n.* (isotypes, S, W).

Lejeunea chaerophylla Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 147. 1884; *Odontolejeunea chaerophylla* (Spruce) Schiffner *in* Engler & Prantl, Nat. Pflanzenfam. **1 (3):** 127. 1893. Type. Peru. San Martín: Tarapoto, *Spruce s.n.* (holotype, MANCH).

Odontolejeunea angustifolia Stephani, Spec. Hep. **5:** 176. 1912. Type. Dominica. *Elliott 1200* (holotype, G).

Dicranolejeunea grossiloba Stephani, Spec. Hep. **5:** 166. 1912. Type. Ecuador. *Unknown collector* (holotype, G).

Odontolejeunea cubensis Stephani, Spec. Hep. **5:** 179. 1913. Type. Cuba. *Wright s.n.* (holotype, G).

Odontolejeunea ecuadoriensis Stephani, Spec. Hep. **5:** 179. 1913. Type. Ecuador. Azuay: *Allioni 6553* (holotype, G).

Odontolejeunea levistipula Stephani, Spec. Hep. **5:** 181. 1913. Type. Brazil. Without loc., *Dusén 8395* (holotype, G).

Odontolejeunea nigrescens Stephani, Spec. Hep. **5:** 181. 1913. Type. Ecuador. Cerier, *Allioni 6557* (holotype, G).

Odontolejeunea paranensis Stephani, Spec. Hep. **5:** 180. 1913. Type. Brazil. Paraná: Etarunandes, *Dusén 4378* (holotype, G).

Odontolejeunea spiniloba Stephani, Spec. Hep. **5:** 180. 1913. Type. Ecuador. Azuay: *Allioni 6588* (holotype, G).

Dicranolejeunea herzogiana Stephani, Biblioth. Bot. **87:** 253. 1916. Type (Kruijt 1988). Bolivia. Cochabamba: Tablas, *Herzog 4603* (lectotype, G).

Odontolejeunea armitagei Pearson, J. Bot. **60:** 217. 1922. Type. Dominica. Mountain Lake, *Armitage s.n.* (holotype, MANCH).

Monoicous or dioicous. *Plants* to 3 cm long × 1–3 mm wide, glossy, usually brownish green. *Branching Lejeunea*-type. *Stems* 0.07–0.15 mm in diam., in cross section composed of 10–12 thin-walled epidermal cells surrounding 10–55 much smaller medullary cells. *Leaves* subimbricate, irregularly crisped-subconvoluted when dry, especially the ventral portion of the leaf, dorsal lobe ovate, 0.5–1.8 × 0.3–1.3 mm, apex rounded-obtuse, dorsal margin plane, ventral upcurved, when flattened forming an angle of 110–180° with the keel, margins toothed all around with 7–24 teeth, teeth usually consisting of 1–10 cells, ventral tooth much larger, consisting of up to 30 cells; median cells ca. 20–35 m, with small cordate trigones and 1(–2) intermediate thickenings on longer cell walls; oil bodies small, homogeneous, *Massula*-type, 6–25 per cell. *Lobules* trapezoid-quadrate to short ovate, ca. 0.2–0.5 long, 1/5–1/3× lobe length, keel curved, free margin with 2–4 erect or incurved teeth, teeth 1–3 cells long. *Underleaves* distant to contiguous, orbicular to transversely ovate, 0.2–0.7 × 0,3–1 mm, (2–)3–5(–7)× stem width, margins usually recurved and weakly to strongly toothed with up to 25 teeth, occasionally entire, bases cordate, folded and seemingly auriculate, the "auricles" rounded or angular, insertion line arched to 0.15–0.3 mm deep. *Androecia* as in the genus. *Gynoecia*: bract lobes larger than leaves, the margins toothed with 10–25 teeth; bracteoles obovate-suborbicular, ca. 0.6–0.9 mm long, margins toothed. *Perianths* with two dentate-ciliate lateral keels and one smooth or slightly dentate ventral keel; beak 2–6 cells long, usually slightly recessed. *Sporophyte* as in the genus. *Vegetative reproduction*: cladia occasionally present, basal leaves with acute apex, margins with numerous small teeth.

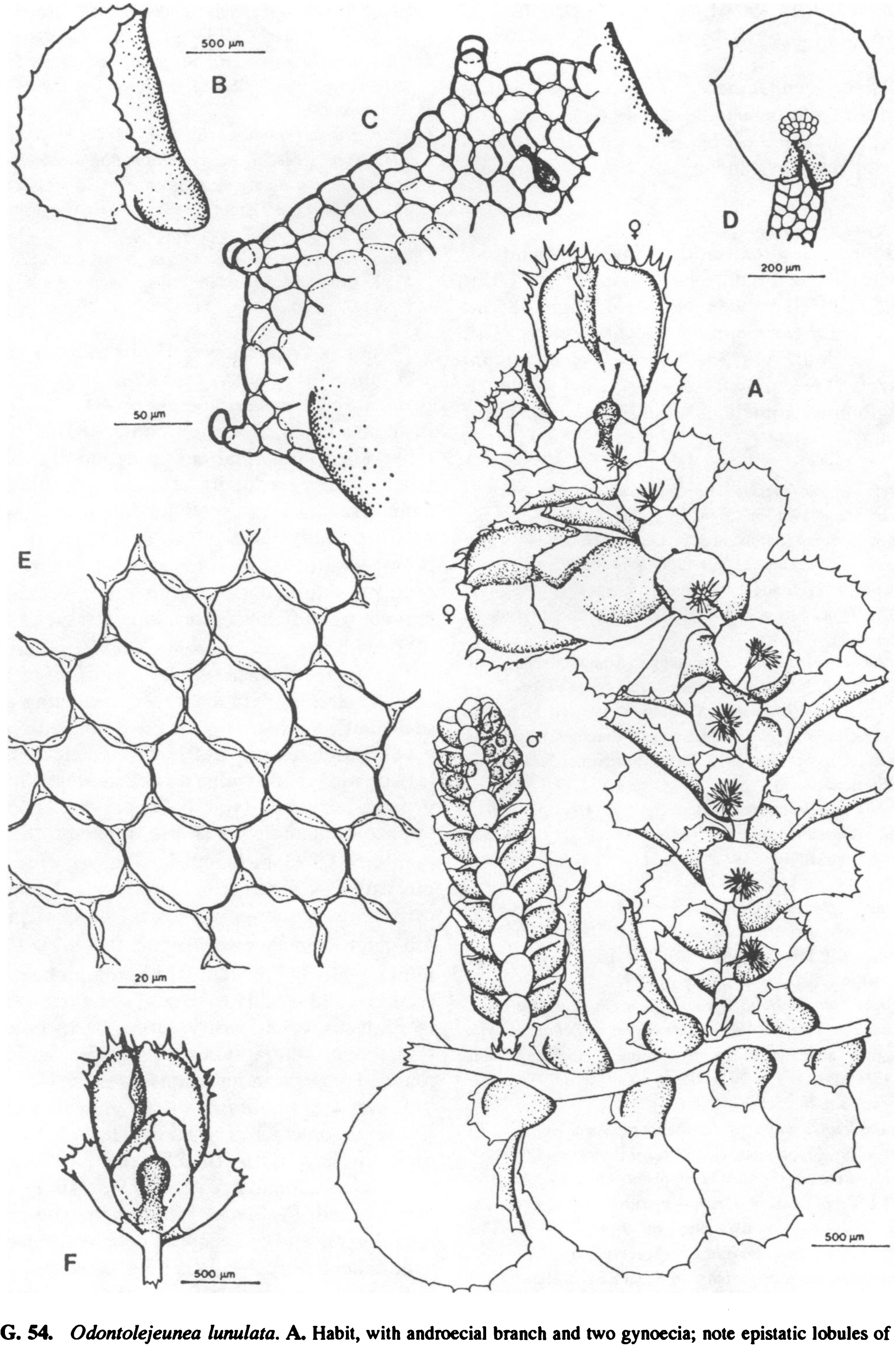

FIG. 54. *Odontolejeunea lunulata.* **A.** Habit, with androecial branch and two gynoecia; note epistatic lobules of male bracts, rhizoid discs on underleaves, and *Lejeunea*-type branching (underleaves removed in main stem). **B.** Leaf. **C.** Lobule free margin. **D.** Underleaf. **E.** Leaf cells. **F.** Gynoecium. From Brazil, *Vital 2591.*

Distribution. Very common throughout tropical America, from sea level up to 3000 m; also in tropical Africa. *Odontolejeunea lunulata* occurs in primary and disturbed forests and in scrub on living leaves, twigs and on trunks, very rarely on soil. The species is one of the most common epiphyllous liverwort species of tropical America. It is also common on bark and in a submontane rain forest in Bolivia, the author observed that *O. lunulata* occurred mainly on bark whereas *O. rhomalea* was common on leaves.

Selected specimens examined. MEXICO. CHIAPAS: Lagunas de Montebello, *Eggers & Frahm MX25,1* (U); Tapachuela, Benito Juarez, *Eggers & Frahm MX34,3* (U). **Oaxaca :** Sierra Juarez above Valle Nacional, *Robinson 10043, 10101, 10116* (US).

GUATEMALA. ALTO VERAPAZ: Cubilquiz, *Türckheim 5067* (G, NY); near Tactic, *Standley 69994* (NY, US).

HONDURAS. ATLÁNTIDA: Tela, *Standley 55586* (S, US). Comayagua: near Siguatepeque, *Morton 7580* (US). **CORTEZ:** N of Lake Yojoa, *Morton 7879, 7884* (US).

COSTA RICA. CARTAGO: Tapanti, *Griffin & Eakin 321-B* (U). **HEREDIA:** Yerba Buena, *Standley & Valerio 49802* (JE). **LIMÓN:** Cairo, *Standley & Valerio 48676* (JE). **PUNTARENAS:** Cordillera de Tilarán, *Eggers CR5,47* (U). **TALAMANCA:** Shirores, *Tonduz 15502* (G).

CUBA. GUANTÁNAMO: Baracoa, *Pócs & Reyes 9064/BZ* (HAC); Campamento Gupeyal, *Schubert s.n.* (JE). **HOLGUIN:** Sierra de Nipe, *Ekman 10090* (UPS). **SANTIAGO DE CUBA:** Gran Piedra, *Pócs & Reyes 9058* (HAC).

JAMAICA. Bath, *Evans 319* (BM, NY, YU); Cinchona, John Crow's Peak, *Britton 221* (NY, YU); St. Elisabeth, *Maxon & Killip 1467* (NY, US, YU); Morce's Gap, *Evans 55* (BM, NY, YU); Hardwar Gap, *Griffin 21753* (U).

HAITI. Massif de la Selle, *Judd 4591b* (JE).

DOMINICAN REPUBLIC. Azua, *Ehrman H6334a* (JE).

PUERTO RICO. Maricao, *Britton et al. 4391* (NY, YU); Mt. Morales, *Howe 1094* (NY, YU); Adjuntas, *Britton & Marble 216* (NY, YU); Luquillo Mts., *Evans 182* (NY, YU), *Blomquist 12568* (NY).

WINDWARD ISLANDS. MONTSERRAT. Chances Pond, *Shafer 926b* (NY, YU). **GUADELOUPE.** Morne Graine-Verte, *Duss 449* (NY); Bois des Banis-Jannes, *Duss 1017* (G, NY); La Desirée, *Duss 303* (G, NY). **DOMINICA.** Morne Trois Pitons, *Elliott 760* (BM), *Schuster 67509a* (US); Laudat, *Lloyd 324a* (NY, YU); Soufrière, *Lloyd 547* (NY, YU). **MARTINIQUE.** Bois de la Médaille, *Duss 1189* (NY); Pitons de Fort de France, *Duss 379* (NY); Deux-Choux, *Duss 401* (NY, YU). **ST. VINCENT.** Richmond Peak, *Elliott 356* (BM). **GRENADA.** Grand Etang, *Thaxter s.n.* (YU).

COLOMBIA. CALDAS: Santa Cecilia, *von Sneidern 5083a* (US). **CHOCÓ:** Pizarro, *von Sneidern 4897a* (US); along road Tutunendo-El Carmen, 100-600 m., *Aguirre & Gradstein s.n.* (COL); Mun. Nuqui, near Arusi, *Aguirre & Gradstein s.n.* (COL). **CUNDINAMARCA:** La Vega, *Apollinaire s.n.* (L); Laguna Pedro-Palo, *Bischler 3026* (COL, U); road Bogotá-Villavicencio, 2000 m, *Bischler 33* (COL, U). **HUILA:** La Plata, *Aguirre et al. 6565* (COL). **PUTUMAYO:** NW of Puerto Asis, *King & Guevara C-1133* (US). **RISARALDA:** Mun. San Antonio de Chami, Geguades, *Gradstein 8635* (COL, U). **SANTANDER:** Las Vegas, *Killip & Smith 16042* (NY, S); Loso, *Killip & Smith 20401* (NY); Charalá, *Killip & Smith 19151* (JE). **TOLIMA:** St. Isabel, *Aguirre & Gradstein 1732* (COL). **VALLE:** Cisneros, *Killip 11478a* (JE); La Cumbre, *Killip 11387* (YU).

VENEZUELA. AMAZONAS: San Carlos del Río Negro, *Spruce s.n.* (BM, G, MANCH, YU), *Delascio et al. 3999* (U); Atabapo, *Guariglia et al. 1442* (NY). **BOLÍVAR:** along Río Cicuta, *Steyermark & Gibson 95787* (US, VEN). **DISTRICT FEDERAL:** Caracas, *Goebel s.n.* (BM). **LARA:** Morán, S of Humocaro Alto, *Steyermark & Carreno E. 111113* (US, VEN). **MÉRIDA:** St. Barbara, *Liesner & Gonzáles 9235a* (MO, U). **SUCRE:** Peninsula de Paria, *Steyermark & Rabe 96286* (VEN, US).

TRINIDAD. Port of Spain, *Thaxter s.n.* (YU); Mt. Tocuche, *Britton et al. 1476* (YU); Valencia, *Britton et al. 1849* (NY, YU); Spring Hill, *Fleming s.n.* (NY).

GUYANA. Bartica, *Richards 492* (BM, YU); Kanuku Mts., Cool Wind Mt., *Jansen-Jacobs et al. 389B* (U); Upper Mazaruni Distr., Jawalla, *Gradstein 4850* (U), Kamarang, *Gradstein 5657, Bryoph. Neotrop. Exsicc. 147* (B, BA, CANM, COL, F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL).

SURINAME. Mapane Cr. area, *Schulz 7726* (U); Brownsberg, *Gradstein 4686* (U); Lely Mts., *Lindeman et al. 556D* (U); Nassau Mts., *Lanjouw & Lindeman 2207* (U).

FRENCH GUIANA. Kourou, *Bekker 2051* (U); Mt. de Cacao, *Aptroot 15588a* (U); Saül, *Cremers 3940* (CAY, U), *Montfoort & Ek 1040-1046* (U); Haute Tampoc, *Cremers 4635* (CAY, JE, U).

ECUADOR. Azuay: Gualaquiza, *Allioni 6471* (G). **CHIMBORAZO:** *Spruce s.n.* (MANCH). **LOS RÍOS:** Hacienda Clementina, Samama, *Harling 187* (S). **NAPO - PASTAZA:** Inchiyacu, *Harling 3611* (S); Mera, *Harling 3234* (S); Santa Bárbara de Sucumbios, *Harling 4181* (S, UPS). **SANTIAGO-ZAMORA:** Méndez, *Harling 2211* (S).

PERU. HUANUCO: Tingo Maria, *Hegewald 8294* (U); near Cerros del Sira, *Dudley 13338Aa* (U). **LORETO:** Maynas, *Timme 4694* (NY). **SAN MARTÍN:** Tarapoto, *Ule 611* (G, L).

BRAZIL. AMAPÁ: Oyapock, *Lützelburg 20170* (JE). **AMAZONAS:** Manaus, *Nelson 19* (NY); road Manaus-Caracarai, *Griffin et al. 561* (FLAS, U); Rio Cunhua, *Prance et al. 16508* (NY); Rio Negro, São Gabriel, *Spruce s.n.* (MANCH). **MINASGERAIS:** Caldas, *Mosén Ff* (G, S, UPS). **PARÁ:** Tanaú, *Spruce s.n.* (MANCH); Serra do Cachimbo, *Reese 16060* (NY, US). **PARANÁ:** Serra do Mar, *Dusén s.n.* (S); Roca nova, *Dusén 14* (YU). **RIO GRANDE DO SUL:**

Santo Angelo, *Lindman s.n.* (S, UPS). **Roraima:** Auaris, *Prance et al. 21516* (NY). **São Paulo:** Apiahy, *Puiggari 846* (G); Alto da Serra, *Hoehne 533* (JE); *Barra Mansa, Schiffner 1839* (UPS); Barra do Turvo, *Vital 2791c* (SP, U); Reserva Florestal de Sete Barras, *Vital 7120* (SP, U).

BOLIVIA. Beni: Ballívian, Serranía del Pilón Lagas, *Gradstein 7146, 7197, 7229* (LPB, U). **Cochabamba:** Espiritu Santo, *Herzog 2792c* (JE).

Reported from Argentina (Misiones) by Reiner-Drehwald (1993).

Although the type specimen of *Odontolejeunea lunulata* is dioicous, the species is more commonly monoicous. *Odontolejeunea lunulata* is the only species of the genus which may produce monoicous populations; the two other species are strictly dioicous. As pointed out by Teeuwen (1989), the polyoicy of *O. lunulata* has caused much confusion as to the correct delimitation of the species. Several of the synonyms listed here, e.g., *O. tortuosa*, *O. sieberiana* and *O. chaerophylla*, are mere monoicous forms of the species.

3. **Odontolejeunea rhomalea** (Spruce) Stephani, Spec. Hep. **5:** 171. 1912; Teeuwen, Nova Hedwigia **48:** 23. 1989; *Lejeunea rhomalea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh **15:** 143. 1884. Type. Ecuador. "Río Verde, fl. Pastasa affluens," *Spruce XL78* (holotype, MANCH).

Odontolejeunea grandiloba Stephani, Spec. Hep. **5:** 181. 1913. Type. Ecuador. Azuay: *Allioni 6466* (holotype, G).

Odontolejeunea obversilobula Herzog, Hedwigia **71:** 339. 1931. Type (Teeuwen, 1989). Venezuela. Amazonas: Río Casiquiare, *von Lützelburg 22263* (lectotype, JE).

Dioicous. *Plants* to 4 cm long × 1.5–3.5 mm wide, glossy green to blackish brown when dry. *Branching Lejeunea*-type. *Stems* 0.12–0.25 mm in diam., in cross section composed of 10–13 epidermal cells surrounding 30–70 much smaller medullary cells, the cell walls ± thickened. *Leaves* imbricate, plane or with upcurved margins when dry, dorsal lobe broadly ovate to suborbicular, 0.7–2 × 0.6–1.8 mm, dorsal margin plane, ventral plane or upcurved, when flattened forming an angle of 90–150× with the keel, margins toothed all around with 10–22 teeth, teeth consisting of 1–10 cells, ventral tooth much larger, of up to 40 cells; median cells ca. 30–45 μm long, frequently somewhat wider than long, orientated in transverse rows, with large cordate trigones and 1(–2) intermediate thickenings on longer cell walls; oil bodies small, homogeneous, *Massula*-type, 15–25 per cell. *Lobules* triangular-ovate to subrectangular, ca. 0.2–0.8 mm long, 1/4–2/5× lobe length, keel concave or almost straight, free margin with (3–)4–6 incurved teeth, teeth 1–3 cells long. *Underleaves* imbricate, orbicular to transversely ovate, 0.4–0.8 × 0,5–1.5 mm, 4–6× stem width, margins plane or recurved, sharply dentate, teeth often recurved, bases cordate, folded and seemingly auriculate, the "auricles" acute-acuminate, insertion line arched to 0.15–0.3 mm deep. *Androecia* as in the genus. *Gynoecia*: bract lobes about as large as leaves, the margins toothed with 12–17 teeth; bracteoles obovate, ca. 0.7–0.9 mm long, margins toothed. *Perianths* with two dentate-ciliate lateral keeds and one smooth or slightly dentate ventral keel; beak 4–7 cells long, not or slightly recessed. *Sporophyte* not observed. *Vegetative reproduction*: cladia occasionally present, basal leaves with rounded apex, margins with numerous small teeth.

Illustration. Teeuwen, Nova Hedwigia **48:** 27, Pl. 5. 1989.

Distribution (Fig. 53). Central and northern South America, from sea level to 3200 m but uncommon in lowland areas. *Odontolejeunea rhomalea* grows in virgin and slightly disturbed humid rain forests, on living leaves or twigs in the understory and in the canopy. The species very rarely grows on soil.

Specimens examined. GUATEMALA. Alto Verapaz: Cobán, *Türckheim 5080* (G); Cubilquitz, *Türckheim 5060, 5063,5066* (BM, G, NY).

COSTA RICA. Talamanca, *Tonduz 6230, 6231, 15542* (G); Río Naranjo, *Tonduz 3082, 15504, 15605* (G); Golfo Dulce, *Tonduz 15564, 15579* (G, NY, S, YU).

COLOMBIA. Santander: Charalá, Virolín, *Castro & Cruz 386* (COL, U). **Valle:** Córdoba, *Killip 5086* (JE, NY).

VENEZUELA. Amazonas: Río Casiquiare, *von Lützelburg 22262, 22263, 22269, 22354* (JE).

GUYANA. Bartica, *Richards 313* (BM, YU); Upper Mazaruni River, Kamakusa, *Long 9* (NY).

SURINAME. Kabalebo Dam project area, *Bekker 1684, 1690A, 1709A* (U).

FRENCH GUIANA. River Comté, between Belizon and Jalbot, *Degelius s.n.* (UPS); near River Arataye, *Cremers 5526* (CAY,U); Saül, *Cremers 3941b* (CAY, JE), *Aptroot 15301g* (U), *Montfoort & Ek 1048-1055* (U), *Gradstein 6107, Bryoph. Neotrop. Exsicc. 148* (B, BA, CANM, COL,

F, FLAS, G, H, JBSD, L, MG, MO, MEXU, NY, PMA, QCA, S, SP, U, USJ, XAL).

ECUADOR. Azuay: Gualaquiza, *Allioni 6549, 6554, 6590, 6594, 6597* (G). **Esmeraldas:** Río San Miguel, *Harling 4701* (S); Río Grande, *Harling 4629* (NY, S). **Napo-Pastaza:** El Topo, *Harling 3409* (S); Río Napo, Almana, *Harling 3645* (S); Río Pastaza, Mera, *Harling 3234* (S). **Zamora-Chinchipe:** *Harling 5886* (S).

PERU. Cuszco: Río Paucartambo, *Killip & Smith 25257* (JE), *25256* (US). **Huanuco:** *Weberbauer 3677* (G). **Loreto:** Pena Blanca, on Río Itaya, *Killip & Smith 29654* (JE, NY, S, US). **San Martín:** Tarapoto, *Spruce s.n.* (MANCH); Rioja, *Frahm et al. 97* (B, U).

BRAZIL. Amapá: Oyapock, Salto Manoa, *von Lützelburg 20199* (JE). **Amazonas:** Manaus, *Ule 580* (G); Rio Juruá, *Ule 550, 551, 552* (BM, G); Rio Uatumã, *Buck 2881* (NY); Rio Negro, Sao Gabriel, *Spruce s.n.* (BM, G, MANCH, NY); Serra Curicuriari, *Buck 2427* (NY). **Roraima:** Uaicá, *Prance et al. 19960* (NY, U). Also recorded from Sao Paulo State, by Vital and Pursell (1992).

BOLIVIA. Beni: Ballívian, Serranía del Pilón Lagas, *Gradstein 7131, 7132, 7135* (U).

The upcurved margins of dried leaves of *Odontolejeunea rhomalea* are a very characteristic feature of this species and are probably induced by the unusual leaf areolation. The leaf cells in this species tend to be wider than long and are arranged in transverse rows, extending from the dorsal to the ventral margin of the leaves. In other species of *Odontolejeunea* they are isodiametrical and arranged in longitudinal rows as usual in the Lejeuneaceae.

Excluded Species

(see Teeuwen, 1989: 29–30)

Odontolejeunea convexistipa (Lehmann & Lindenberg) Schiffner = *Cyclolejeunea convexistipa* (Lehmann & Lindenberg) Evans

Odontolejeunea integerrima Stephani = *Cyclolejeunea integerrima* (Stephani) Stephani

Odontolejeunea mimula Stephani = *Cyclolejeunea mimula* (Stephani) Stephani

Odontolejeunea mirabilis Stephani ex Goebel, nom. nud. = *Cyclolejeunea peruviana* (Lehmann & Lindenberg) Evans

Odontolejeunea paulina Stephani = *Cyclolejeunea paulina* (Stephani) Stephani

Odontolejeunea peruviana (Lehmann & Lindenberg) Stephani = *Cyclolejeunea peruviana* (Lehmann & Lindenberg) Evans

Odontolejeunea stachyclada (Spruce) Stephani = *Cyclolejeunea convexistipa* (Lehmann & Lindenberg) Evans

Odontolejeunea subbifida Stephani = *Cyclolejeunea chitonia* (Taylor) Evans

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INDEX OF SCIENTIFIC NAMES

New names and new combinations are in **boldface** and synonyms in *italics*.