

A Taxonomic Monograph of the Genus *Acrolejeunea* (Hepaticae)

with an Arrangement of the Genera
of Ptychanthoideae

(Studies on Lejeuneaceae subfam. Ptychanthoideae III)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
IN DE WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE RIJKSUNIVERSITEIT TE UTRECHT, OP
GEZAG VAN DE RECTOR MAGNIFICUS PROF. DR.
S.J. GROENMAN, VOLGENS BESLUIT VAN HET
COLLEGE VAN DEKANEN IN HET OPENBAAR TE
VERDEDIGEN OP MAANDAG 20 OKTOBER 1975
DES NAMIDDAGS TE 4.15 UUR

DOOR

STEPHAN ROBBERT GRADSTEIN

geboren op 31 oktober 1943 te Krimpen aan de IJssel



J. CRAMER · 1975

In der A.R. Gantner Verlag Kommanditgesellschaft
FL-9490 VADUZ

PROMOTOR: DR. P.A. FLORSCHÜTZ

PREFACE

At the completion of this thesis I wish to express my sincere gratitude to my Promotor, Dr. P.A.Florschütz, for his continual support and cordial friendship, and for his constructive criticism on the manuscript.

I am greatly indebted to Professor Dr. M.H.Fulford (Cincinnati, U.S.A.) and Dr. R.Grolle (Jena, D.D.R.) for their invaluable guidance and advice. Part of this work was carried out when I was a research assistant of Dr. Fulford in 1970-71.

Thanks are due to Professor Dr. F.Verdoorn for his interest in this work, which follows the footsteps traced by him long ago, and for putting at my disposal pertinent hepaticological literature; and to Professor Dr. F.A.Stafleu for valuable advice concerning language and nomenclature.

Finally I wish to thank all those who assisted in the preparation of the manuscript, particularly Mr. T.Schipper for skillfully inking my pencil drawings published here, Dr. A.Touw for making available base maps from the Rijksherbarium, Leiden, Dr. T. van der Hammen and Mr. A.M.Cleef for suggested improvements concerning the introductory chapters, Mrs. J.R.A.J.Hendriks-Holla, Miss E.G.Henken, and Mrs. A.Holla-Smit for preparing the typescript, and lastly my wife for critically reviewing the English text and for tolerating a life dominated by *Acrolejeunea*.

Aan de nagedachtenis van mijn vader
Aan mijn moeder

TABLE OF CONTENTS

Introduction	9
Part I: A taxonomic monograph of the genus <i>Acrolejeunea</i>	
History	12
Morphology and Anatomy	15
1. Leaves	15
2. Cells	18
3. Stem structure	20
4. Underleaves and primary rhizoid disc	21
5. Branching	23
6. Gametoecea	26
7. Sporophyte and sporeling development	28
8. Vegetative reproduction	32
Subdivision	35
1. Species, subspecies and varieties	35
2. Subgenera and sections	38
3. Conspectus	40
4. Phenetic diagram	42
Distribution	43
Evolutionary trends	46
Generic relationship	50
TAXONOMIC TREATMENT	52
<i>Acrolejeunea</i>	52
Key to the species of <i>Acrolejeunea</i>	55
Subgenus <i>Acrolejeunea</i>	59
Section <i>Pusillae</i>	59
Section <i>Acrolejeunea</i>	63
Subgenus <i>Isolejeunea</i>	83
Section <i>Regulares</i>	83
Section <i>Isolejeunea</i>	103
Excludenda	125
Types not available for this study	130
Part II: An arrangement of the genera of <i>Ptychanthoideae</i>	
1. Circumscription of the <i>Ptychanthoideae</i>	134
2. Generic classification	142
3. Synopsis	145
4. Concluding remarks	147

References	152
Index of Names	160
Plates I-XXIV	

INTRODUCTION

The present study was initiated a few years ago by Dr. R. Grolle (Jena) who discovered that *Acrolejeunea* (Spruce) Schiffn. was probably the correct name for a tropical liverwort genus to which in this century the name *Ptychocoleus* Trev. was applied. Since replacing the name *Ptychocoleus* by *Acrolejeunea* would necessitate a considerable number of nomenclatural changes, I was asked to reexamine the taxonomy of the group.

I soon found that *Ptychocoleus* as traditionally understood is heterogeneous and consists of two well-defined genera: *Acrolejeunea* (Spruce) Schiffn. and *Schiffneriolejeunea* Verd. (Gradstein 1974a). In order to determine their taxonomic affinities, I decided to review the generic subdivision of the subfamily Ptychanthoideae (Lejeuneaceae) to which they belong. The present work comprises the taxonomic monograph of *Acrolejeunea* and the review of the subfamily. The monograph of *Schiffneriolejeunea* will be published separately.

For the present study I have examined specimens from the following herbaria (abbreviations of institutional herbaria according to Index Herbariorum ed. 6):

AAU, ABSH, B. BM, BP, BR, C, CHR, COLO, DUKE, EGR, F, FH (+ FH-Tayl., FH-Schiffn.), FLAS, G, GRO, H, JE, K, L, M, MANCH, NICH, O, PC (+ PC-Mont.), PI, PRC, PRE, S, SP, STR, TNS, TO, U, UPS, US, W, WELT, YU, and the private herbaria from Dr. Margaret H. Fulford (Cincinnati), Dr. R. Grolle (Jena), Dr. E. Hegewald (Dortmund), Dr. H. Hürlimann (Basel), Dr. E. W. Jones (Kirtlington), Dr. N. Kitagawa (Nara), and Dr. C. Vanden Berghen (Brussel).

I express my gratitude to the directors and curators of the herbaria for making the specimens available. I am particularly indebted to Dr. Suzanne Jovet-Ast and Dr. Hélène Bischler (Paris), Dr. Geneva Sayre (Cambridge, U.S.A.), Dr. C. E. B. Bonner (Geneva), Dr. A. Bresinski (München), Mr. A. Eddy (London), Dr. G. L. Smith and Dr. W. C. Steere (New York), Dr. A. Touw (Leiden), Dr. O. Vitikainen (Helsinki), and Dr. B. O. van Zanten (Groningen) for their hospitality and generous assistance upon my visits to their institutions for the study of *Acrolejeunea* and *Schiffneriolejeunea*. Financial assistance from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), the Centre National de la Recherche Scientifique (C.N.R.S.), and the "Miquel Fonds" for these travels is gratefully acknowledged.

Searching for records of *Acrolejeunea* and *Schiffneriolejeunea* I have gone through large amounts of unrevised specimens of "holostipous Lejeuneaceae"

from recent explorations. This effort proved extremely fruitful since it yielded many new data on morphological variation and geographic distribution. For sending unrevised materials I am indebted to:

Dr. Hélène Bischler (Paris) for her *Holostipae* from Colombia (collected 1956-59);

Dr. D.Griffin III (Gainesville) for his *Holostipae* from tropical America (collected 1968-1974);

Dr. R.Grolle (Jena) for various unrevised collections;

Dr. and Mrs. E.Hegewald (Dortmund) for their *Holostipae* from Peru (collected 1973);

Dr. H.Hürlimann (Basel) for his *Holostipae* from New Caledonia, Tonga, Fiji and Tahiti (collected 1950-52);

Frère Maurice Onraedt (Malonne) for his *Holostipae* from Madagascar, Réunion and Seychelles (collected 1969, 1971 and 1973-74). He also kindly sent me specimens recently collected by Mr. G.Cremers (O.R.S. T.O.M., Tananarive) on Madagascar;

Dr. T.Pocs (Eger) for his *Holostipae* from Vietnam (collected 1963-1966) and Tanzania (collected 1969-73).

The study of fresh material, collected by colleagues in the field, yielded data on such critical characters as oil body and sporophyte structure. Living specimens from Brazil were provided by Dr. D.M.Vital and Dr. G.L.Smith; from tropical West Africa by Mrs. Fr.Ketelaars-van Eindhoven and Dr. G.K.Berrie; from Colombia by Mr. A.M.Cleef and Dr. P.A.Florschütz; from Malesia by Mr. H.J.M.Sipman. I am most indebted to all colleagues afore mentioned, and also to Dr. E.W.Jones for putting at my disposal his unpublished observations on oil bodies in African *Acrolejeunea*, *Schiffneriolejeunea* and *Archilejeunea*.

I

A TAXONOMIC MONOGRAPH OF THE GENUS
ACROLEJEUNEA

In his epoche-making treatment of the liverworts of tropical South America, SPRUCE (1884) published *Acro-Lejeunea* as one of his 37 subgenera of *Lejeunea* Lib. The genus *Lejeunea* sensu Spruce is almost equivalent to the family of Lejeuneaceae Casares-Gil, currently comprising over 75 accepted genera in c. 5 subfamilies. *Acro-Lejeunea* was established to include a number of species previously assigned to *Phragmicoma* Dum., a genus which was characterised by SPRUCE and later authors as an "agglomeration of species of various distinct types" (SPRUCE l.c.: 71). The subgenus *Acro-Lejeunea*, which belongs to the *Holostipae* Spruce (possessing undivided underleaves), was essentially characterised by the perianth being terminal on a stem or a long branch, lacking subfloral innovations, being more or less inflated, and bearing 4-5 or 7-10 smooth plicae. This circumscription reflects the fundamental importance of the gynoecium for the delimitation of SPRUCE's subgenera.

SPRUCE included 12 species in *Acro-Lejeunea*: *Phragmicoma torulosa* (Lehm. & Lindenb.) Lehm. & Lindenb., *Phr. polycarpa* (Nees) Nees, *Phr. juliformis* (Nees) Nees, *Lejeunea linguaeifolia* Tayl., *L. domingensis* Tayl., *L. marsupiiifolia* Spruce (sp. nov.) from tropical America, and *Phragmicoma fertilis* (Nees) Nees, *Phr. hasskarliana* Gott., *Phr. tumida* (Nees) Nees & Mont., *Lejeunea malaccensis* Tayl., *L. peradeniensis* Mitt., *L. terminalis* Spruce (sp. nov.) from Southeast Asia.

Subsequent taxonomic studies on tropical liverworts by STEPHANI and SCHIFFNER contributed to the rapid increase in size of the group. Due to their effort to revise the collections of Lejeuneaceae in the classical herbaria of LINDENBERG in Vienna (STEPHANI 1890) and of GOTTSCHKE in Berlin (SCHIFFNER 1894, 1897; herbarium destroyed in 1945), most of the earlier described species of Lejeuneaceae got to be placed in the subgenera of SPRUCE. In 1889, STEPHANI listed 24 species in the subgenus *Acro-Lejeunea*, including *Phragmicoma aulacophora* Mont. from Tahiti, *Phr. securifolia* (Nees) Nees from Norfolk I., *Phr. emergens* Mitt. from Rodriguez I., and 5 further species from Africa. The subgenus had now become truly pantropical in distribution.

SCHIFFNER (1893), in his classical treatment of the Hepaticae in Engler & Prantl, *Die Natürlichen Pflanzenfamilien*, assigned 38 species to *Acrolejeunea*, which he formally raised to generic rank. Thus, within ten years the number of species in *Acrolejeunea* had increased more than threefold. EVANS (1908) revised some of the South American species assigned to *Acrolejeunea* and reviewed the delimitation and taxonomic affinities of the genus. His placing the genus next to *Brachiolejeunea* has been followed by most later authors. At the same

time EVANS reduced *Acrolejeunea* to synonymy under the almost forgotten genus *Ptychocoleus* Trev. (1877) by choosing *Acrolejeunea aulacophora* (Mont.) Schiffn. as the lectotype of *Ptychocoleus*.

STEPHANI (1912) adopted the name *Ptychocoleus sensu* Evans in his monumental *Species Hepaticarum* and listed 85 species in this group, thus making it the largest genus of the *Holostipae*. STEPHANI's treatment is the only existing comprehensive study of *Ptychocoleus*, but unfortunately his descriptions are vague or incorrect. Thirty new species of *Ptychocoleus* were described in this treatment, from which only three or four survived subsequent revisions (including this revision). The name change from *Acrolejeunea* to *Ptychocoleus* has apparently been a rapid course of action, because all STEPHANI collections of this group (over 500 !) are labelled "*Acro-Lej*" or "*Acrolej*" in his handwriting. The adoption of the name *Ptychocoleus* in the *Species Hepaticarum* was apparently decisive for its general future use. Except for PEARSON, who described two new species as "*Acrolejeunea*" in 1922, no author between 1912 and 1972 (VAN DEN BERGHEN) has ever again used the name *Acrolejeunea*.

VERDOORN (1932, 1933, 1934) revised the Asian and Australasian species assigned to *Ptychocoleus*. He classified the species from that area into 8 sections, using characters of the leaves (lobe and lobule), female bracts, and perianth (VERDOORN 1934c: 128-148): 1. sect. *Arcuatae* (2 spp.), 2. sect. *Cristatae* (1 sp.), 3. sect. *Dentatae* (2 spp.), 4. sect. *Minores* (1 sp.), 5. sect. *Mediae* (4 spp.), 6. sect. *Saccatae* (4 spp.), 7. sect. *Regulares* (3 spp.), 8. sect. *Brachiolejeuneoides* (1 sp.). By redefining the species in the group and providing keys and extensive lists of synonyms, he paved the way for the present monograph. VAN DEN BERGHEN (1948) and JONES (1954) produced useful revisions of African species described in *Ptychocoleus*. After their studies the total number of accepted or unrevised binomials in *Ptychocoleus* became c. 50.

The circumscription of *Ptychocoleus* as given by EVANS (1908, 1918) remained unchallenged until data on the oil bodies of the group became available. The diagnostic value of the oil body type for the delimitation of genera and families of liverworts was demonstrated by MÜLLER (1939). ARNELL (1953) reported large, segmented oil bodies in the cells of South African *Ptychocoleus pappeanus* (Nees) Steph., each oil body being composed of a number of small droplets. SCHUSTER and HATTORI (1954) demonstrated the presence of small, homogeneous oil bodies in the cells of *Pt. heterophyllus* Evans from Florida and *Pt. nipponicus* from southern Japan. Because of the apparent presence of two different types of oil bodies in *Ptychocoleus*, SCHUSTER (in SCHUSTER & HATTORI, l.c.) placed *Pt. pappeanus* in a

new genus *Phragmilejeunea* Schust. Besides the oil body type, this genus was characterised by the lobule having only one tooth and the perianth virtually lacking any keels. In 1961 SCHUSTER transferred the African *Pt. molleri* to *Phragmilejeunea*. At the same time he stressed the close relationship between *Phragmilejeunea* and the poorly known monotypic genus *Schiffneriolejeunea* Verd. from Celebes.

MIZUTANI (1961) and BISCHLER (1965) added to our knowledge of the morphology of the genus. MIZUTANI provided a useful morphological diagnosis of *Ptychocoleus*, which for the first time included data on the sporophyte. He also noted the presence of two different branching types. BISCHLER carefully studied the anatomy of the stem in a number of species, and tried to define VERDOORN's sections anatomically. MIZUTANI (1969) advocated the presence of two natural groups within the southeastern Asiatic members of *Ptychocoleus*. The groups, which were not given nomenclatural status, were said to differ in the number of perianth keels, in the form and outline of the female bracts and bracteoles, and in the form of the lobule and the number of its teeth.

GRADSTEIN (1974) demonstrated that the genus *Ptychocoleus* Trev. sensu Evans is to be divided into two different genera. The taxonomic concept of these genera follows logically from the earlier concepts of *Ptychocoleus* held by SCHUSTER and MIZUTANI. The genera were distinguished on the basis of structural differences in the stem, the oil bodies, the androecium, and the perianth. The characters derived from the stem and the androecium were new. The species of *Ptychocoleus* with segmented oil bodies were transferred to *Schiffneriolejeunea* Verd. (1933), which was united with *Phragmilejeunea* Schust. (1954). The group of species with homogeneous oil bodies, including the lectotype of *Ptychocoleus* sensu Evans (*Pt. aulacophorus*) was referred to *Acrolejeunea* (Spruce) Schiffn. In a preliminary conspectus ten species were listed in each genus. *Acrolejeunea* (Spruce) Schiffn. was re-established as a nomenclaturally correct name, and *A. torulosa* (Lehm. & Lindenb.) Schiffn. was chosen as the lectotype. *Ptychocoleus* Trev. was shown, by GROLLE (in GRADSTEIN l.c.), to have been incorrectly lecto-typified by EVANS, and was reduced to synonymy under *Frullanoides* Raddi (= *Brachiolejeunea* subg. *Plicolejeunea* Schust.).

MORPHOLOGY AND ANATOMY

In the last decades a wealth of new morphological and anatomical data has considerably improved our concepts of liverwort taxonomy. The progress in this field was dealt with in excellent reviews by MÜLLER (1951), FULFORD (1964), and SCHUSTER (1966). An up to date review of progress in the Lejeuneaceae is not available although useful morphological discussions and taxonomic evaluations were provided by MIZUTANI (1961) and SCHUSTER (1963).

In this treatment I will discuss the morphology and anatomy of *Acrolejeunea* against the background of the developing new concepts. For this reason some aspects of morphology and anatomy are placed in a wider perspective than others. The main characters which I use in my taxonomic treatment of *Acrolejeunea* are discussed briefly with the introductory taxonomic remarks (p. 37). Some of the morphological concepts discussed here are expanded taxonomically in the chapter on the classification of the genera of Ptychanthoideae (Part II).

1. Leaves (Pl.I)

The mature leaves in *Acrolejeunea* are complicate-bilobed with a large dorsal lobe and a small inflated ventral lobule (Pl.I:1). The leaf is attached to the axis along a S-shaped line of insertion. The insertion-line of the lobe is usually c. 1,5 x the length of the insertion-line of the lobule, and covers half to almost the entire length of the lateral merophyte ⁺) (Pl.I:3,5). The lateral merophytes are interlocking along the dorsal midline of the stem. The interlocking pattern, which is common in the Lejeuneaceae (EVANS. 1935), is obvious because of the presence of a continuous dorsal row of cortical cells (Pl.I:4). This row of cells is alternatively associated with the dorsal base of the leaves of each lateral merophyte.

In plants with closely imbricated leaves (lobe insertion-line always covering the entire length of the merophyte) the lateral merophytes meet dorsally along a straight longitudinal line or along an oblique zig-zag line (Pl.I:2).

⁺) Merophyte = segment of the leafy axis in Jungermanniales which arises from a cutting face of the apical cell. Since the apical cell has three cutting faces (two lateral, one ventral) each plant consists of three merophytes (Douin 1925)

In plants with weakly imbricated leaves (lobe insertion-line usually covering only $1/2-3/4$ x the length of the merophyte) the lateral merophytes always meet along a straight longitudinal line (Pl.I:4). These different merophyte patterns are obvious from the differences in the arrangement of the dorsal cortical cells. I have observed an oblique zig-zag arrangement in all species of *Acrolejeunea* sect. *Acrolejeunea*, and in *Brachiolejeunea* subg. *Plicolejeunea*. In other genera of Ptychanthoideae the merophytes meet dorsally along a straight longitudinal line. The variation observed in the merophyte patterns in Ptychanthoideae demonstrates the plasticity of the outline of the free surface of the lateral merophytes in leafy liverworts. A careful comparative study of the ontogeny of the merophytes is necessary to understand this variation.

The juvenile leaf in *Acrolejeunea* has three hyaline papillae ("slime papillae"). Two of them are associated with the outer ends of the insertion-line of the leaf, the third one is located at the apex of the lobule (Pl. I:1). This is the usual position of the slime papillae in the Lejeuneaceae. The hyaline papilla at the ventral leaf base represents the stylus, which in contrast to Frullaniaceae is not elaborated in Lejeuneaceae (except *Cololejeunea*). STOTLER (1969) and STOTLER & CRANDALL-STOTLER (1974) reported the presence of a fourth hyaline papilla at the apex of the leaf lobe in *Frullania* and *Bryopteris*. This papilla is apparently lacking in *Acrolejeunea*.

A characteristic feature of the leaves in *Acrolejeunea* is the difference in appearance between the dry and the moist state. When dry the leaves are suberect, strongly convoluted, and more or less wrapped around the stem. When moistened, the leaves spread out widely and become strongly convex with the dorsal margin assuming a subvertical position. In *Acrolejeunea* sect. *Acrolejeunea* and sect. *Regulares* the dorsal margin of the lobe tends to curve backwards from its subvertical position, giving the leaves a distinctly squarrose appearance. The marked difference between the dry and the moist state of the leaves is typical for several other genera of Ptychanthoideae as well (see Part II).

The lobule in *Acrolejeunea* is c. $2/5-2/3$ x the length of the lobe, and consists of an inflated, convex portion along the keel and a flattened portion along the free margin (Pl.I:1). A "water-sac" is formed by the inflated portion of the lobule and the adjacent tissue of the lobe. Towards the apex of the lobule the inflated portion narrows down gradually, leaving a narrow opening into the water-sac between the apex and the keel. At the base of the lobule, the inflated portion is attached to the axis by c. 10 cells. The width of the flattened portion varies considerably

within a species, or even within a single plant. In stem leaves the flattened portion is usually developed more conspicuously than in the branch leaves. The transition from the inflated portion into the flattened portion is gradual or abrupt (Pl.I:6,7). When abrupt, the flattened portion tends to become deeply concave and strongly appressed to the lobe, whereas the free margin curves upwards and away from the surface of the lobe. This is seen in *A.mollis*, *A.pycnoclada*, *A.recurvata*, *A.heterophylla*, e.o.

The keel, which connects the lobule with the lobe, is gradually curved or almost straight. In species of *Acrolejeunea* subg. *Isolejeunea* the surface of the keel is sometimes "rough" owing to projecting cells. When the leaf is detached from the stem and spread out, the keel stands at an angle of $90-180^{\circ}$ to the ventral margin of the lobe. In *A.heterophylla* and *A.aulacophora* the angle is $90-120^{\circ}$ ($\sim 140^{\circ}$). In other species, e.g. *A.emergens*, the angle is much wider and as a result the keel forms an almost straight line with the lobe.

The free margin is either flat or upcurved, but never incurved like in some other genera of Ptychanthoideae (*Caudalejeunea*, *Lopholejeunea*). At apex the free margin and the keel meet each other at an oblique or straight angle. When straight (Pl.XV:4,5,6), the free margin ends abruptly at the junction of the keel and the ventral margin of the lobe. When oblique (Pl.VIII:3), the free margin usually continues into the ventral margin of the lobe over a short distance. This continuation of the free margin is less pronounced than in allied genera, e.g. *Mastigolejeunea*, where it is difficult to determine where the free margin ends and the ventral margin of the lobe begins. The free margin in *Acrolejeunea* bears one to ten teeth. Within a species the teeth may vary considerably in number, length, form, and position. A proper understanding of this variation is essential for the taxonomist working with this group. Sometimes the teeth are erect and clearly visible, sometimes they are inflexed and almost invisible (Pl.VII:8). When plants are growing in relatively moist habitats, the teeth tend to become reduced in size. This is particularly obvious in *A.emergens*. The striking variation in the denticulation of the lobule in this species is illustrated in Plate X. Reduction of the entire lobule as a response to moist habitats - a phenomenon often occurring in hygrophytic species of Lejeuneaceae - is never seen in *Acrolejeunea*. Apparently this is correlated to some extent with its preference for relatively xerophytic habitats.

A small, pyriform hyaline papilla is normally found at or near the proximal base of the first tooth on the inner surface of the lobule (cf.Pl.X:5). According to MIZUTANI (1961) this hyaline papilla in the Lejeuneaceae

is always proximal in position to the first tooth. He clearly demonstrated that in genera with a "distal" hyaline papilla - e.g. *Omphalanthus*, *Cheilo-lejeunea* - the hyaline papilla has seemingly become associated with the second tooth due to reduction of the first tooth. An exception to this rule is found in *A.pycnoclada*. In this species the first tooth is situated at the extreme end of the free margin, whereas the second tooth is inserted at the place where the first tooth is normally found (Pl.XVI:2-5). Consequently, the hyaline papilla is inserted at the proximal base of the second tooth. In dried material the hyaline papilla at the lobule apex tends to degenerate and is often hard to find. Therefore it seems to be much more convenient to apply the terms "first tooth", "second tooth", etc. in a numerical sense only and to avoid connecting these terms by definition with the position of the hyaline papilla. In the past the term "apical tooth" was often used for the first tooth of the lobule. I propose to use the term "apical tooth" in a more restricted sense for the tooth of the lobule bearing the hyaline papilla at its proximal base. Thus, it appears that in *Acrolejeunea* the apical tooth is generally the first tooth on the lobule, except in *A.pycnoclada*.

2. Cells (Pl.I)

The cells in the leaf lobe of *Acrolejeunea* are elongate-hexagonal and arranged in more or less diverging rows (Pl.I:8;X:2). The cells in the centre of the lobe are c. 30-40 x 20-25 micron except in *A.arquata*, which has smaller cells. Towards the base of the lobe the cells become slightly larger, but a vitta, as in *Thysananthus* sect. *Vittatae* Verd., is never formed. Along the margin of the lobe a row of smaller subquadrate cells is always present. Ocelli (ZWICKEL 1932) are entirely lacking in *Acrolejeunea*.

The cell walls are smooth and colourless or yellowish, rarely are they reddish-brown pigmented (*A.arquata*). The walls are usually slightly bulging outwardly, giving the leaf surface a somewhat glistening appearance. They consist of a thin middle lamella, with collenchymatic thickenings ("trigones") and elliptical to orbicular intermediate thickenings. Intermediate thickenings are either scarce or frequent. Normally not more than one intermediate thickening is observed on each longer cell wall except in *A.securifolia*, which occasionally has two.

The trigones in the leaves are always heart-shaped ("cordate"), possessing

two convex sides and one concave side. "Semicordate" trigones, possessing two concave sides and one convex side may also be observed. The cordate shape is already present in very young leaves and is apparently initiated in an early stage of leaf development. The lumen of each cell is bordered by three or four convex trigone sides and two or three concave sides. The position of concave and convex sides seems to be correlated with the shape of the cell. In elongate-hexagonal cells with truncate ends the concave sides are usually situated at one end of the cell (Pl.I:10), whereas in cells with acute ends the concave sides are always located at either end of the cell (Pl.I:9). Both cell types occur in each leaf lobe. Cordate trigones are seen in several genera of Ptychanthoideae and they are characteristic for the tribus Ptychantheae emend. Gradst. (Part II). The occurrence of cordate trigones in *Acrolejeunea* was noted earlier in descriptions by EVANS (1908), VANDENBERGHEN (1948), and SCHUSTER (1954).

The size of the trigones varies considerably in response to habitat conditions. Some species however have always small trigones (*A. aulacophora* and *A. securifolia*), whereas in others (*A. arcuata*, *A. parvula*) they are rather large. Often they tend to become large and orbicular in shape in the upper cells of the perianth. In the sect. *Acrolejeunea* trigones and intermediate thickenings tend to become larger towards the dorsal margin of the leaves.

Oil bodies are present in all cells of the leaves, underleaves, and stem cortex. They tend to degenerate rapidly when the plant dries up. They were described previously in *A. emergens* (VANDENBERGHEN 1948, sub *Ptychocoleus confertissimus*), *A. heterophylla* (SCHUSTER 1954), *A. pusilla* (SCHUSTER & HATTORI 1954), and *A. tjibodensis* (INOUE 1967, sub *Ptychocoleus sarawakensis*). I have observed oil bodies in four additional species of *Acrolejeunea*: *A. aulacophora*, *A. fertilis*, *A. pycnolada* and *A. torulosa*. In all species the oil bodies are homogeneous and usually ellipsoid to fusiform in shape (cf. Pl.VIII:8). In median leaf cells their number varies from 7 to 20. Along the leaf margin and in stem cortex cells the oil bodies are smaller and almost spherical. It should be noted that ellipsoid oil bodies may appear to be spherical when they are laying in transverse position in the cells. Upon degeneration the oil bodies first become septate and subsequently disintegrate into numerous minute granulae. One should not confuse degenerating homogeneous oil bodies, which have become septate, with oil bodies which are normally segmented !

3. Stem structure (Pl.II)

In the past fifteen years much emphasis has been put upon the importance of the stem structure for distinguishing genera and higher units within Lejeuneaceae (BISCHLER 1961, 1965, 1967; SCHUSTER 1963). EVANS (1935) was the first to study the anatomy of the stem in the family. He outlined the major evolutionary lines of stem development (p.46). BISCHLER (1965) studied the anatomy of the stem in *Ptychocoleus*, including 8 species which are now assigned to *Acrolejeunea*. For the present study, transverse stem sections were made in all species of *Acrolejeunea*. The stem in *Acrolejeunea* (Pl.II) measures 50-200 micron in diameter, which is about 0,1 x the width of the leafy plant. In transverse section the stem is orbicular-ovate to quadrate in shape. There is a distinct cortex, consisting of one layer of almost thin-walled cells surrounding somewhat smaller medullary cells with distinct trigones. The walls of the stem cells are colourless or yellowish and never show any trace of secondary pigmentation. There are 10-22 longitudinal rows of cortical cells and 7-40 longitudinal rows of medullary cells which are much longer than cortical cells and have wide, truncate ends.

In transverse section the dorsal cortical cells are c. 1,5 x larger than medullary cells. The size of the ventral cortical cells varies. In symmetric stems they are as large as the dorsal cortical cells, whereas in asymmetric stems they are smaller than the dorsal cortical cells. Asymmetric stems are found in all species of *Acrolejeunea* except for *A. aulacophora*, *A. fertilis*, and *A. securifolia* (sect. *Regulares*), which have symmetric stems (Pl.II:4,5). In the sect. *Acrolejeunea* the difference in size between dorsal and ventral cortical cells is particularly pronounced (Pl.II:1,2).

The ventral merophyte surface is usually four cells wide (Pl.III:2). In large mountain forms of *A. recurvata* and *A. emergens* the ventral merophyte becomes up to ten cells wide. In *A. parvula*, which is one of the smallest species of the genus, the ventral merophyte is sometimes only two cells wide (Pl.XVII:2). Thus, it appears that the width of the ventral merophyte in *Acrolejeunea* is not a very stable character.

The attachment of the leaves and the underleaves to the stem is anatomically quite interesting. At the dorsal base of the lobe the leaf is always attached to the stem by two long and narrow cells (Pl.II:3). When the leaf is detached these cells appear as small cells surrounded by larger cortical cells (Pl.I:2,4). Along the insertion of the lobe then cortical cells are enlarged and often "protrude" into the leaf base (Pl.II:5). At the base of the underleaf there are always four large, U-shaped cells (Pl.II:6),

which are only visible in transverse stem section. The anatomy of the underleaf is dealt with in the next paragraph.

4. Underleaves and primary rhizoid disc (Pl.III)

The underleaves in the genus *Acrolejeunea* are always undivided and orbicular to transversally ovate in shape (Pl.III:1). The apex is widely rounded or truncate, and plane or recurved. When recurved the apex may become retuse (*A. recurvata*). The central region of the underleaf is sometimes gibbous. The bases are cuneate, rounded, or slightly auriculate, and the line of insertion is arched or almost straight. Large auricles as seen in *Brachiolejeunea* and *Marchesinia* are never present in *Acrolejeunea*. The cells in the underleaf are almost uniformly elongate-hexagonal, and the cell walls have thickenings as the leaves.

At the base of the underleaf a small disc of bulging cells is present (Pl.III:2). The bulging cells are rhizoid initial cells, giving rise to a short bundle of unicellular rhizoids (Pl.III:1), which firmly attach the plant to the substrate. Often the apices of the rhizoids proliferate into a hand-shaped pattern (Pl.III:1), apparently providing a better attachment. The disc, which was called "paramphigastrium" by SCHIFFNER (1929), is to be distinguished from the specialised "Haftscheibe" in epiphyllous species of Lejeuneaceae, which consists of a conspicuous circular mat of partially connate rhizoids protruding from a paramphigastrium. WINKLER (1968) introduced the terms "primäre Rhizoidplatte" for paramphigastrium, and "sekundäre Rhizoidplatte" for Haftscheibe. Following WINKLER, I propose to use the terms "primary rhizoid disc" and "secondary rhizoid disc".

The anatomy of the underleaf base and the primary rhizoid disc in Lejeuneaceae was studied independently by WINKLER (1968, 1970) and BISCHLER (1969). The anatomy is to be studied by means of transverse and longitudinal sections. Both authors showed that the underleaf is always attached to the stem by large, U-shaped cells (Pl.III:3S). These cells are also involved in sustaining the primary rhizoid disc (Pl.III:3,4). The disc is connected with the adjacent ventral cortical cells by means of rectangular cells (Pl.III:3i). Between these rectangular cells and the underlying medullary cells somewhat modified cortical cells are present (Pl.III:3mc).

Following BISCHLER (l.c.) the U-shaped cells are called "superior central cells" and the connecting rectangular cells "inferior central cells". In a previous paper (GRADSTEIN 1974b) I called the superior central cells "rhi-

zoid disc initial cells", because BISCHLER (1.c.) and WINKLER (1970) suggested that the superior central cells might play an important role in the development of the primary rhizoid disc. So far, however, we have no morphogenetic evidence for this assumption. The origin of the superior and inferior central cells also remains uncertain, although WINKLER (1970) suggested that the superior central cells belong to the underleaf.

We still know very little about the taxonomic value of the structure of the underleaf base. Yet, the data provided by WINKLER and BISCHLER are quite interesting. They demonstrated that in genera of Ptychanthoideae there are usually four inferior central cells whereas in Lejeuneoideae there are only two. This agrees with the ventral merophyte being normally four cells wide in Ptychanthoideae and two cells wide in Lejeuneoideae (MIZUTANI 1961). In Ptychanthoideae it is often difficult to distinguish between inferior central cells, adjacent underleaf cells, and cortical cells (WINKLER 1.c.). I would suggest a study of the number of superior central cells in this subfamily to give better results. BISCHLER (1.c.) reported the presence of two superior central cells in some genera of Lejeuneoideae.

WINKLER (1970) demonstrated that in some genera of Ptychanthoideae (*Symbiezidium*, *Odontolejeunea*) an intermediate layer of cells is present between the superior central cells and the primary rhizoid disc. The underleaf base in these genera is therefore "tristratose", and belongs to the *Symbiezidium*-type, whereas in genera lacking an intermediate layer of cells the underleaf base is "bistratose" and belongs to the *Stictolejeunea*-type. GRADSTEIN (1974b) showed that in *Caudalejeunea* the underleaf base is either bistratose (*C. grolleana*) or pluristratose, consisting of three or more layers or cells (*C. aristiloba*).

In the genus *Acrolejeunea* the structure of the underleaf base appears to be very uniform. The primary rhizoid disc consists of 8-15 thinwalled or slightly thick-walled rhizoid initial cells. These cells are usually larger than the surrounding underleaf cells. In transverse section I have always counted four superior central cells (Pl.II:6;III:4). These cells are readily distinguishable because of their large size. *Acrolejeunea* seems to have four inferior central cells as well, although they are not always distinct (see above). In *A. parvula*, which has a two cells wide ventral merophyte, there are distinctly four inferior central cells (Pl.XVII:2). Apparently the number of these cells is much stabler in *Acrolejeunea* than the width of the free surface of the ventral merophyte.

The underleaf base in *Acrolejeunea* is always bistratose and therefore belongs to Winkler's *Stictolejeunea*-type.

5. Branching (Pl.III)

In most species of *Acrolejeunea* two types of branches are found: the *Lejeunea*-type branch and the *Frullania*-type branch. Previously the genus was considered to possess *Lejeunea*-type branches only (e.g. SCHUSTER 1963). It is true that *Lejeunea*-type branches are the more common type of branches in *Acrolejeunea*. *Frullania*-type branches are particularly common in plants creeping loosely over the substrate with long, pseudo-dichotomously branched, sterile stems. Often these stems sprout from dense patches of fertile plants. *Frullania*-type branches in *Acrolejeunea* are most robust and longer than *Lejeunea*-type branches. This was also noted in *Brachiolejeunea*, by EVANS (1908:157).

JONES (1970: 76) suggested that in *Dicranolejeunea* the development of *Frullania*-type branches results from luxuriant growth of the plants. It is remarkable that only in the smallest species of *Acrolejeunea* (*A. parvula* and *A. pusilla*) I did not observe *Frullania*-type branches. Is there indeed a correlation in Lejeuneaceae between the size of the plant or stem and the presence of *Frullania*-type branches? The virtual absence of *Frullania*-type branches in the Lejeuneoideae, which are generally much tinier than the Ptychanthoideae, is indeed quite suggestive of this correlation.

Gametoecia in *Acrolejeunea* are almost exclusively produced on *Lejeunea*-type branches, although in *A. fertilis* and *A. securifolia* I occasionally observed androecia on *Frullania*-type branches. In *A. tjibodensis* and in *A. allisonii* I once found a gynoeceium on a *Frullania*-type branch.

The development and morphology of the branching types in Lejeuneaceae was carefully studied by CRANDALL (1969). The *Frullania*-type branch develops at the stem apex from the ventral half of a three-celled lateral merophyte, and therefore the branch replaces the lobule portion of the associated leaf. The *Lejeunea*-type branch develops below the stem apex in the ventral half of a differentiated lateral merophyte and originates from a cortex cell, which is covered by a few cells from the adjacent ventral leaf-base (Pl.II: 2,3). Upon branch development the overlaying leaf cells, called "brace-cells", differentiate into a distinct sheath ("collar") at the base of the branch. The collar is usually divided into lobes. Because of the presence of a collar, the *Lejeunea*-type branch is called "gyrothecal" (CRANDALL l.c.). The *Frullania*-type branch lacks a collar and is called "athecal".

The first leafy appendage of the *Frullania*-type branch in *Acrolejeunea* is morphological quite peculiar (Pl.III:5). It is largely inserted on the ventral side of the branch and resembles an underleaf. It is bilobed, however,

and bears a small lobe at the side turned away from the main stem. Several authors (e.g. EVANS 1912, CRANDALL 1969, HAMLIN 1973) paid attention to the morphology and ontogeny of this appendage of the *Frullania*-branch in liverworts. Sometimes it resembles an underleaf, sometimes it is highly modified, and its position on the branch varies too. It may even be inserted largely on the main stem. Most authors suggest it to be a modified underleaf except for HAMLIN (1973), who claims a styler origin for this appendage in *Frullania* and related genera.

I am convinced that in *Acrolejeunea*, and possibly in the other genera of Lejeuneaceae as well, the ventral portion of the appendage (which is the main portion) represents an underleaf, because in several species I found a rhizoid disc at the base which sometimes produced rhizoids. A longitudinal section of the base of the *Frullania*-type branch in *A. aulacophora* (Pl.III:6) shows that the ventral base of the appendage is anatomically similar to the ventral base in underleaves (see previous paragraph). However, it is hard to believe that the entire appendage is a modified underleaf. From the picture (Pl.III:5) one gets the impression that the appendage is an underleaf which is fused with the first lateral leaf. This leaf might have been a primary leaf, lacking differentiation into lobe and lobule. My assumption is of course hypothetical, because I have no ontogenetic evidence to prove it. Of interest is the fact that in *Marchesinia brachiata* the first branch appendage is sometimes fused with the underleaf of the main stem (CRANDALL 1969: fig. 348). This shows that the first branch appendage has indeed the ability to become fused with other leafy appendages.

CRANDALL (l.c.) suggested that the position and form of the first appendage of the *Frullania*-type branch is often constant within a genus. This is true for *Acrolejeunea*.

The genus *Acrolejeunea* is generally considered to be essentially different from its closest allies by the absence of innovations. Innovations are branches which originate just below the inner female bract. The associated bract is often partially inserted on the innovating branch. The absence or presence of innovations is one of the classical Sprucean characters to delimit the genera of Lejeuneaceae. The absence of innovations appears to be correlated with an increase in the number of female bracts (EVANS 1907 : 23).

Innovations in the Lejeuneaceae are athenal branches belonging to the *Radula*-type (except in *Trocholejeunea*, which has *Frullania*-type innova-

tions). CRANDALL (1969) showed that the *Radula*-type innovations in the family are ontogenetically very similar to *Lejeunea*-type branches. The absence of a collar in the *Radula*-type innovation is apparently caused by the absence of leaf brace-cells at the base of the inner female bracts.

The above statement that innovations are absent in *Acrolejeunea* is not entirely true. In *A. torulosa* (Suriname, Lanjouw 124), *A. emergens* (type of *Ptychocoleus renauldii* var. *victoriae*), and *A. fertilis* (Pl.III:7), I once observed a single innovation. In all cases the innovation was a sexual, *Radula*-type branch, originating below an apparently unfertilized archegonium. Thus, it appears that *Acrolejeunea* might be characterized better by the absence of innovations in fertilized gynoecia.

SCHUSTER (1966: 459) reported the occurrence of innovations in unfertilized gynoecia of the genus *Tennoma*, which normally lacks innovations. He also reported innovations in several genera of Ptychanthoideae normally lacking innovations (*Lopholejeunea*, *Caudalej.*, *Stictolej.*), but unfortunately no data on the gynoecia of the specimens were provided (SCHUSTER 1963: 33).

Of interest in *Acrolejeunea* is the frequent occurrence of "pseudo-innovations". This term was introduced by VERDOORN (1934: 127), in his key to the Asiatic species of *Ptychocoleus*, for branches originating lower than innovations, between subinvolutural female bracts. Pseudo-innovations were reported in *A. fertilis* by VERDOORN (l.c.) and in *Ptychocoleus renauldii* var. *victoriae* (= *A. emergens*) by JONES (1954, 1957). I observed pseudo-innovations in several collections of *A. torulosa*, *A. emergens* (Pl.III:8), *A. fertilis*, *A. pycnoclada* and *A. tjibodensis*. Usually these branches are reduced in length and hidden by the bracts. The leaves of these branches are sometimes anormal in shape (Pl.III:8). In *A. torulosa* and *A. emergens* pseudo-innovations occasionally are flagelliform shoots producing caducous leaves. I presume that pseudo-innovations normally are *Radula*-type branches, because I never found a collar at the base of these branches. In small pseudo-innovations the presence or absence of a collar was often difficult to ascertain, though.

Small pseudo-innovations may occur in fertilized gynoecia. The fact that fertilized gynoecia in *Acrolejeunea* never produce innovations but occasionally produce pseudo-innovations which are inhibited in growth, suggests an inhibitive action of fertilization upon branch development in the gynoecial region. So far pseudo-innovations have been reported only in *Acrolejeunea*, but I expect them to occur in other genera with more than one series of female bracts (lacking innovations !) as well.

6. Gametoecia (Pl.IV)

Gametoecia are known in all species of *Acrolejeunea*. *A. mollis* and *A. allisonii* are paroicous species, having sexual branches with male bracts just below the female bracts. Truly dioicous species are *A. arcuata*, *A. tjibodensis*, *A. parvula*, *A. recurvata*, *A. heterophylla* and *A. pusilla*. The remaining species are usually autoicous, but in almost all of them collections of apparently unisexual plants were found as well. It is often difficult to ascertain whether a taxon is autoicous or dioicous, because the male bracts very much resemble the leaves, and seasonal differences in the development of androecia and gynoecia are likely to occur (JONES, in litt.)

The androecium consists of a slightly modified leaf ("bract") enveloping a single antheridium (Pl.IV:1,2). The androecia are produced on long, leafy *Lejeunea*-type branches in terminal spikes, which often become intercalary through continued growth of the branch. Rarely are the antheridia produced on *Frullania*-type branches. The androecial spike (=male spike) in *Acrolejeunea* is composed of 2-50 (!) series of bracts and bracteoles. Long spikes, made up of 15-50 series of bracts, are predominantly produced in dioicous plants, or on separate male branch systems in autoicous plants. Autoicous plants with androecia on branches close to the gynoecium usually have shorter spikes, made up of only 5-15 series of bracts. In paroicous plants the male spike consists of only 2-4 series of bracts.

The male bracts differ from the preceding branch leaves by the slightly smaller lobe and the more strongly inflated lobule, which is almost devoid of teeth (Pl.IV:2). The lobes tend to become smaller towards the apex of the male spike. In an earlier publication (GRADSTEIN 1974a) I showed that the male bracts in *Acrolejeunea* have "epistatic" lobules, whereas in *Schiffneriolejeunea* the lobules are "hypostatic". Epistatic lobules are characterised by the free margin - in ventral view - curving behind the lobule of the younger bract, whereas in hypostatic lobules the free margin is distinctly overlapping the younger bract. The difference between epistatic and hypostatic lobules thus reminds of the difference between succubous and incubous leaves, although no significant differences were found in the insertion of the two types of lobules. Each genus of Ptychanthoideae usually has only one type of androecial lobule (see Part II). The male bracteoles are similar to underleaves, or slightly smaller and somewhat more flattened. The cells in bracts and bracteoles are not different from the cells in leaves and underleaves.

I found in *Acrolejeunea* only one antheridium per bract. EVANS (1918) and

VANDENBERGHEN (1948) reported two antheridia per bract, in *A. heterophylla* and *A. emergens* respectively. The mature antheridium is ovoid and c. 150 micron in diameter (Pl.IV:3). The antheridium is attached to the stem by a curved, uniseriate stalk, which is about as long as the antheridium.

The gynoecium in *Acrolejeunea* is found on stems or on elongated *Lejeunea*-type branches, and consists of a single archegonium surrounded by a perianth and 2-6 series of bracts and bracteoles. The bracts are complicate bilobed and larger than the preceding leaves. They increase in size towards the inner series. The lobule of the bracts is elongated beyond the keel and tends to become as long as the lobe. In species with 4-6 series of bracts, e.g. *A. torulosa*, *A. emergens* and *A. fertilis* p.p., the lobule increases very gradually in length towards the inner series. Length and shape of the lobule in the inner bract are very stable. In species with only 2-3 series of bracts, e.g. *A. sikkimensis*, *A. recurvata* and *A. fertilis* p.p., the lobule increases rapidly in length and consequently the length and shape of the lobule in the inner bract varies considerably. The mature inner bracts and bracteoles have entire margins. They are sometimes spreading widely around the perianth forming an involucre, which resembles a "flower" (JONES 1954). The inner bracteole is larger than the underleaves and undivided.

The gynoecial axis is usually slightly swollen. In the paroicous *A. mollis* this swelling is sometimes very pronounced and as a result the gynoecial axis is twice the diameter of the preceding androecial axis (Pl.IV:4). A similar swelling has apparently not yet been reported in other genera of Lejeuneaceae.

The archegonium is flask-shaped and has a very long neck of c. 16 superimposed cells in 5-6 longitudinal rows. The juvenile perianth consists of three portions (Pl.IV:5): 1) a basal portion, which is made up of regularly arranged quadrate-rectangular cells; 2) a central portion, which consists of smaller, rather irregularly arranged cells; 3) a beak, which has apparently already completed its development and measures almost half the length of the juvenile perianth. The venter of the archegonium is surrounded by the basal and central portion of the perianth, whereas the base of the archegonial neck is surrounded by the beak. The beak is crowned by a few slime papillae.

After fertilization, the expanding venter (= calyptra) and the archegonial neck become entirely enclosed in the rapidly growing perianth (Pl.IV:6,7). From the central portion of the juvenile perianth a number of plicae differentiate. In *A. torulosa* and several other species the central portion is more or less compressed and the plicae are sharp and of varying height and length (Pl.IV:6,8). They are much stronger developed on the ventral surface

of the perianth than on the dorsal surface. This type of perianth is called "anisoplicate". The young plicae, particularly the larger ones, are "rough" along their backs because of proliferating cells (Pl.IV:9).

Sections of the perianth in *A. torulosa* (Pl.IV:7,8) show that the basal portion is inflated, whereas the central portion is compressed, although a slight swelling of the ventral surface is always observed. This swelling is reminiscent of the primitively trigonous condition of the perianth in the Ptychanthoideae (SCHUSTER 1961: 158), characterised by the presence of two lateral keels and one wide ventral keel. The ventral keel is distinct in several species of *Acrolejeunea* with anisoplicate perianths, e.g. *A. pusilla*, *A. emergens*, *A. sikkimensis* and *A. fertilis* p.p. The plicae are often produced as narrow folds on the edges of the widely rounded ventral keel. Mature anisoplicate perianths have 4-10 smooth plicae, except in *A. pusilla* and *A. emergens* var. *confertissimus* in which the juvenile "rough" condition of the plicae has persisted.

In *A. pycnoclada* and related species the perianth is always entirely inflated (Pl.IV:10,11). The plicae are very uniform in height and length and they are smooth along their backs from early stages of development on. This type of perianth is called "isoplicate". Mature isoplicate perianths normally have 8-10 plicae, but a smaller number may also be present. *A. arcuata*, for example, often has only 5 large, conspicuously swollen plicae.

The mature perianth is either hidden by the bracts or emergent. When emergent, the basal portion of the perianth is often elongated and forms a short stalk. The stalk-like elongation of the perianth base - a common phenomenon in Lejeuneaceae (e.g. SCHIFFNER 1894: 187) - occurs simultaneously with the development of the sporophyte. The perianth is obovoid to cylindrical or obpyriform in shape, and one layer of cells thick except for the base where there are 2-3 layers. The beak is 3-12 cells long. The cell-wall thickenings are basically similar to those in the leaves and become increasingly larger towards the apex of the perianth.

7. Sporophyte and sporeling development (Pl.V)

The study of herbarium material does not permit an adequate taxonomic investigation of the sporophyte in Lejeuneaceae. Seta and foot in particular are thin structures which are shrunken almost irreversibly when dry. Another difficulty is the rarity of mature sporophytes. In most species

(autoicous and dioicous !) mature sporophytes were present in less than 10% of the collections. The highest rate of mature sporophytes was found in *A. fertilis* and *A. pycnoclada* (both autoicous): in 15% out of 100-125 different collections. Sporophytes remain unknown in *A. heterophylla* and *A. recurvata*, both of which are dioicous.

It is generally assumed that genera of Lejeuneaceae have very uniform sporophytes. I do not know any publication on Ptychanthoideae in which a species is distinguished from its congeners by a sporophytic character. Some intrageneric variation in the sporophyte is to be observed, though, as becomes evident from the descriptive data given below. At present it is very difficult to assess the taxonomic significance of the observed variation. We badly need a comparative investigation of the sporophyte in the Lejeuneaceae, aiming at an adequate description of the intrageneric variation and at finding taxonomic characters. In practice such a study will be difficult to perform, but the results might be invaluable.

The sporophyte in *Acrolejeunea* is basically similar to the sporophyte described in *Brachiolejeunea laxifolia* (FULFORD 1961) and *Dicranolejeunea axillaris* (STOTLER & CRANDALL-STOTLER 1969). The development of the sporophyte takes place entirely within the calyptra, which is one layer of cells around the developing capsule and several layers thick around the developing seta and foot. The outer cells of the calyptra are larger than the inner cells, and measure c. 25-30 micron in diameter. At its base, the calyptra is rather wide and plump and not distinctly narrowed into a stalk. The foot consists of few large, bulging cells in c. three vertical layers (Pl.V:1). The foot gradually continues into seta, which as a rule consists of 16 outer cells and 4 inner cells in cross section (Pl.V:2). I made only few sections but found no irregularities in the number of cells. MIZUTANI (1961) reported slight irregularities in the number of cells in the seta of *A. pusilla*.

Upon elongation of the seta, the capsule is elevated up to 2 mm above the perianth (Pl.V:1). The outer cells of the elongated seta are unevenly or evenly tiered (Pl.V:1). Inner and outer cells are always arranged on different vertical levels, hence the seta is not articulate. An articulate seta has all cells arranged on the same vertical level after elongation, and is consequently entirely and regularly segmented transversally. Some authors (e.g. STOTLER & CRANDALL-STOTLER 1974) have used the term "articulate" to indicate that the outer cells of the seta are evenly tiered. I should prefer to use the term "articulate" in the more restricted sense given above. Articulate setae are much more common in Lejeuneaceae than

non-articulate setae.

The mature capsule is dark-brown, globose, and 0,3-0,55 mm in diameter. Upon dehiscence the capsule splits over 4/5 of its length into four valves (Pl.V:1,2). As an abnormality, I observed a capsule with only two valves in *A. pusilla* (Kodama 18289). Normally the valves are 0,5-0,6 mm long, and spread backwards entirely or at least in the upper half to an erecto-patent position. The inner side becomes convex and bears a few elaters at the apex. *A. pusilla* has distinctly smaller, c. 0,3-0,35 mm long valves which remain suberect after dehiscence with the inner side \pm concave. In *A. pycnoclada* I observed large, spreading valves and small, suberect valves. The variation observed here is quite interesting because widely spreading valves are typical for Ptychanthoideae whereas suberect valves are characteristic for Lejeuneoideae (see Part II).

The valves in *Acrolejeunea* consist of two layers of cells, whereas the capsule base is three to four layers of cells thick. The outer cells of the valves are arranged radially. They have asymmetrically nodulose trigones and intermediate thickenings, which tend to become confluent (Pl.V:3, 4,5). Considerable interspecific differences in the size of the thickenings are observed but too few observations are available to permit taxonomic conclusions. In the centre of the lower half of the valves the outer cells are smaller, \pm irregularly arranged, and thin-walled (Pl.V:3,6). They gradually continue into the thin-walled cells of the capsule base.

The inner surface of the valves has several longitudinal ridges and is covered by an orange-brown, reticulate layer of thickening (Pl.V:6) The inner cells of the valves are slightly smaller than the outer cells. Usually each inner cell shows several pores in the layer of thickening. This is the "plurifenestrate" pattern, described and illustrated in *Lopholejeunea muelleriana* by SCHUSTER (1966) and in many other genera of Ptychanthoideae by MIZUTANI (1961). The pores are variable in diameter and ill defined in *Acrolejeunea*. Their outline is difficult to observe with the light microscope. Some cells have only one, large pore. This is the "monofenestrate" pattern, described in *Frullania* by SCHUSTER (l.c.). In *A. mollis* and *A. allisonii* the cells tend to be monofenestrate in the upper half of the valve and plurifenestrate in the lower half of the valve (Pl. V:20,26). STOTLER & CRANDALL-STOTLER (1974) reported the occurrence of both patterns of thickening in sporophytes of *Bryopteris*. SCHUSTER's call for further study is still valid here: "A detailed comparative investigation of the capsule wall would surely prove fruitful, but has not yet been undertaken" (SCHUSTER 1963:47).

Mature, but unopened capsules have 36 elaters, which are vertical in position and attached to the capsule base and the apical region of the valves. After dehiscence each valve bears 9 elaters in a very regular pattern (Pl. V:2). The length of the elater is correlated with its place of attachment and with the total length of the valves. In most species the elaters are 250-350 micron long and c. 12 micron wide, but in *A. pusilla* the elaters are only 120-200 micron long. Usually the elaters are monospiralled by a yellowish-brown, 4-5 micron wide thickening band, but in *A. mollis* bispiralled elaters were observed as well. VAN DEN BERGHEN (1972) reported the occurrence of monospiralled and bispiralled elaters in *A. emergens*.

The mature spores have undergone precocious germination as is usual in the Lejeuneaceae, and consequently they are green and relatively large, 45-60 micron in length, roundish to angular or somewhat longer than wide (Pl.V:7,8). The surface of the spores is covered by numerous small, bluntish papillae and 5-10 scattered "rosettes" consisting of radially oriented coarse, sharp papillae.

Sporeling development was observed in *A. torulosa* (Vital 2846, Brazil). The protonema develops entirely within the expanded spore wall and consists of a globose to ovoid mass of c. 10-15 cells (Pl.V:8). Outgrowth of the sporeling takes place at one side of the spore, whereas at the opposite side a rhizoid germinates (Pl.V:8). Growth of the sporeling takes place from an apical cell with three cutting faces (Pl.V:8a). The first series of leaves consists of primary leaves, whereas in the second series the first juvenile leaf appears (Pl.V:9). The primary leaves are flat and undivided, whereas the juvenile leaves are strongly saccate with subequal lobe and lobule. Underleaves are absent in the series of primary leaves. Their initiation apparently starts with the formation of juvenile leaves.

The type of sporeling development pattern observed in *A. torulosa* is similar to FULFORD's *Lopholejeunea*-type. The *Lopholejeunea*-type occurs in several genera of Ptychanthoideae (FULFORD 1956, NEHIRA 1974; see Part II).

The sporeling grows by a pendular segmentation, resulting in the presence of two underleaves within each series of leaves (Pl.V:10). The pendular sequence of segmentation is characteristic of juvenile stages of development in liverworts, and is apparently replaced by a spiral sequence (one underleaf in each series of leaves) when the plant turns into the adult phase of development (CRANDALL 1969).

8. Vegetative reproduction (Pl.VI)

Some species of *Acrolejeunea* are able to propagate vegetatively by means of deformed caducous leaves arising from upright, flagelliform shoots. This mode of vegetative reproduction is a rare phenomenon in Jungermanniales. According to SCHUSTER (1966) it is only known in some epiphytic genera of Jubulineae, e.g. *Acrolejeunea*, *Rectolejeunea*, and *Frullania* (*F. bolanderi*). In *Acrolejeunea* it occurs in *A. emergens*, *A. heterophylla*, *A. pusilla*, *A. recurvata*, and *A. torulosa*. This group of species constitutes the subgenus *Acrolejeunea*. No vegetative reproduction of any kind was observed in the other species of the genus.

Vegetative reproduction of *Acrolejeunea* was described in *A. heterophylla* by EVANS (1918: 147-148). The peculiar upright flagellae were noticed earlier by SPRUCE in an annotation on one of his Amazonian collections of *A. torulosa*: "*Acrolej. torulosa* var. - *sterilis* , rami in flagella foliis orbata sed foliolis lato-cuneatis squarrosa patulis obstructa abeuntes". SPRUCE apparently did not publish this observation, and failed to recognize the function of these flagellae. My observations are based on a study of fresh material of *A. torulosa*. Additional data were obtained from dried material of the other species of the subgenus.

Flagellae in *Acrolejeunea* are usually produced terminally on leafy *Lejeunea*-type branches (Pl.VI:1). Occasionally they constitute an entire *Lejeunea*-type branch. In fertile plants they often arise terminally from a male branch or laterally from a female branch. They may even arise as pseudo-innovations! When fresh they stand upwards, away from the substrate, and measure 0,5-5 mm in length. The flagellae are greenish in colour when young, turning brownish on age. Normally they are unbranched (Pl.VI:2a,b), but in some East African collections of *A. emergens* they are pinnately branched with numerous short lateral flagellae (Pl.VI:2c). Unbranched flagellae in these collections are often short and clustered near the apex of stems or branches (Pl.VI:2b). When curving upwards the flagelliform shoot sometimes undergoes a torsion in left-hand direction. This torsion is usually less than 180° , but in the type-collection of *A. torulosa* var. *obtusata* the torsion was c. 270° .

Young leaves get entirely detached at the apical region of the shoot, which is usually curved. The remaining underleaves are smaller than normal underleaves and densely imbricated due to the very short internodes of the flagelliform shoot (Pl.VI:3). In *A. pusilla* the underleaves of the flagellae are relatively unmodified, flat, and appressed to the axis. In *A. re-*

curvata the underleaves are very small, often narrower than the axis. Consequently the flagellae in this species have a barren appearance. In *A. heterophylla* and *A. emergens* the underleaves are more or less squarrose, especially near the apex of the shoot, and the margins are curved inwards. *A. torulosa* has strongly squarrose underleaves which differ from the underleaves of *A. heterophylla* and *A. emergens* by the margins, which are often folded outwardly, away from the axis. The insertion line of the underleaves is always straight and the base is entirely devoid of rhizoids, although a rudimentary rhizoid disc consisting of one or two cells may still be present.

Transverse and longitudinal sections of the flagelliform shoot (Pl.VI:3, 4) show that the medullary cells and the ventral cortical cells are essentially similar to the cells of the leafy stem, although they are shorter in length and more strongly variable in width (especially the medullary cells!). In contrast, the cortical cells of the lateral merophytes get conspicuously altered. In surface view they are usually wider than long and strongly protuberant. They tend to become arranged in oblique rows in long flagellae which have undergone a torsion.

At the apical region of the shoot the cortical cells are pale-greenish, but soon the cell walls turn brownish and the cell lumina become filled with slime. Oil bodies and chloroplasts tend to degenerate. Narrow grooves on the rough surface of the shoot mark the original insertion line of the caducous leaves. In fresh material a few slime papillae are seen in the grooves. The deformation of the cortical cells in the lateral merophytes is apparently correlated with the complete detachment of the leaves. Developmental studies are needed for a better understanding of this process of detachment and deformation.

In all species of *Acrolejeunea* the caducous leaves average 0,2-0,3 mm in length. The lobule is weakly convex to almost flat and has 1-3 small teeth. Great variation is observed in the length of the lobule. In *A. emergens* and *A. heterophylla* the lobule is c. $1/3$ x the length of the lobe (Pl.VI:6), whereas in *A. pusilla* the lobule is $1/2-4/5$ x the length of the lobe (Pl.VII:5,6,7). In these species the caducous leaf superficially resembles a small branch leaf. In *A. recurvata* the lobule is always reduced to a small fold with one single tooth (Pl.VI:5), whereas in *A. torulosa* the lobule is usually almost as long as the lobe (Pl.VI:7). In the latter species a long rhizoid arises from the apex of the keel in the apical region of the caducous leaf. The caducous leaf in *A. torulosa* represents the most strongly deformed type of caducous leaf in the genus. It is a minute

flask-like body, produced by hundreds in a single patch of the species.

When dispersed, the caducous leaves in all species tend to produce rhizoids as a means of attachment. Most species have short rhizoids, not exceeding 50 micron in length, which arise from cells on the back of the keel, especially near the base of the caducous leaf (Pl.VI:6). A long apical rhizoid is only observed in *A. torulosa*.

Germination of gemmalings takes place in the lower half of the caducous leaf, from the outer surface of the lobule or the lobe. (Pl.VI:7;VII:5). When from the lobe, the gemmalings are produced close to the keel. Apparently a caducous leaf produces only one new plant. I was struck by the low percentage of caducous leaves from which gemmalings arise. In a patch of plants with flagellae usually hundreds of caducous leaves are present, which are easily observed when the entire patch is soaked in water in a petri dish. At best I found germination in c. 10% of the caducous leaves, but usually the percentage is much lower. In the species studied I mostly found gemmalings in early stages of development, lacking a distinct shoot (Pl.VI:8). A few later stages were found in *A. torulosa* (Pl.VI:9). The rarity of later stages of development was already noted by EVANS (1918).

The gemmalings in *Acrolejeunea* develop directly from a dedifferentiated cell, without the intervention of a protonemal stage (EVANS l.c.). In this respect they are similar to regenerants (FULFORD 1956). Regeneration from adult stems or leaves was not observed in *Acrolejeunea*, although it is known to occur in related genera, e.g. *Mastigolejeunea* (FULFORD 1943) and *Schiffneriolejeunea* (pers. obs.).

The gemmaling in *A. torulosa* has one series of primary leaves and underleaves preceding the juvenile series (Pl.VI:9,10). The primary underleaves are somewhat wider than the juvenile underleaves, but otherwise they resemble each other morphologically. Like in the sporeling a pendular sequence of segmentation is present. A remarkable difference between gemmaling and sporeling is the presence of primary underleaves in the gemmaling and their absence in the sporeling. This difference is also observed in other groups of liverworts (FULFORD 1957), although in some genera (*Calypogeia*, *Ptilidium*) sporelings have primary underleaves as well. CRANDALL (1969) demonstrated that the formation of primary underleaves depends on the width of the ventral merophyte, which in turn is determined to some degree by the size of the ventral cutting face of the apical cell. Exactly which factors control the development of primary underleaves remains open to question.

SUBDIVISION

The subdivision of the genus *Acrolejeunea* presented here is entirely based on the gametophyte, because sporophyte differentiating characters could not be found. The characters that could be successfully employed for distinguishing species or intraspecific taxa are mainly derived from the lobule, the under-leaf, the means of vegetative reproduction, and the gynoeceum. Subgenera and sections are mainly distinguished by the absence or presence of vegetative reproduction, by the perianth, and by stem structure.

The selection of taxonomic characters was largely based on the study of morphological variation in herbarium collections. Personally I have not been able to observe the morphological behaviour of the plants in nature nor in culture. It is well known that liverworts usually have great somatic plasticity (SCHUSTER 1966:314-318), which makes it very difficult to find "good" specific or intraspecific characters. BUCH (1928) described the basic patterns of phenotypic variation in liverworts. Valuable accounts of variation in species of *Acrolejeunea* were provided by VERDOORN (1934c) and JONES (1954), who were able to study the species in the field. These and other studies provided important background information for my taxonomic evaluation of the morphological variation in *Acrolejeunea*.

1. Species, subspecies and varieties

The genus *Acrolejeunea* is divided into 15 species, 4 subspecies, and 2 varieties. I have accepted as species those morphological entities which are distinguished by at least two correlated diagnostic characters. In a few cases this definition of the species seems to break down in this treatment because of the apparent existence of one or two "intermediate" collections, e.g. between *A. torulosa* and *A. emergens*, and between *A. securifolia*, *A. aulacophora* and *A. fertilis*. As the correct interpretation of the intermediate plants is dubious (see notes under the species), I have maintained these taxa on the species level.

The species of *Acrolejeunea* and related groups may have large areas of distribution (see chapter on distribution). They are not necessarily confined to one continent. Widespread species, e.g. *A. emergens*, *A. securifolia*, and *A. pycnolada*, tend to be more variable than species with limited areas of distri-

bution, e.g. *A. pusilla* and *A. mollis*. This is also seen in species of higher plants (VAN STEENIS 1957). A remarkable exception in *Acrolejeunea* is *A. aulacophora*, which is distributed discontinuously from East Africa to the Central Pacific (Pl. XXII), and yet shows very little morphological variation throughout its vast range.

The morphological variation within a species is either continuous or discontinuous. When more or less continuous, I have treated the intraspecific variation in its entirety in the species description. Notable patterns of intraspecific variation are discussed separately. These discussions may serve as a guide and stimulus for subsequent biosystematic investigations. GILMARTIN (1974) accused taxonomists of having neglected the description of intraspecific variation. He advocated the use of numerical methods for these purposes. There is no doubt about the great value of numerical methods for detecting discriminative characters and taxonomic relationships. I do not believe, however, that for the mere description of intraspecific variation these methods should be favoured, as long as we do not combine them with biosystematic methods of investigation.

When clear-cut intraspecific discontinuities were found, I applied two categories: subspecies and varieties. In my interpretation both categories have the same morphological standing. Each of them is distinguished by one or two diagnostic morphological characters. If two, e.g. *A. securifolia* ssp. *caledonica*, the intraspecific level was chosen to express more properly its taxonomic relationship (see below). Since taxonomic interpretation of intraspecific morphological variation in liverworts is very difficult and subjective (SCHUSTER 1966), I do not think we should worry about morphologically different intraspecific levels. Difficulties abound in circumscribing our species and in the rare case of subspecies requiring subdivision into varieties one might as well consider upgrading the taxonomic levels.

The difference between subspecies and varieties in this treatment is essentially geographical. Subspecies are allopatric forms with "geographic distributions of their own which are distinct from the area occupied by the other subspecies of the same species" (LAWRENCE 1951). Varieties are sympatric forms, and usually they have limited areas of distribution. Subspecies are described in *A. pycnoclada* and *A. securifolia*. In the latter species, the morphological individuality of the subspecies varies, and one of them, *A. securifolia* ssp. *caledonica*, might just as well be treated as a separate species. I have treated this taxon on the subspecies level mainly to express the close relationship to the other subspecies of *A. securifolia*. This procedure was recommended for higher plants by VAN STEENIS (1957) and for animals by MAYR (1969): "It is pre-

ferable for various reasons to treat allopatric populations of doubtful rank as subspecies. The use of trinomials conveys two important pieces of information: 1) closest relationship, and 2) allopatry. Such information is very valuable, particularly in large genera " (MAYR l.c.:197). Geographic subspecies as defined above have only rarely been distinguished in bryophytes. Partly this is due to the fact that only few monographic studies have been made, justifying the distinction of geographic intraspecific taxa. Examples of recent bryological works in which geographic subspecies were distinguished are the treatments of the *Frullania tamarisci* complex by HATTORI (1972), and of the Hypnodendraceae by TOUW (1971). The application of the geographic subspecies category in liverwort taxonomy was discussed by SCHUSTER (1966, 1972).

The distinction of species, subspecies and varieties in *Acrolejeunea* is mainly based, as was stated above, on character states of the lobule, the underleaf, the means of vegetative reproduction, and the gynoeceum.

- a. Lobule. This is the most important taxonomic tool for distinguishing species in *Acrolejeunea* and other genera of Lejeuneaceae. Particularly important are the shape of the lobule and the shape and number of its teeth. In several species the lobule is considerably variable, e.g. in *A. emergens* (Pl.X).
- b. Underleaf. Particularly important characters are the shape of the underleaf and the recurvature of the margins. These characters have been proved useful for distinguishing subspecies, e.g. *A. pycnoclada* ssp. *latistipula* and *A. securifolia* ssp. *caledonica*. In other species, e.g. *A. recurvata*, the underleaf is strongly variable in these respects.
- c. Vegetative reproduction. The species of the subgenus *Acrolejeunea* are sometimes distinguished by the shape of the caducous leaf (*A. torulosa*) or by the flagellae (*A. recurvata*). These characters have not yet been employed previously in *Acrolejeunea*.
- d. Female bracts and bracteole. Some species are distinguished by the shape of the female involucre, e.g. *A. pycnoclada* and *A. arcuata*. In *A. fertilis* the female bracts are quite variable in shape, whereas in the section *Acrolejeunea* their shape is almost uniform.
- e. Perianth. The diagnostic value of the perianth for distinguishing the subgenera of *Acrolejeunea* is discussed in the next paragraph. With respect to distinguishing species, the perianth provides good characters in a few cases only. The length of the beak is a character of *A. pycnoclada*, whereas *A. pusilla* and *A. emergens* var. *confertissima* are distinguished by the rough plicae. When mature the perianth is sometimes longly emergent,

which serves to distinguish *A. allisonii* and *A. securifolia* ssp. *pallida*. Several authors, e.g. STEPHANI (1912), employed the number of plicae as a diagnostic specific character. In my experience this character should be treated with great care, because it varies considerably within a species. In all species of the section *Acrolejeunea*, and also in *A. fertilis*, *A. parvula* and *A. arcuata*, the number of plicae varies from 5 to 10. In species with a seemingly constant number of plicae, especially those which have 9-10 plicae, one should always be alert on finding specimens with a deviating (lower) number of plicae. The shape of the plicae varies as well, and generally I have been quite reluctant to distinguish taxa solely by this character. *Ptychocoleus coroniformis* KODAMA & KITAGAWA (1974) for example, distinguished from *A. arcuata* by its expanded plicae, is reduced here to synonymy under the latter species.

A final remark should be made on the taxonomic value of the sexuality in *Acrolejeunea*. In Lejeuneaceae the autoicous or dioicous condition was used by several authors, e.g. SPRUCE, EVANS and JONES, as an important taxonomic tool for distinguishing species. SCHUSTER (1972) discussed the significance of the sexuality of the liverwort plant for the process of speciation, and advocated using the rank of subspecies for taxa differing only in sexuality. Some authors, e.g. VERDOORN (1934c) and MIZUTANI (1961) seldom refer to sexuality in their studies on Lejeuneaceae. BISCHLER (1969) warns against an over-appreciation of the sexuality as a taxonomic character in *Leptolejeunea*:

"La valeur distinctive attribuée à ce caractère a souvent été exagérée" (p.284).

In *Acrolejeunea* it is often difficult to determine the sexuality of the plants (p.26). Several species are apparently both autoicous or dioicous. Examples are *A. emergens*, *A. torulosa*, and *A. securifolia*. Therefore I have not as a rule used sexuality as a diagnostic taxonomic character. In many cases, however, the sexuality of the plants provides supporting evidence for separating morphological entities, e.g. *A. tjibodensis* and *A. parvula* (dioicous) versus *A. pycnoclada* ssp. *vuonoclada* (autoicous), and *A. securifolia* ssp. *securifolia* (autoicous) versus ssp. *hartmannii* (dioicous). The paroicous condition is rare, and characterises the New Zealandian endemics *A. mollis* and *A. allisonii*. A single paroicous collection was found in *A. securifolia* ssp. *pallida*, which is normally autoicous, and in *A. emergens*.

2. Subgenera and sections

I have divided the genus *Acrolejeunea* into two subgenera: sub. *Acrolejeunea*

and subg. *Isolejeunea*. The subg. *Acrolejeunea* contains the species which are able to reproduce vegetatively by means of caducous leaves, whereas the species of the subg. *Isolejeunea* are lacking any device of vegetative reproduction. The absence or presence of vegetative reproduction - considered a significant character for delimitating genera of Lejeuneaceae (SCHUSTER 1963) - is the only diagnostic difference between both groups, although characters of the perianth are important as well. The species of the subg. *Acrolejeunea* differ from most species of the subg. *Isolejeunea* by the anisoplicate perianth, which is more or less compressed in the upper half (Pl.IV:7,8). In transverse section the presence of a wide ventral keel becomes apparent. This keel is reminiscent of the primitively trigonous condition of the perianth in Ptychanthoideae. The perianth in subg. *Isolejeunea* is entirely inflated and isoplicate (Pl.IV:11), except in *A. sikkimensis*, which has a compressed-anisoplicate perianth and in *A. fertilis* and *A. parvula* which have both types of perianth. The subgenera have very different patterns of geographical distribution (Pl.XXI).

Each of the subgenera is divided into two sections: sect. *Acrolejeunea* and sect. *Pusillae* in subg. *Acrolejeunea*, and sect. *Isolejeunea* and sect. *Regulares* in subg. *Isolejeunea*. The sections are not always sharply delimited but they represent clusters of closely related species. Characters of the stem in transverse section serve to delimit the sections diagnostically (Table I).

	A	B	C	D
Sect. <i>Pusillae</i>				
<i>A. pusilla</i>	†	4	10-12	7-9
Sect. <i>Acrolejeunea</i>				
<i>A. torulosa</i>	†	4-6	16-22	24-33
<i>A. emergens</i>	†	4-8	12-20	20-40
<i>A. recurvata</i>	†	4-10	15-22	25-35
Sect. <i>Regulares</i>				
<i>A. sikkimensis</i>	†	4	13-14	c. 20
<i>A. fertilis</i>	=	4-6	14-17	24-30
<i>A. aulacophora</i>	=	4	14-16	22-27
<i>A. securifolia</i>	=	4	14-16	25-30
Sect. <i>Isolejeunea</i>				
<i>A. mollis</i>	†	4	14-15	c. 20

<i>A. parvula</i>	≠	2-4	11-15	10-14
<i>A. pycnoclada</i>	≠	4	13-17	15-20
<i>A. tjibodensis</i>	≠	4	c. 14	c. 20
<i>A. arcuata</i>	≠	4	15-17	14-15

Table I: Stem of *Acrolejeunea* in transverse section. A: cortical cells uniform in size (=) or dorsally larger (≠); B: width of the ventral merophyte (number of cells); C: number of cortical cells; D: number of medullary cells.

The species of the sect. *Acrolejeunea* have heavier stems with a larger number of cortical and medullary cells than the species of sect. *Pusillae*. The peculiar oblique zig-zag pattern of the dorsal cortical cells (Pl. I:2) is typical for the sect. *Acrolejeunea*. In the subgenus *Isolejeunea* sections are distinguished by the number of medullary cells and the size of the cortical cells. In sect. *Regulares* there is a larger number of medullary cells and the cortical cells are uniformly larger than the medullary cells, whereas in sect. *Isolejeunea* only the dorsal cortical cells are distinctly larger than the ventral cortical cells. *A. sikkimensis* belongs stem-anatomically in the sect. *Isolejeunea* (see Table I). Yet, I have placed this species in the sect. *Regulares* because of its overall affinity to *A. fertilis*.

For a comprehensive circumscription of the sections and subgenera the reader is referred to the taxonomic treatment of the genus. Morphologically the two subgenera are connected by sect. *Acrolejeunea* and sect. *Regulares*, which have in common the squarrose leaves, the relatively large number of medullary cells, and the tendency of the lobule to produce more than three teeth. The phenetic relationships are therefore best expressed by placing the sections in the following linear order: sect. *Pusillae* - sect. *Acrolejeunea* - sect. *Regulares* - sect. *Isolejeunea*.

3. Conspectus

Subg. *ACROLEJEUNEA*

Vegetative reproduction by means of caducous leaves. Perianth + compressed in the upper half, anisoplicate. Tropical America, Africa, and S.E. Asia

(not in Malesia); 0-1500 m.

I Sect. *Pusillae* Gradst. sect. nov.

Stem with 10-12 longitudinal rows of cortical cells and 7-9 longitudinal rows of medullary cells. Dorsal cortical cells arranged in straight longitudinal rows. Leaves not squarrose.

- (1) *A. pusilla* (Steph.) Grolle & Gradst.

II Sect. *Acrolejeunea*

Stem with 12-22 longitudinal rows of cortical cells and 20-40 longitudinal rows of medullary cells. Dorsal cortical cells arranged zig-zag in oblique rows. Leaves squarrose.

- (2) *A. torulosa* (Lehm. & Lindenb.) Schiffn.

a. var. *torulosa*

b. var. *obtusa* Gradst. var. nov.

- (3) *A. heterophylla* (Evans) Grolle & Gradst.

- (4) *A. emergens* (Mitt.) Steph.

a. var. *emergens*

b. var. *confertissima* (Steph.) Gradst. comb. nov.

- (5) *A. recurvata* Gradst. sp. nov.

Subg. *ISOLEJEUNEA* Gradstein. subg. nov.

Vegetative reproduction absent. Perianth mostly entirely inflated and isoplicate, more rarely + compressed and anisoplicate. Palaeotropics, but rare in continental Africa; 0-3500 m.

III Sect. *Regulares* (Verd.) Gradst. comb. nov.

Stem with 20-30 longitudinal rows of medullary cells. Cortical cells + uniform in size. Leaves often squarrose.

- (6) *A. sikkimensis* (Mizut.) Gradst. comb. nov.

- (7) *A. fertilis* (Reinw., Blume & Nees) Schiffn.

- (8) *A. aulacophora* (Mont.) Steph.

- (9) *A. securifolia* (Nees) Watts

a. ssp. *securifolia*

b. ssp. *hartmannii* (Steph.) Gradst. comb. nov.

c. ssp. *caledonica* (Steph.) Gradst. comb. nov.

d. ssp. *pallida* (Aongstr.) Gradst. comb. nov.

IV Sect. *Isolejeunea*

Stems with 10-20 longitudinal rows of medullary cells. Ventral cortical cells smaller than dorsal cortical cells. Leaves not squarrose.

- (10) *A. allisonii* Gradst. sp. nov.

- (11) *A. mollis* (Hook & Tayl.) Schiffn.
- (12) *A. pycnolada* (Tayl.) Schiffn.
 - a. *ssp. pycnolada*
 - b. *ssp. latistipula* Gradst. ssp. nov.
- (13) *A. parvula* (Mizut.) Gradst. comb. nov.
- (14) *A. tjibodensis* (Verd.) Grolle & Gradst.
- (15) *A. arcuata* (Nees) Grolle & Gradst.

4. Phenetic diagram

In Pl. XX the species of *Acrolejeunea* are depicted as discs of variable size, which are arranged in accordance with their morphological affinities. Continuous lines are drawn between closely related pairs of species, whereas intersectional relationships are shown by broken lines. The size of the discs is roughly correlated with the size of the areas of geographic distribution of the species. In each disc the major geographical areas in which the species occur are indicated by means of abbreviations. Intraspecific taxa are drawn as subdivisions of the discs in such a fashion, that subspecies are marked by continuous lines, whereas varieties are marked by broken lines. The chart was drawn without the purpose of suggesting phylogenetic relationships. It is possible, though, to recognize evolutionary trends in the genus. These trends are discussed in a following chapter.

The chart reminds of the phenetic diagram of the System of the Angiosperms presented by PULLE in his Compendium (1938). According to STAFLEU (1971) the first diagram of this kind was constructed as early as 1789 by GISEKE to illustrate the Linnean system of the plant kingdom. Surprisingly few botanists employed this type of phenetic diagram in their publications. In my opinion this diagram is a very elegant means of systematic illustration, because various sorts of taxonomic information (morphology, geography, ecology, cytology, etc.) may be incorporated in the chart. A good example is the chart of the sectional subdivision of the genus *Pinus* by VANDERBURGH (1973), in which the diagnostic morphological characters are shown by standard abbreviations in the discs.

DISTRIBUTION

The genus *Acrolejeunea* is pantropical in distribution, ranging in altitude from sealevel up to 3500 m. The highest records are from the Himalayas (Sikkim), Borneo (Mt. Kinabalu) and New Guinea. The northernmost limits of distribution are in Japan, Kinkazan I. (38° N. Lat.) at sealevel and in the Himalayas at 3500 m. South of the equator the genus reaches down to 42° S. Lat. on Tasmania and the South Island of New Zealand. In America the limits are Central Florida and Sao Paulo State respectively, whereas in Africa the genus reaches north to the southern border of the Sahara, and south to Mt. Mlanje (Malawi) and southeastern Madagascar. Within the tropics the genus is still unknown from most of the Caribbean area, from the west coast of tropical South America (Colombia, Ecuador), from southern India and parts of Indo-China, from a number of pacific and eastern Malesian islands (Celebes), and from northern Australia. The centre of the present-day distribution of the genus is Southeast Asia where 9 species are found. New Guinea is particularly rich in species: *A. arcuata*, *A. fertilis*, *A. pycnoclada*, *A. securifolia*, and *A. tjibodensis* (all belonging to subg. *Isolejeunea*).

The two subgenera of *Acrolejeunea* have entirely different patterns of distribution. Subg. *Isolejeunea* is palaeotropical (Pl.XXI) and occurs mainly in Southeast Asia, Australasia, and the Pacific. Two species extend westwards to continental Africa. Within the family Lejeuneaceae this pattern of distribution is also found in the genus *Ptychanthus* (VERDOORN 1934c). Subg. *Acrolejeunea* has a discontinuous, tricentric range (Pl.XXI), occurring in tropical America, tropical Africa, and Southeast Asia (Indo-China and Japan). The species occurring in America, Africa, and Indo-China belong to the sect. *Acrolejeunea*, whereas the single Japanese species constitutes the sect. *Pusillae*. The tricentric distribution pattern of subg. *Acrolejeunea* is found in other groups of Lejeuneaceae as well, e.g. *Bryopteris* (FULFORD 1951, STOTLER & CRANDALL-STOTLER 1974), and *Brachiolejeunea* subg. *Plicolejeunea* (GROLLE 1966).

On the species and subspecies level many different types of distribution patterns are observed. The geographical diversification is demonstrated in the list given below. SCHUSTER (1966) postulated that in liverworts monoicous (=autoicous or paroicous) taxa tend to be distributed more widely than dioicous taxa. This is explained by the assumption that effective migration is much more difficult for taxa with unisexual spores than for taxa with bisexual spores.

To check this hypothesis for *Acrolejeunea*, the sexuality of each taxon is listed in conjunction with its area of distribution. The size of the areas decreases from 1 to 9.

1. Pluriregional

a. Afro-Indopacific. Pl. XXII

A. pycnoclada ssp. *pycnoclada* (autoicous); 0-1500 m.

b. Afro-Australpacific (disjunct). Pl. XXII

A. aulacophora (autoicous); 0-800 m.

c. Afro-American. Pl. XXI

A. emergens (autoicous or dioicous); 0-1500 m.

2. Tropical South America. Pl. XXI

A. torulosa (autoicous or dioicous); 0-100(-800) m.

3. Indo-Malesia. Pl. XXII

A. fertilis (autoicous); 0-250 m.

4. Malesia.

A. tjibodensis (dioicous)

A. arcuata (dioicous)

Both species occur more or less disjunct at higher altitudes between 1200 and 3500 m.

5. Eastern Malesia. Pl. XXII

A. securifolia ssp. *hartmannii* (dioicous); 0-1500 m.

6. Australasia. Pl. XXII

A. securifolia ssp. *securifolia* (autoicous or dioicous); 0-100 m.

7. Indo-China

A. recurvata (dioicous); 350-1500 m. Pl. XXI

A. parvula (dioicous); 0-2000 m. Pl. XXII

8. Central America and Florida (disjunct). Pl. XXI

A. heterophylla (dioicous); 0-100 m.

9. Endemic

Seven species and subspecies have distribution patterns which might be qualified as endemic. Except for *A. sikkimensis*, which is known from only one collection, they are all known from five or more collections.

a. New Zealand.

A. allisonii (paroicous); 250-750 m.

A. mollis (paroicous); 0-700 m. Pl. XXII

- b. New Caledonia. Pl. XXII
A. securifolia ssp. *caledonica* (dioicous); 0-750 m.
- c. Southern Central Pacific. Pl. XXII
A. securifolia ssp. *pallida* (dioicous); 0-100 m.
- d. New Guinea
A. pycnoclada ssp. *latistipula* (dioicous); 1200-1600 m.
- e. Japan. Pl. XXI
A. pusilla (dioicous); 0-300(-900) m.
- f. Sikkim
A. sikkimensis (autoicous); c. 3500 m.

SCHUSTER'S hypothesis that widely distributed taxa are monoicous, whereas narrowly distributed taxa are more often dioicous apparently holds for *Acrolejeunea*, although there are some notable exceptions: *A. mollis*, *A. allisonii*, and *A. sikkimensis*. *A. mollis* and *A. allisonii* are paroicous endemics which probably evolved in relatively recent times in rather dry subtropical bush areas of northern New Zealand. *A. sikkimensis* is an autoicous endemic from the Himalayas. It is the most primitive species of the genus. Therefore I presume that it is an old relict species, which used to be distributed more widely in earlier times. Evolutionary trends in *Acrolejeunea* are considered in the next chapter.

EVOLUTIONARY TRENDS

A phylogenetic interpretation of the phenetic relationships in the genus *Acrolejeunea* requires assumptions as to which characters are more primitive and which are more advanced. We will primarily consider those characters which serve to distinguish between sections and subgenera, and as such could indicate major lines of evolutionary development. With respect to stem structure, EVANS (1935) postulated that in Lejeuneaceae: 1) heavy stems are more primitive than thin stems, 2) stems lacking differentiation into cortex and medulla are more primitive than stems with a distinct cortex and medulla. The cortical cells in advanced genera of Lejeuneaceae are usually distinctly larger than medullary cells and uniform in size.

I have called stems with uniformly enlarged cortical cells "symmetric" stems (p.20). They are found in *Acrolejeunea* sect. *Regulares*. Most species of *Acrolejeunea* have "asymmetric" stems, which have only the dorsal cortical cells distinctly larger than the medullary cells. It seems logical to assume that symmetric stems are more advanced than asymmetric stems. BISCHLER (1965) showed that asymmetric stems are found in almost half the number of genera of Ptychanthoideae.

MIZUTANI (1961) and SCHUSTER (1963) independently listed primitive and advanced characters in Lejeuneaceae. With respect to characters of the perianth and of reproduction, they assumed that a trigonous perianth and the absence of vegetative reproduction are primitive.

From the foregoing it appears that the subg. *Isolejeunea* is more primitive than the subg. *Acrolejeunea*, because it has no means of vegetative reproduction. Within the subg. *Isolejeunea* the species of the sect. *Regulares* are the more primitive because of their heavy stems, although their stem is usually symmetric. *A. sikkimensis* is the only species of the sect. *Regulares* with an asymmetric stem. This would place *A. sikkimensis* at the lowest level of the evolutionary scale in *Acrolejeunea*. Another primitive character of this species is its more or less trigonous, 5-plicate perianth.

A. sikkimensis is an endemic species from the Himalayas in Sikkim, where it was collected only once, at an altitude of c. 3500 m. This is the highest altitude for a species of *Acrolejeunea*. The species was found hanging from a twig with *Frullania musciocola*. Further data on the habitat are unfortunately lacking. The pendulous habit of the species is unique, because all other species of *Acrolejeunea* have a prostrate habit of growth. According to SCHWEINFURTH

(1957) and TROLL (1974) the vegetation commonly found between 3000 and 3900 m in Sikkim is a wet Coniferous-Rhododendron cloud forest. If *A. sikkimensis* was indeed collected in this type of forest, this would provide an explanation for the pendulous habit because many taxa of Lejeuneaceae have this type of growth pattern in cloud forests, e.g. *Taxilejeunea*, *Omphalanthus*, *Thysananthus*, *Schiffneriolejeunea*, *Ptychanthus*, e.o. The genus *Acrolejeunea* only rarely occurs in cloud forests.

Starting with *A. sikkimensis* the morphological evolution in *Acrolejeunea* apparently takes two directions. Each direction corresponds with a subgenus:

1. Development of an entirely inflated, isoplicate perianth and a symmetric stem leads from *A. sikkimensis* into the other species of the section *Regulares*. The species of the section *Regulares* have squarrose leaves except for certain pacific forms of *A. securifolia*, which is considered the most advanced species of this section. The sect. *Isolejeunea* is more advanced than the sect. *Regulares* because of its flattened leaves and its thinner stems. By its asymmetric stem the sect. *Isolejeunea* is more primitive than the sect. *Regulares*, though. The most primitive species of the sect. *Isolejeunea* seems to be *A. parvula*, because this is the only species of the section in which the perianth is still trigonous (especially in mountain forms from northern Thailand).
2. Development of vegetative reproduction leads into the subgenus *Acrolejeunea*. The species of this subgenus are very closely related except for the endemic *A. pusilla*, which is placed in a separate section *Pusillae*. By its thin stem and its flattened leaves *A. pusilla* is more advanced than the species of the sect. *Acrolejeunea*, although by its perianth and its simple caducous leaves *A. pusilla* is rather primitive as well. Sporophytically *A. pusilla* is more advanced than the species of the sect. *Acrolejeunea* because of its short capsule valves, which remain suberect after dehiscence. This character is also found in the sect. *Isolejeunea* (*A. pycnoclada*!) near the end of the other line of evolutionary development in *Acrolejeunea*.

Within the family of Lejeuneaceae, *Acrolejeunea* and its relatives are usually considered to be primitive, ancient groups (SCHUSTER 1963). By its preference for rather dry habitats, especially at lower altitudes, *Acrolejeunea* differs from most other genera of the family, which usually abound in moist tropical forests. Its absence from the relatively recently evolved, Angiosperm-dominated tropical rainforest might also argue for an old age of the genus (SCHUSTER 1969 63).

The genera of Lejeuneaceae are considered to have originated in the tropics

(FULFORD 1951, SCHUSTER 1969), except for some primitive genera. FULFORD (1951) and STOTLER & CRANDALL-STOTLER (1974) showed that the primitive genus *Bryopteris* (Lejeuneaceae) has a tricentric distribution pattern - including S. America, Africa, and the Sikkim-India area -, which resembles the distribution pattern of certain mesozoic conifers (FULFORD 1964). Therefore they assumed that *Bryopteris* originated in the old southern land-mass ("Gondwana-land"), and migrated northwards into tropical areas after the Mesozoic break-up of the Gondwana-continent. Subsequent species diversification took place on the drifting continents, whereas climatic changes affected the areas of distribution of the species. A Gondwana origin was postulated for other groups of bryophytes with similar tricentric distribution patterns as well, e.g. the *Hyprum curvifolium* group (ANDO 1972).

The geographical distribution of *Acrolejeunea* (Pl. XXI) strongly suggests a Gondwana origin. The subg. *Acrolejeunea*, which has a tricentric distribution like *Bryopteris*, probably originated in West Gondwanaland and subsequently migrated northwards to C. America, Indo-China and Japan. Prior to the Oligocene the group should have reached Florida (U.S.A.), where one species (*A. heterophylla*) now persists in the central Floridan "Oligocene Island" region.

The subg. *Isolejeunea* is represented by primitive species in relatively cool mountain forests of continental S.E. Asia (*A. sikkimensis* and *A. parvula*), and by more advanced species in warm (sub)tropical areas of Australasia and the Pacific (*A. aulacophora*, *A. securifolia*, *A. mollis*, *A. allisonii*). RAVEN & AXELROD (1974) argued that the Indian continent served as a migration route for tropical organisms from West Gondwanaland to Australasia up to the close of the Early Cretaceous time. Thus, I presume that the subg. *Isolejeunea* originated in the eastern part of West Gondwanaland, including India, and subsequently migrated to Malesia and Australasia. Southeast Asia became its center of diversification, with 7 out of 10 species of the subgenus.

The sect. *Regulares* evolved at lower altitudes (except for *A. sikkimensis*!) and includes closely related, autoicous species which are widely distributed. The sect. *Isolejeunea* has a more diversified pattern of evolution. In Malesia one species evolved at lower altitudes: *A. pycnoclada*. This species is autoicous and widely distributed (Pl. XXII). At higher altitudes two related dioicous species evolved: *A. tjibodensis* and *A. arcuata*. These taxa actually persist on higher peaks of Malaya, Sumatra, W. Java, N. Borneo, Luzon, and New Guinea. When the sect. *Isolejeunea* reached New Zealand, two closely related paroicous species evolved: *A. mollis* and *A. allisonii*. Phenotypically these species closely resemble *A. securifolia* (Pl. XX), and therefore they are juxtaposed in

the systematic treatment. In the picture of migration and evolution in *Acro-lejeunea* subg. *Isolejeunea* presented here, these species are placed at different ends of evolutionary lines of development. Consequently, their morphological resemblance should reflect convergence rather than close phylogenetic relationship.

SPRUCE (1884) juxta-posed *Acro-lejeunea* and *Lopho-lejeunea*, mainly because both groups lack innovations. EVANS (1908) placed *Acrolejeunea* ("*Ptychocoleus*") close to *Brachiolejeunea* because of the general morphological similarity of the two genera. His arguments still hold: "The absence of subfloral innovations will at once distinguish it (*Ptychocoleus*) from *Brachiolejeunea*, but the genera agree so closely in the characters derived from the lobe of the leaves, from the underleaves, and from the bracts and perianth that it would be superfluous to describe these organs in detail for *Ptychocoleus*. There are also no essential differences in colour, in general habit, or in cell-structure" (EVANS l.c. :161-162). Recent authors have usually followed EVANS' classification, although some authors preferred to place the genus in an alphabetical arrangement (VERDOORN 1934c, BISCHLER 1965).

The genus *Brachiolejeunea* sensu EVANS consists of three elements: *Br.* subg. *Brachiolejeunea*, *Br.* subg. *Plicolejeunea* Schust. and the genus *Trocholejeunea* Schiffn. *Br.* subg. *Brachiolejeunea* is restricted in distribution to the American Andes, *Br.* subg. *Plicolejeunea* has a tricentric distribution area similar to the area of the sect. *Acrolejeunea* (America-Africa-E. Asia), whereas *Trocholejeunea* occurs in Southeast Asia (excl. Malesia) with extensions into the Pacific (VERDOORN 1934c).

It appears that *Trocholejeunea* is closely related to *Acrolejeunea* subg. *Isolejeunea*. Diagnostic differences are the presence of a *Frullania*-type innovation and a heavier seta in *Trocholejeunea* (MIZUTANI 1961). Recent reports on chromosome numbers in Lejeuneaceae (MOORE 1972) show that both groups have different chromosome numbers: *Acrolejeunea pusilla* and *A. emergens* have $n=9$ (the usual number in the family), whereas *Trocholejeunea sandwicensis* has $n=16$. Further counts may show whether the chromosome number is consistently different in both groups. Two species are assigned to *Trocholejeunea*: 1) *T. sandwicensis* from continental S.E. Asia (0-1500 m) and some pacific islands, and 2) *T. infusata* from mountains in continental S.E. Asia (1000-3000 m). Sterile *T. sandwicensis* is very similar to *A. fertilis* (sect. *Regulares*), whereas sterile *T. infusata* is sometimes almost indistinguishable from *A. tjobodensis* (sect. *Isolejeunea*). Apparently *Acrolejeunea* subg. *Isolejeunea* and *Trocholejeunea* have undergone parallel evolution: (see also Pl.XX):

altitude:	Malesia:	continental S.E. Asia:
0-1000 m.	<i>Acrolejeunea</i> <i>fertilis</i> (sect. <i>Regulares</i>)	<i>Trocholejeunea</i> <i>sandvicensis</i>
	↑↓	↑↓
1000-3000 m.	<i>Acrolejeunea</i> <i>tjibodensis</i> (sect. <i>Regulares</i>)	<i>Trocholejeunea</i> <i>infuscata</i>

As CRONQUIST (1969) pointed out, evolutionary parallelism is often indicative for close taxonomic relationship.

Brachiolejeunea subg. *Plicolejeunea* is less closely related to *Acrolejeunea* than *Trocholejeunea*. In tropical America *Brachiolejeunea* (*Plicolejeunea*) *corticalis* and *Acrolejeunea* *torulosa* (sect. *Acrolejeunea*) resemble each other when sterile. Subg. *Plicolejeunea* differs from sect. *Acrolejeunea* essentially by 1) presence of two *Radula*-type innovations, 2) winged female bracts, 3) absence of caducous leaves 4) blackish pigmentation, and 5) diandrous male bracts (personal obs.). Data on sporophyte and chromosome number in subg. *Plicolejeunea* are still lacking. It is noteworthy that both groups have fundamentally similar patterns of geographic distribution (see above). Further discussion of the affinities between both groups should await a revision of the subg. *Plicolejeunea*.

The third group in *Brachiolejeunea* sensu EVANS, Br. subg. *Brachiolejeunea*, differs more from *Acrolejeunea* than the other two groups. Other genera of Ptychanthoideae are only remotely allied to *Acrolejeunea*. The position of the genus in the subfamily is demonstrated in Part II in conjunction with a new arrangement of the genera of Ptychanthoideae.

TAXONOMIC TREATMENT

ACROLEJEUNEA (Spruce) Schiffn.

in Engl. & Prantl, Nat. Pfl.-fam. I, 3(1): 128 (1893); Schiffner (1898): 283; Bonner (1962): 15; VandenBerghen (1972): 104; Gradstein (1974a): 327.

Lejeunea subg. *Acrolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 115 (1884); Stephani (1889): 166.

Lectotype species: *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. (fide Gradstein 1974a).

Heterotypic synonym:

Ptychocoleus Evans, Bull. Torrey Bot. Cl. 35: 161 (1908) non Trev. (1877); Stephani (1912): 19; Evans (1918): 146; Verdoorn (1934c): 124; VandenBerghen (1948): 37; Jones (1954): 396; Schuster & Hattori (1954): 27; Schuster (1961): 161; Mizutani (1961): 168; Schuster (1963): 106; VandenBerghen (1965): 152; Bischler (1965): 430; Mizutani (1969): 136.

Lectotype species: *Ptychocoleus aulacophorus* (Mont.) Trev. (= *Acrolejeunea aulacophora* (Mont.) Steph.).

Plants dioicous, autoicous, or paroicous, almost without a particular smell or taste (in *A. fertilis* slightly peppery), growing in appressed mats, rarely pendulous (*A. sikkimensis*!), green with hardly any lustre or yellowish-green and golden-tinged, rarely reddish-brown pigmented, when dry becoming dull yellowish-brown or whitish-brown, more rarely dark brown. Leafy stem up to 4 cm long, 0.5-2 mm wide, irregularly branched, with branches of the *Lejeunea*-type or *Frullania*-type, the *Lejeunea*-type branches short or long, vegetative or sexual, sometimes microphyllous or upright and flagelliform (producing caducous leaves), the *Frullania*-type branches long and usually vegetative, with the dorsal half-leaf partially inserted on the branch and the first branch underleaf unequally bifid (fused with the first branch leaf?), the gynoecea without innovations (except when unfertilized!) but occasionally with pseudo-innovations of the *Radula*-type.

Stem c. 0.1 x the diameter of the leafy plant, 0.06-0.25 mm in diam., rather fragile; ventral merophyte (2-)4-6(-10) cells wide; dorsal cortical cells arranged in straight longitudinal rows or oblique zig-zag rows, the lateral merophytes interlocking dorsally; stem in transverse section with (10-)12-22 almost thin-walled cortical cells surrounding (7-)14-40 medullary cells with collenchymatic wall-thickenings of variable size, the dorsal cor-

tical cells larger than the medullary cells and larger than, or as large as the ventral cortical cells, the cell walls without pigmentation; medullary cells in longitudinal section tapering to relatively wide, truncate ends.

Leaves incubous, with a large dorsal lobe and a smaller ventral lobule, imbricated, when dry appressed and more or less wrapped around the stem with the apex suberect, when moist obliquely to widely spreading, becoming subvertical in position and strongly convex to squarrose with the dorsal margin curving backwards. Lobe asymmetrically ovate orbicular to oblong, 0.5-1.4 mm long, the dorsal base cordate to weakly auriculate, not arching beyond the stem, the margins without teeth, the apex rounded to obtuse, never acute, the apex and ventral margin plane or incurved, the keel rounded, smooth or rough by projecting cells; cells arranged in diverging rows, elongate-hexagonal, the median cells 20-45 x 15-30 μm , at leaf base slightly larger, towards the margins becoming gradually smaller, at the margins subquadrate, c. 15 μm ; vitta and ocelli absent; trigones and intermediate thickenings present, the trigones small to large, cordate or semicordate, rarely almost orbicular, the intermediate thickenings occasionally to frequently present on longer cell walls, elliptical to orbicular, usually one, rarely two on each wall; cuticula smooth; oil bodies present in all cells of leaves, underleaves, and stem cortex, in the lobe 7-20 per cell, homogeneous and colourless, ellipsoid to fusiform, up to 9 μm long, upon degeneration becoming septate and subsequently desintegrating into minute granulae.

Lobule 2/5-2/3 x the length of the lobe, never reduced, ovate to rectangular or semiorbicular, with an inflated portion along the keel and a non-inflated portion along the free margin, the free margin plane or upcurved, not incurved, arched at base and sometimes auriculate, towards the apex with 1-9 erect or inflexed teeth, beyond the apex abruptly ending or continuing over a short distance into the ventral margin of the lobe; hyaline papilla inserted on the inner side of the lobule at the proximal base of the apical tooth or 1-3 cells below it; cells of the lobule slightly smaller than the cells of the lobe and arranged irregularly.

Underleaves imbricated to distant, 3-5 x the width of the stem, orbicular to subquadrate or transversally ovate, sometimes gibbous, the apex undivided, rounded to weakly retuse, plane or recurved, the margins entire and usually plane, the bases cuneate, rounded or slightly auriculate, the line of insertion straight or arched; underleaf base with 4 superior central cells, bistratose, the primary rhizoid disc consisting of up to 15 bulging cells giving rise to short bundles of pale rhizoids.

Androecia terminal or intercalary on *Lejeunea*-type branches, rarely on

Frullania-type branches, the bracts and bracteoles in 2-50(!) series, the bracts very much resembling leaves but usually slightly smaller in size, the lobules more strongly inflated, epistatic, almost without teeth, enveloping one globose antheridium subtended by a curved, uniseriate stalk; bracteoles similar to underleaves, present throughout the male spike.

Gynoecium on a short or long, *Lejeunea*-type branch (very rarely *Frullania*-type!), the gynoecial portion of the axis slightly to conspicuously swollen, the bracts and bracteoles in (1-)2-6 series, never connate, increasing in size towards the inner series, the margins without teeth; inner bract suberect to widely spreading, shallowly to deeply (to 2/3) bifid, the lobule elongated beyond the keel, smaller to almost as large as the lobe, the lobe at apex widely rounded to narrowly obtuse, the lobule at apex rounded to sharply acute or acuminate; inner bracteole usually as long as the bract, orbicular-obovate to elliptical or obspathulate, sometimes distinctly gibbous, undivided, the apex widely rounded to weakly retuse, plane or recurved.

Perianth immersed or emergent to 1/2(-2/3) of its length, obovate-cylindrical to obpyriform, sometimes shortly stalked, + bilaterally compressed with the ventral side swollen, or entirely inflated, anisplicate or isoplicate in the upper half with (4-)5-10 plicae (2 lateral, (0-)1-3 dorsal, 2-5 ventral), the plicae usually smooth on their backs, rarely "rough" with rudimentary wing-like projections; beak 3-12 cells long; basal cells large and thin-walled with small trigones, apical cells much smaller, often with large trigones.

Calyptra entirely enveloping the young sporophyte, the upper portion (surrounding the capsule) 1(-2)-stratose, the lower portion (surrounding seta and foot) 3-7-stratose, the outer calyptral cells about twice as wide as the inner cells, the calyptral stalk very short.

Mature sporophyte exerted up to 2 mm above the perianth, the foot consisting of few bulging cells in c. 3 layers, the seta not articulate, with (14-) 16 evenly or unevenly tiered longitudinal rows of outer cells and 4(-8) longitudinal rows of inner cells, the capsule globose, dark brown, splitting to 4/5 of its length into 4 valves; valves widely spreading, rarely suberect, each valve bearing 9 elaters at apex, bistratose, the outer cells with asymmetrically-nodulose trigones and intermediate thickenings except for the centro-basal cells which are thin-walled, the inner cells covered by an orange-brown, mono- to irregularly plurifenestrate sheath of thickening, the capsule-base 3-4-stratose, of thin-walled cells; elaters 36 per capsule, 130-400 μ m long, 12-15 μ m wide, with one or two spirals, the spirals yellowish-brown, 4-6 μ m wide, sometimes rudimentary; spores with precocious germination, ellipt-

ical or almost isodiametrical, 40-60 μm long, angular when dry, the spore-coat covered with numerous short bluntish papillae and 6-12 rosettes of radially oriented coarse, sharp papillae.

Sporelings of the *Lopholejeunea*-type, lacking primary underleaves.

Vegetative reproduction (in subg. *Acrolejeunea*) by means of modified caducous leaves produced on upright flagelliform shoots; gemmalings with primary underleaves.

Chromosomes: $n=9$ (known in *A. emergens* and *A. pusilla*).

Distribution: PANTROPICAL, ranging in altitude from sealevel up to 3500 m.; highest records from the Himalayas (Sikkim), North Borneo (Mt. Kinabalu), and New Guinea. The main centre of diversity is South East Asia with 9 species.

Ecology: mostly epiphytic, drought tolerant; preferably growing on stems or twigs of living trees or shrubs in rather open mesophytic to xerophytic woods or bush, in savannas, along roadsides or beaches, and in cultivated areas (plantations, gardens, etc.), more rarely in moist riparian woods or high altitude forests (1500-3500 m.); rarely growing on decaying wood, on rocks, or on soil (calcareous!); not epiphyllous.

Differentiation: important diagnostic characters are underlined in the description.

KEY TO THE SPECIES OF ACROLEJEUNEA ⁺)

1. Upright flagellae producing caducous leaves present.....2.
1. Upright flagellae absent.....7.
2. Flagellae with widely spreading to squarrose-recurved underleaves.....3.
2. Flagellae with appressed or obliquely spreading underleaves.....5.
3. Lobule with 2-4 teeth. Keel forming an almost straight line with the ventral margin of the lobe.....
-4. *A. emergens* (Africa, America)

⁺) plants in moist condition; leaves and underleaves from stem, not from branches.

3. Lobule with (4-)5-8 teeth. Keel usually forming an angle of 120-150° with the ventral margin of the lobe.....4.
4. First tooth of the lobule 2-4 cells long, erect or curved, separated from the second tooth by more than two margin cells.....2. *A. torulosa* (America)
4. First tooth 1 cell long, usually inflexed, separated from the second tooth by one or two margin cells.....3. *A. heterophylla* (C.America, Florida)
5. Stem with leaves less than 1 mm wide.....1. *A. pusilla* (Japan)
5. Stem with leaves 1-2,5 mm wide.....6.
6. Underleaf apex recurved-retuse, rarely plane. Lobule with (3-)4-6 teeth. Flagellae seemingly barren, with minute underleaves.....5. *A. recurvata* (Indo-China)
6. Underleaf apex plane. Lobule with 2-4 teeth. Flagellae with distinct underleaves.....4. *A. emergens* (Africa, America)
7. Lobule with 3-10 teeth (teeth sometimes inflexed and rather invisible!).....8
7. Lobule with 1-3 teeth.....13.
8. Lobule semi-orbicular, with semi-circular free margin and regularly spatiated teeth (or lobule ovate in plants from Ceylon: p. 89).....9.
8. Lobule ovate to triangular or rectangular, the free margin not semi-circular in outline.....10.
9. Lobule with 4-10 erect or partially inflexed teeth, all or at least some teeth 2-3 cells long; inner female bracteole gibbous.....7. *A. fertilis* (Indo-Malesia)
9. Lobule with 3-5 inflexed teeth, each tooth only 1 cell long; inner female bracteole not gibbous.....8. *A. aulacophora* (Pacific, Australasia, Africa)
10. Leaves distinctly squarrose: the dorsal leaf margin curving backwards.....11.
10. Leaves not or weakly squarrose.....13.
11. Plants from Africa or America.....3.
11. Plants from continental S.E.Asia.....12.
12. Leaves barely overlapping. Underleaves longer than wide, with flat apex.....6. *A. sikkimensis* (Sikkim)
12. Leaves closely imbricated. Underleaves wider than long, with + recurved apex.....5. *A. recurvata* (Indo-China)
13. First tooth of the lobule situated at the extreme end of the free

- margin (Pl.XVI:2-5). Female bracteole cucullate, the bracts often also cucullate. Beak of the perianth 8-12 cells long.....12. *A. pycnoclada* (Pacific, Indo-Malesia, Africa)
13. First tooth of the lobule not situated at the extreme end of the free margin. Female bracteole and bracts not cucullate. Beak of the perianth 3-8 cells long.....14.
14. Lobule more than 2,5 x longer than wide. Plants often reddish-brown.....15. *A. arcuata* (Malesia)
14. Lobule less than 2,5 x longer than wide. Plants not reddish-brown.....15.
15. Plants very small: stem with leaves less than 1 mm wide. Dioicous.....16.
15. Plants larger.....17.
16. Lobule apex oblique, with 2 teeth.....1. *A. pusilla* (Japan)
16. Lobule apex + truncate, with 1 tooth.....13. *A. parvula* (Indo-China)
17. Underleaves with deeply arched insertion-line and + recurved apex. Dioicous.....18.
17. Underleaves with shallowly curved insertion-line and flat, rarely weakly recurved apex. Paroicous or autoicous, rarely dioicous.....19.
18. Leaf apex incurved, dorsal leaf base auriculate. Lobule with 2-3 narrow, linear teeth.....14. *A. tjiobodensis* (Malesia)
18. Leaf apex flat or weakly incurved, dorsal leaf base not auriculate. Lobule with 1-2(-3) wide teeth.....9c. *A. securifolia* ssp. *caledonica* (N. Caledonia)
19. Lobule with one prominent tooth.....20.
19. Lobule with two or more teeth.....22.
20. Plants paroicous: with 2-4 series of male bracts below the gynoecium (New Zealand only).....21.
20. Plants autoicous or dioicous.....9d. *A. securifolia* ssp. *pallida* (S.C.Pacific)
21. Underleaves 0,6-0,8 mm wide. Perianth distinctly emergent. Female bracts bifid to 1/2.....10. *A. allisonii* (New Zealand)

21. Underleaves 0,5 mm wide. Perianth not emergent. Female bracts bifid to 1/5.....11. *A. mollis* (New Zealand)
22. Lobule of the inner female bract + as large as the lobe. Perianth entirely inflated, isoplicate. Flagellae absent.....
.....9. *A. securifolia* (E.Malesia, Australasia,
Pacific)
22. Lobule of the inner female bract shorter and smaller than the lobe. Perianth more or less compressed above, anisoplicate. Flagellae usually present.....
.....4. *A. emergens* (Africa, America)

Subg. 1. *ACROLEJEUNEA*

Plants with vegetative reproduction by means of caducous leaves. Perianth anisoplicate, more or less compressed in the upper half except for a swelling of the ventral side. Outer cells of the seta unevenly tiered.

Distribution: tropical AMERICA, AFRICA, S.E. ASIA (not in Maleisia!)

Sect. 1. *Pusillae* Gradst. sect. nov.

Caulis in sectione transversali cellulis corticalibus 10-12, cellulis medullaribus 7-9. Lobi foliorum non squarrosi.

Type species: *Acrolejeunea pusilla* (Steph.) Grolle & Gradst.

Stem in transverse section with 10-12 cortical cells and 7-9 medullary cells. Dorsal cortical cells arranged in straight longitudinal rows. Leaves not squarrose. Lobule $1/2-2/3$ x the length of the lobe, with 1-2 teeth. Female bracts in 1-2 series, the lobule of the inner bract c. 0,5 mm long. Perianth with 4-5 plicae.

Distribution: this section contains only *A. pusilla* from Japan.

1. *ACROLEJEUNEA PUSILLA* (Steph.) Grolle & Gradst. (Pl.VII)

in Gradst., J.Hattori Bot.Lab. 38: 332 (1974).

Archilejeunea pusilla Steph., Spec.Hep. 4: 731 (1911); Verdoorn (1934c): 47
Typus: Japan, Oshima, Faurie 640, VII.1900 (G holo not seen, PC!).

Heterotypic synonym:

Ptychocoleus nipponicus Hatt., Bot.Mag.Tokyo 57: 358 (1943); Hattori (1951): 43, 84; Mizutani (1961): 169; Bischler (1965): 431; Tatuno & Nagatomo (1969): 48.

Typus: Japan, Kagoshima, Yakushima I., Hattori 8077, X.1940 (TNS holo not seen).

Plants dioicous, small, up to 2 cm long, 0,7-0,9 mm wide, greenish, becoming brownish when dry, irregularly branched; branches always of the *Lejeunea*-type, occasionally becoming erect and flagelliform (producing caducous leaves), microphyllous branches and (pseudo-)innovations not seen.

Stem fragile and thin, up to 0,1 mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells (sub)rectangular, the dorsal cortical cells larger, arranged in straight rows; stem in transverse section with 10-12 cortical cells surrounding 7-9 medullary cells, the dorsal cortical cells c. 25µm high, the ventral cortical cells and the medullary cells 15-20 µm, the

cells moderately thick-walled, with yellowish walls.

Leaves (laxly) imbricated, appressed and only slightly clasping the stem when dry, when moist obliquely spreading, strongly convex, not squarrose. Lobe asymmetrically ovate orbicular, 0,4-0,6 mm long, 0,4-0,5 mm wide, inserted along $(1/2-3/4)$ x the length of the merophyte, the dorsal base almost straight, the apex rounded, the ventral margin plane or slightly incurved, forming a nearly straight line with the keel; keel arched at base, smooth, at an angle of $45-60^\circ$ with the axis, not decurrent; median leaf cells arranged in indistinctly diverging rows, $30-35 \times 20-25 \mu\text{m}$, at leaf base slightly larger, at leaf margin forming a row of smaller, (sub)quadrate cells; trigones medium-sized, intermediate thickenings frequent, 1-2 per cell; oil bodies (MIZUTANI 1961) homogeneous, 15-20 per cell, ellipsoid to spherical, $1,5-2 \times 1,5-6 \mu\text{m}$.

Lobule relatively large, $1/2-2/3$ x the length of the lobe, ovate with an oblique apex, 0,3-0,4 mm long, 0,2-0,25 mm wide, widely inflated along the keel and gradually flattened above; free margin \pm plane, gradually curved towards apex and continuing into the incurved ventral margin of the lobe, sinuate-dentate, (1-)2 erect teeth, the teeth 1-2(-3) cells long, separated from each other by 2-4 margin cells; hyaline papilla one cell below the base of the first tooth.

Underleaves barely overlapping, small, orbicular to subquadrate, 0,15-0,25 mm in diam., plane, the apex rounded to truncate, the bases weakly cuneate, the line of insertion almost straight; cells $15-20 \times 18-24 \mu\text{m}$, at the margins smaller; rhizoid disc often rudimentary.

Androecia in short spikes terminal or intercalary on long stems or branches, the bracts in 2-5 series, \pm similar to leaves but the lobe slightly smaller and the lobule more strongly inflated, monandrous; bracteoles similar to underleaves.

Gynoecium terminating a stem or branch, the bracts and bracteoles in 1-2 series, hardly larger than leaves and underleaves; inner bract obliquely to widely spreading (not squarrose), unequally bifid with a relatively small lobule and a rounded keel, the lobe concave, ovate, c. 0,8 mm long, with a rounded apex, the lobule not or weakly elongated beyond the keel, ligulate and flat, $0,55(-0,6) \times 0,2-0,25 \text{ mm}$, with a narrow obtuse to truncate apex, the teeth reduced to a single cell; inner bracteole ovate-ligulate, erect or deflexed, shorter than the bracts, 0,5-0,7 mm long, the apex rounded to slightly retuse. Perianth emergent, widely obovate, $0,8 \times 0,5 \text{ mm}$, \pm compressed with the ventral side inflated, with 4-5 sharp and very unequal plicae: two wide lateral keels, extending over the whole length of the perianth and \pm rough at their backs by proliferating cells, two sharp ventral plicae,

inserted on the edges of a wide, rounded keel and extending half-way down the perianth, and one small dorsal plica, which is sometimes absent; beak 2-4 cells long.

Sporophyte: seta (MIZUTANI 1961) not articulate, 4-5 cells thick, the outer cells in 14-16 longitudinal rows, the inner cells in 4-8 rows; capsule tiny, split nearly to base into 4 (rarely 2!) valves, the valves c. 350 μ m long, not widely spreading but remaining suberect, pale-brownish; spores c. 50 μ m, elaters short, c. 130-170 μ m long, with one yellowish-brown spiral which is sometimes developed rudimentary.

Vegetative propagation by means of caducous leaves produced on specialised flagelliform branches or on shoots terminating leafy, sterile branches; flagellae up to 1 mm long, with 5-15 small, appressed underleaves; caducous leaves much smaller than branch leaves, 0,1-0,2(-0,3) mm long, the lobule 2/3-4/5 x the size of the lobule, with 2 teeth.

Chromosomes: n=9 (TATUNO & NAGATOMO 1969).

Distribution: JAPAN (see map in MIZUTANI 1961: 286).

The species is not uncommon in the lowlands of southern Japan, ranging in altitude from sea level up to 300 m. (-900 m. (?): Kumamoto, Mayebara 3192). Due to the relatively mild climate along the east coast of Japan, the species reaches north as far as Kinkazan I., near Sendai, at c. 38°30' N. Lat., where the mean January temperature is about 0°C. (MIZUTANI l.c.: 289).

Ecology: on stems of trees in broad-leaved evergreen forests.

Differentiation: *A. pusilla* is the only species of the genus occurring in Japan. It is a peculiar little plant which differs from other species of the genus in quite a number of characters, including 1) the very small size, 2) the obliquely spreading leaves, which are not squarrose, 3) the large leaf-lobule, which has only (1-)2 teeth, 4) the weakly differentiated female bracts, which have relatively small lobules, and 5) the widely obovate perianth, which has only 4-5 very unequal, + rough plicae.

The species is interesting too by its sporophyte. The seta, described by MIZUTANI (1961), shows irregularities in the number of cells in transverse section. Most important is the decrease in the number of outer rows of cells (14-16), because the Ptychanthoideae are supposed to have 16 outer cells, whereas the Lejeuneoideae have only 12. The valves of the mature capsule in *A. pusilla* are relatively short and do not spread widely as in the other species of the genus (except for some specimens of *A. pycnoclada*). In this

respect the species also resembles *Lejeuneoideae*. In other respects, e.g. thickening pattern of the valves, morphology of spores and elaters, etc. the species is not different from the *Ptychanthoideae*.

Variation: morphologically *A. pusilla* is a very stable species.

Note: caducous leaves had not yet been reported in this species although MIZUTANI depicted a short flagella (1961: fig. XI,2).

Specimens seen (*A. pusilla*):

Kagoshima: Yakushima I., Hattori 8069, X.1940 (TNS); Ibusuki-gun, Kaimon-mura, Iwatsuki s.n., I.1956 (NICH).

Miyazaki: Aoshima I., Hattori s.n., XI.1952 (NICH); Tomishima, Amakawa s.n., III.1952, Hep.Jap. 244 (COLO,G,GRO,H,JE,M,NICH,S,W); Nichinan, Iwatsuki & Mizutani s.n., VII.1969, Hep.Jap. 887 (COLO,NICH,U).

Kumamoto: Hitoyoshi, Mayebara 618, VIII.1947 (NICH,NY,S); *ibid.* Mayebara s.n., III.1950, Hep.Jap. 191 (COLO,G,GRO,H,M,NICH,S,W); Itsuki, Mayebara 3192, VIII.1951 (S); Kuma-Gun Watari, Mayebara s.n., VIII.1947, Hep.Jap. 43 (NY,S).

Tsushima I.: Mt. Tatera, Inoue 19400, III.1969 (TNS).

Kochi: Shikoku, Mt.Yokogura, Hattori 4179, VII.1940 (TNS); Tosa, None Mt., Yoshinaga 4, XI.1903 (YU); Tsudai-mura, Sawaragi 7641, III.1956 (NY).

Wakayama: Tomogashima I., Kodama 9359, IX.1955 (NICH); Kotonoura, Kodama 4993, XI.1953 (W); Nakanokawa, Samoto, Kitagawa 2569, III.1959 (S,W).

Mie: Ohé, Nanto-cho, Kodama 43939, IV.1972 (U); Aominé-yama Mt., Toba, Kodama 18289, VII.1962 (U).

Saitama: Chichibu, Nagatoro, Inoue 5678, VII.1956 (TNS).

Miyagi: Kinkazan I., Higuchi 25389-90, III.1953 (NICH).

Sect. 2. Acrolejeunea

Stem in transverse section with 12-22 cortical cells and 20-24 medullary cells. Dorsal cortical cells arranged zig-zag in oblique rows. Leaves squarrose. Lobule $2/5-1/2$ x the length of the lobe, with 2-8 teeth, the hyaline papilla one or two cells below the base of the apical tooth. Female bracts in 2-6 series, the lobule of the inner bract c. 1 mm long. Perianth with (4-)5-10 plicae.

Distribution: tropical America, Africa, and Indo-China.

2. ACROLEJEUNEA TORULOSA (Lehm. & Lindenb.) Schiffn. (Pl.VIII)

- in Engl. & Prantl, Nat.Pfl.-fam. I, 3(1): 128 (1893); Schiffner (1894): 188; Gradstein (1974a): 333.
Jungermannia torulosa Lehm. & Lindenb., in Lehmann, Nov.Min. Cogn.Stirp.Pug. 6: 41 (1834).
Lejeunea torulosa Dum., Rec. d'Obs.: 12 (1835) nom. nud.
Phragmicoma torulosa (Lehm. & Lindenb.) Lehm. & Lindenb., Syn.Hep.: 294 (1845); Stephani (1889): 166, (1890): 9.
Ptychocoleus torulosus (Lehm. & Lindenb.) Trev., Mem.Reale Ist.Lomb.Sci.Mat. Nat., Ser. 3,4: 405 (1877); Evans (1908): 165, (1912): 62, (1918): 149; Stephani (1912): 37.
Lejeunea (subg. *Acrolejeunea*) *torulosa* (Lehm. & Lindenb.) Spruce, Trans. & Proc.Bot.Soc.Edinburgh: 117 (1884); Stephani (1890): 133.
Marchesinia torulosa (Lehm. & Lindenb.) Kuntz, Rev.Gen.Pl.II: 837 (1891).
 Typus: Guiana, "Hb. Hooker" (S holo, BM,FH,MANCH,NY,PC,W,YE).

Heterotypic synonym:

- Lejeunea polyphylla* Tayl., London J.Bot. 5: 390 (1846); Syn.Hep. (1847): 751; Stephani (1889): 19, (1890): 16; Evans (1902): 115.
Lejeunea torulosa var. *polyphylla* (Tayl.) Spruce, Trans. & Proc.Bot.Soc. Edinburgh 15: 118 (1884).
Symbiezidium polyphyllum (Tayl.) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 403 (1877).
Archilejeunea polyphylla (Tayl.) Steph., Spec.Hep. 4: 717 (1911).
 Typus: Brazil, Belem, on bark of coffee-trees, "J.L.R." s.n. (J.L.Richard?), II.1841 (FH-Tayl. holo, BM,MANCH,W) "Hab. Cincinnati" in descr.orig. pro err. (fide Evans (1902): 115).

Plants autoicous or (seemingly?) dioicous, medium-sized, up to 4 cm long, 1,25-1,8 mm wide, green, becoming dull yellowish-brown to darkish- or grayish-brown when dry, irregularly branched; branches short or long, rarely microphyllous, mostly of the *Lejeunea*-type, originating at straight angles with the axis and curving towards the stem apex or ascending and becoming flagelliform (producing caducous leaves), long vegetative branches of the *Frullania*-type infrequently present.

Stem 0,12-0,17 mm in diam.; ventral merophyte 4(-6) cells wide, the ventral cortical cells rectangular, 35-55 x 22-30 μ m; dorsal cortical cells

arranged zig-zag in oblique rows; stem in transverse section with 16-22 thin-walled cortical cells surrounding 24-34 medullary cells, the dorsal cortical cells 30-35 μm high, the ventral cortical cells 20-27 μm high, the medullary cells 15-27 μm in diam., the walls of the medullary cells slightly thickened and somewhat darker in colour than the walls of the cortex.

Leaves closely imbricated, clasping the stem when dry, when moist widely spreading-falcate and squarrose. Lobe ovate-orbicular, 0,7-1,2 mm long, 0,7-1,0 mm wide, inserted along the whole length of the merophyte, the dorsal base not or weakly auriculate, the apex rounded or subobtusate, plane, the ventral margin plane or upcurved, when spread out forming an angle of 140-160° with the keel; keel smooth, at an angle of 45-75° with the axis, curved near the base, not decurrent; median leaf-cells 25-35 x (16-)20-27 μm larger towards leaf base, at the margins small and subquadrate, 14-18 μm high; trigones small to medium-sized, intermediate thickenings usually scarce, more frequent near the margins of the lobe; oil bodies homogeneous, 7-15 in median leaf cells, ellipsoid to fusiform, 2 x 4-7(-9) μm (sphaerical when seen from the side), in marginal leaf cells shorter, in stem cells very small and sphaerical, up to 25 per cell.

Lobule ovate-triangular with an oblique apex, 0,35-0,5 mm long, 0,25-0,35 mm wide, 2/5-1/2 x the length of the lobe, inflated along the keel, rather abruptly flattened towards the free margin, the flattened part often becoming concave; free margin plane or upcurved, gradually curved towards the apex of the lobule and shortly continuing into the ventral margin of the lobe, with 5-7 teeth; first tooth 2-4 cells long, usually curved outwardly, more rarely erect or partly inflexed, separated from the second tooth by 3-5 free margin cells, the other teeth 1-2 cells long, erect or inflexed, separated from each other by (1-)2-3 free margin cells; hyaline papilla three cells below the proximal base of the first tooth.

Underleaves imbricated, plane or slightly gibbous, transversally ovate to obovate, 0,25-0,5 mm long, 0,5-0,8 mm wide, the apex rounded to truncate, rarely notched, plane, the bases rounded or slightly auriculate, the line of insertion arched, 0,08-0,15 mm deep; median cells (21-)25-30(-34) x 15-25 μm , at the margins smaller and subquadrate; rhizoid disc elliptical, made up of a few large, rather thick-walled cells.

Androecia on short or long *Lejeunea*-type branches, usually close to the female branch; bracts and bracteoles in 6-10 series, the bracts resembling leaves but the lobe slightly smaller than the leaf-lobe and the lobule more strongly inflated, with reduced teeth; bracts monandrous.

Gynoecium terminating a short *Lejeunea*-type branch, without innovations but sometimes with short, sterile pseudo-innovations of the *Radula*-type;

bracts and bracteoles in (3-)4-5(-6) series, densely crowded, becoming larger and more or less bilaterally compressed towards the inner series, the lobule becoming longer and erect; inner bract squarrose above, subequally bifid to $1/3$, with a sharp keel, the lobe obovate, 1,1-1,4 mm long, widely rounded at apex, the lobule narrow oblong, $2/3-3/4$ x the length of the lobe rounded or notched at apex; inner bracteole erect, obovate-subquadrate, as long as the bracts, the apex widely rounded to truncate, plane or rarely narrowly recurved. Perianth not emergent when mature, obovate, c. 1,0 x 0,7 mm, inflated below, compressed or weakly inflated (when old!) above, anisoplicate, with 5-10 smooth plicae in the upper half: 2 lateral plicae, 2-5 narrow ventral plicae which are inserted on a wide ventral keel, and (1-)2-3 small dorsal plicae; beak 6-7 cells long.

Sporophyte seta with 16 unevenly tiered outer cells; capsule split to near base into 4 widely spreading valves; spores green, angular when dry, 40-50 μ m long, covered with numerous short, bluntish papillae and a few rosettes; elaters 350-400 μ m long, c. 14 μ m wide, with one brownish, c. 4 μ m wide spiral. Sporeling of the *Lopholejeunea*-type.

Vegetative reproduction by means of caducous leaves produced on ascending flagelliform shoots which arise with or without torsion from short leafy or male branches; flagellae unbranched, with strongly squarrose and outwardly folded underleaves without rhizoid disc; caducous leaves \pm saccate, about three to five times smaller than branch-leaves, usually with subequal lobe and lobule, the lobe 0,2-0,4 mm long, 0,2-0,3 mm wide, the lobule 0,15-0,2 mm wide, with 2 teeth; a long apical rhizoid arising from the sinus at the junction of lobe and lobule.

Distribution (Pl.XXI): tropical SOUTH AMERICA, C. AMERICA (Honduras).

Probably common in the Amazon and Orinoco basin. The species seems to occur mainly in lowland areas (0 - 100 m) but data on the altitudinal distribution are scarce. In Honduras collected at c. 800 m.

Ecology: on bark of living trees in savannas, pastures, and in xerophytic to mesophytic forests. Along the Amazon and its tributaries also occurring in seasonally flooded riparian forest (igapo). In Sao Paulo State growing in xerophytic shrubby secondary forests (cerradaos). In Brazil the species often grows together with *A. emergens*!

Differentiation: *A. torulosa* is distinguished from its allies (e.g. *A. heterophylla* and *A. emergens*) by 1) its lobule, which has 5-8 teeth, and 2) its small caducous leaf, which has a subequal lobe and lobule and a long

rhizoid protruding from the sinus between lobe and lobule. Further differences are discussed under *A. heterophylla* and *A. emergens*. *A. torulosa* was defined by SPRUCE (1884) and EVANS (1918) as having a lobule with 2-8 teeth. Spruce distinguished two varieties: var. *torulosa* with 2-4 teeth, and var. *polyphylla* (Tayl.) Spruce with 5-8 teeth. The type of *Acrolejeunea torulosa*, of which beautiful fruiting material is kept in the Stockholm herbarium (holo), has a lobule with 6-7 teeth and is therefore similar to var. *polyphylla* (Tayl.) Spruce. All neotropical plants named *A. torulosa*, which have a lobule with only 2-4 teeth (var. *torulosa* sensu Spruce), appear to be similar to the African *A. emergens*.

When sterile, *A. torulosa* might be confused with *Brachiolejeunea corticalis*, which has almost similar leaves and underleaves. *Br. corticalis* differs mainly by 1) its more blackish colour when dry, 2) the less squarrose leaves, 3) the stem, which is more rigid, and 4) the absence of caducous leaves.

Variation: *A. torulosa* varies in size, in characters of the lobule, in the width of the underleaves, and in the number of perianth plicae. The variation in the lobule is correlated with the size of the plant (EVANS 1918). Small plants usually have ovate leaves with a relatively narrow apex and a rather sharp angle at the junction of the ventral margin of the lobe and the keel. The lobule is usually sharply divided into a narrow sac and a wide non-inflated portion which tends to become deeply concave. Furthermore the first tooth is slenderer than the other teeth and curved outwardly.

Large plants (including the type of *A. torulosa* and *A. polyphylla*!) have wider, more orbicular leaves, in which the ventral margin forms an almost straight line with the keel. The lobule is more gradually flattened and the first tooth is usually erect and not very different from the other teeth. Sometimes the teeth are very irregularly developed, especially towards the base of the free margin. Large plants are usually fertile and autoicous, and only rarely produce caducous leaves (absent in the type collections). They somewhat resemble *A. emergens*. The small plants on the other hand are often sterile and seemingly dioicous, and produce great quantities of caducous leaves. They have much more affinity to *A. heterophylla*. This affinity is most obvious in *A. torulosa* var. *obtusa*.

Note: in some collections from the Amazonas and Sao Paulo State (Griffin 48 & 212; Sioli 40; Vital 2088) *A. torulosa* and *A. emergens* are growing intermingled. Both species are very distinct in these collections and can be distinguished almost with the naked eye by the more flattened appearance of *A. emergens*. *A. torulosa* is represented in these collections by its small

form with the outwardly curved first tooth. On the other hand, it appears that forms which are morphologically intermediate between both species occur as well in the coastal regions of Brazil. Two intermediate collections were seen (Vital 2109 & 2846). These plants have 5-7 lobule teeth like in *A. torulosa* and caducous leaves resembling those in *A. emergens*. The intermediate form apparently does not grow together with typical forms of either species.

It thus appears that my delimitation of *A. torulosa* and *A. emergens* is not entirely satisfactory. Nevertheless, I have kept both taxa on the species level in this treatment because the number of intermediate collections is very small. More collections of *A. torulosa* and *A. emergens* from tropical America are wanted to achieve a better understanding.

Key to the varieties of *A. torulosa*.

- a. Inner female bract with widely rounded apices.....var. *torulosa*
- b. Inner female bract with narrowly obtuse apices.....var. *obtusa*

2a. *A. torulosa* var. *torulosa*

see under the species

2b. *A. torulosa* var. *obtusa* Gradst. var. nov. (Pl.VIII)

A typo differt lobis lobulisque bractearum feminearum angustibus obtusis vel apiculatis, foliis inferioribus parvis basi cuneatis subdecurrentibus. Typus: British Guiana, Rupununi river basin, near mouth of Chairwair creek, on tree trunk at edge of forest, A.C.Smith 2397, XI.1937 (NY holo, FH, Fulford, K, S, U, US).

The type material consists of relatively small plants, with young sporophytes. The distinguishing characters of this variety are 1) the narrowly obtuse to apiculate apex of lobe and lobule in the inner female bracts, and 2) the cuneate, almost decurrent underleaves. By its bracts and its small size the variety resembles *A. heterophylla*.

Distribution: only known from the type.

Specimens seen (*A. torulosa* var. *torulosa*):

HONDURAS. Morazan: Quebrada de St. Clara, Standley & Williams 169 (F).
TRINIDAD. Piarco Savanna, E.G. Britton et al. 119, II.1920 (FH, NY, US, YU);
Princetown, Broadway 9137, XII.1932 (Fulford ex BM).

VENEZUELA. Guarica: San Carlos, *Rudd* 407, XI.1943 (Fulford); Orinoco: Esmaralda, *Serrote*, *Lützelburg* 22552, X.1928 (JE); *ibid.* 23109, X.1928 (W).

GUIANA (without further indications): ex hb. Hooker (BM, FH, MANCH, NY, PC, S, W, YU); *Leprieur* s.n., ex hb. Stephani (BM).

SURINAME. ex hb. Hampe (BM); Berg en Dal, *Suringar* s.n., IV.1885 (L); Charlesburg, *Lanjour* 124, VII.1933, *Hep. Sel. Crit. Verdoorn* 436 (BM, FH, Fulford, JE, L. MANCH, NY, S, US, W, YU).

FRENCH GUIANA. St. Jean du Marouï, *Rey* 38, 1909 (PC).

BRAZIL. Para: Belem, *J.L.R.* s.n., II.1841 (BM, FH, MANCH, W); Caripi, Obidos, & Maypures, "Silva Amazonica", *Hep. Spruc. Am. And.* 117 (BM, NY, YU); *Spruce* s.n., several collections (BM, M, MANCH, NY, US, W); Amazonas: road Manaus-Caracarai, Campina forest, *Griffin et al.* 48 p.p., 1974 (FLAS, U); road Manaus-Itacoatiara, *Griffin* 212 p.p., VII.1974 (FLAS, U); Manaus, Estrada Maua, *Smith et al.* P 11728, IV.1971 (NY, U); Rio Negro, in monticulo Canapuna, *Spruce* L95 (MANCH); Rio Cururu, *Stoll* 40 p.p., VI.1942 (GRO); Sao Paulo: Nova Independencia near Andradino, *Vital* 2085 & 2086, V.1972 (NICH, SP, U).

PERU. Loreto: Iquitos, *Hegewald* 6322 & 6354, VII.1973 (Hegewald, U).

Intermediate between *A. torulosa* and *A. emergens*:

BRAZIL. Espirito Santo: Piuma, Lake Piabanha, *Vital* 2846, I.1974 (SP, U); Sao Paulo: Rancharia, *Vital* 2109, V.1972 (NICH, SP, U).

3. ACROLEJEUNEA HETEROPHYLLA (Evans) Grolle & Gradst. (Pl.VII)

in Gradst., *J. Hattori Bot. Lab.* 38: 332 (1974).

Ptychocoleus heterophyllus Evans, *Amer. J. Bot.* 5: 44 (1918); Evans (1922); 32; Schuster (1954): 52.

Typus: U.S.A., Florida, Semiole Co., Robinson's Spring, 8 miles S. of Sanford, on live oak, *S. Rapp* s.n., 8.V.1917 (YU holotype).

Plants dioicous, small, 1-2,5 cm long, 1-1,3 mm wide, yellowish-green and golden-tinged when alive (SCHUSTER 1954), becoming yellowish-brown when dry, irregularly branched; branches mostly of the *Lejeunea*-type, short, sometimes becoming erect and flagelliform (producing caducous leaves), occasionally a longer *Frullania*-type branch present, microphyllous branches absent.

Stem 0,09-1,3 mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells (sub)rectangular, 35-45 x 20-35 μ m, the dorsal cortical cells subquadrate, 25-40 μ m, arranged zig-zag in oblique rows.

Leaves closely imbricated, clasping the stem when dry, when moist widely spreading and squarrose. Lobe ovate-suborbicular, (0,6-)0,7-C,9(-1) mm long, 0,45-0,65 mm wide, inserted along the whole length of the merophyte, the dorsal base not auriculate, the apex (sub)obtuse, plane, the ventral margin almost plane, at an angle of 90-120(-140) $^{\circ}$ with the keel; keel curved and smooth, at an angle of 45-60 $^{\circ}$ with the axis, arched near the base, not decurrent; median leaf cells 24-30(-35) x 17-23 μ m, cells slightly larger

towards leaf base, at the margins small and subquadrate, 12-15 μm high; trigones medium-sized, intermediate thickenings frequently present on longer cell walls, one on each wall; oil bodies (SCHUSTER 1954) homogeneous, in the leaf centre 7-12 per cell, bacilliform to narrowly fusiform, more rarely ovoid to broad-ellipsoid, 2(-3) \times 3-5(-8) μm , in marginal leaf cells usually smaller and almost sphaerical.

Lobule ovate-triangular with an oblique apex, 0,35-0,5 mm long, 0,25-0,3 mm wide, c. 1/2 \times the length of the lobe, inflated along the keel and rather abruptly flattened towards the free margin, the flattened part usually wider than the sac; free margin plane or upcurved, weakly curved, not or only very shortly continuing into the ventral margin of the lobe, with (4-)5-8 teeth, the teeth usually completely inflexed and closely spatiated, more rarely partially inflexed only, each tooth consisting of a single sphaerical cell attached to an enlarged margin cell and separated from the next tooth by only 1-2 margin cells; hyaline papilla 2 cells below the proximal base of the first tooth.

Underleaves weakly imbricated, plane, orbicular to transversally ovate, 0,3-0,4 mm long, 0,35-0,5 mm wide, 3 \times the width of the stem, the apex rounded to truncate, the bases rounded, the line of insertion arched, up to 0,1 mm deep; median cells 21-27 \times 13-18 μm , the cells somewhat longer towards the base, smaller and quadrate at the margin; rhizoid disc orbicular to elliptical, consisting of up to 15 large, bulging cells.

Androecia in spikes terminal or intercalary on *Lejeunea*-type branches; bracts and bracteoles in 6-15 series, the bracts closely imbricated, squarrose and falcate, slightly smaller than the leaves, the lobule relatively large and conspicuously inflated, the free margin without teeth except for the erect apical tooth; bracteoles similar to the underleaves; bracts monandrous.

Gynoeceum terminating a short *Lejeunea*-type branch, without pseudo-innovations; bracts and bracteoles in 3-5 series, densely crowded, becoming larger and more or less bilaterally compressed towards the inner series; inner bract widely spreading to squarrose above, subequally bifid to 1/4, the lobe widely ovate, 1,2 \times 0,9 mm, the margins tapering to an obtuse to subacute apex, the lobule erect and almost as long as the lobe, oblong, 1,1 \times 0,6 mm, obtuse at apex, separated from the lobe by a narrow, sharp sinus; inner bracteole erect, suborbicular, as long as the bracts, 1,1 \times 1 mm, rounded at apex, the margins plane. Perianth not emergent when mature, obovate, 1,1 \times 0,7 mm, inflated below, compressed above, in the upper half with 5-6 unequal plicae or c. 10 subequal plicae, the plicae narrow and smooth; beak 5-6 cells long.

Sporophyte unknown.

Vegetative propagation by means of caducous leaves produced on ascending flagelliform shoots terminating short, leafy or male branches; flagellae up to 5 mm long, curved at apex, with 15-50 small underleaves, the underleaves more or less squarrose with the margins slightly incurved; caducous leaves basically similar to stem-leaves but c. 3x smaller, the lobe 0,3 x 0,25 mm, the lobule 0,15 x 0,1 mm, with 1-3 short erect teeth; a few rhizoids arising from cells along the keel.

Distribution (Pl.XXI): FLORIDA, CENTRAL AMERICA. A typical lowland species, in Central America occurring along the Caribbean coast, especially along the Gulf of Honduras. In Florida the species occurs mainly in the central part of the state, which is the so-called "Oligocene Island" region (SCHUSTER 1954). Because of this distribution pattern, SCHUSTER reckons *A. heterophylla* to the "old tropical" flora, which invaded Florida in pre-pleistocene times.

Ecology: on bark of living trees in relatively open, xerophytic to mesophytic forests; also on decaying wood and in swamps. The ecology of the species in Florida has been described in some detail by SCHUSTER (1954): "the species occurs both in deep hammock forests and in open turkey-oak forests. It is, in fact, somewhat less frequent on shaded, damp bark in the hammocks than on dry, exposed, somewhat insolated bark in open oak woods. In the rich and mesophytic hammock forests, it has been found on bark of *Quercus nigra*, *Persea borbonia*, and even on that of the cabbage-palm, *Sabal palmetto*. The more frequent occurrences, in oak forests peripheral to the hammock-forests, are almost always on either live-oak (*Q. virginiana*) or on turkey-oak (*Q. laevis*). When on the latter hosts, the species is a very pronounced xerophyte, occurring with *Frullania kunzei* and *oboordata*, *Leucolejeunea conchifolia* and *unciloba*, *Microlejeunea bullata* and *Cololejeunea minutissima*".

Differentiation: the distinguishing characters of *A. heterophylla* include 1) the small size of the plants, 2) the dioicous inflorescence, 3) the rather sharp angle (90-120°) between the keel and the ventral margin of the lobe, 4) the lobule, which has 4-8 closely inserted, more or less inflexed teeth consisting of only one cell, and 5) the inner female bracts, which are narrowly obtuse at apex. The species is closely related to *A. torulosa* and *A. emergens*. From *A. emergens* the species is readily distinguished by the characters given here. Specimens of *A. heterophylla* having lobules with only partly inflexed teeth are likely to be confused with *A. torulosa*. The most reliable difference between these two species is the shape of the caducous leaf.

Variation: the specimens known from Florida (USA) are always sterile and usually smaller than the Central American specimens. They differ further in the more orbicular shape of the underleaves (transversally ovate in C. America) and in the lobule having only 4-5 teeth (5-8 in C. America). Perianths have been seen in only two collections: Nicaragua (Hamilton s.n.) with 10-plicate perianths, and Honduras (Punta Gorda, unknown coll.) with 5-6-plicate perianths. The variability in the number of plicae observed in *Acrolejeunea* indicates that this variation has no taxonomic standing.

Note: the holotype-material of *Ptychocoleus heterophyllus* Evans (YU) was collected by Rapp, "May 1917" (EVANS 1918). Many herbaria have topotype material, which was distributed as "Hepaticae of Florida, S.Rapp nr. 38", dated "April 1917", "March 1918", or "March 1919". Duplicates of the holotype, dated "May 1917", have not been found.

Specimens seen: (*A. heterophylla*):

USA. Florida: Semiole: Sanford, Rapp s.n., III.1911, V.1912, V.1917 (YU); *ibid*, Rapp Hep.Flor.38, IV.1917 "III.1918", "III.1919" (ABSH, BM, FH, K, NY, PRC, U, US); Marion: Ocala Nat.For. Juniper Springs, Schuster 22090, XII.1951 (NY); *ibid*.31910b, XII.1953 (ABSH, H, NY); *ibid*.31940, XII.1953 (DUKE); Dade(?): Royal Palm Park, M.S.Taylor s.n., III.1929 (YU). Further reports from Marion, Lake, and Hillsborough Co. in Schuster (1954)

GUATEMALA. Izabal: Puerto Barrios, Steyermark 39828, IV.1940 (F, Fulford).

BRITISH HONDURAS. Punta Gorda, unknown coll.nrs.9,63,79,81,84,97,100,110 & 112, XI.1932 (Fulford ex MO).

HONDURAS. P.Wilson 569, 1903 (NY, YE); Morazan, Le Montanita, Stanley 12355, X.1946 (F).

NICARAGUA. Sandy Bay, Hamilton 224 & 225, I.1920 (DUKE, FH, YU).

4. *ACROLEJEUNEA EMERGENS* (Mitt.) Steph. (Pl. IX, X)

in Engl., Die Pflanzenwelt Ostafrikas, C: 65 (1895); VandenBerghen (1972): 104; Gradstein (1974b): 332.

Paragmitocoma emergens Mitt., Philos.Trans. 168: 397 (1879); Mitten (1887): 323; Stephani (1889): 166.

Lejeunea (subg. *Acrolejeunea*) *emergens* (Mitt.) Steph., Bull.Soc.Roy.Bot.Belg. 32: 119 (1894).

Ptychocoleus emergens (Mitt.) Steph., Spec.Hep. 5: 24 (1912); VandenBerghen (1948): 43; Jones (1954): 406; VandenBerghen (1965): 153; Bischler (1965): 431.

Typus: Rodriguez I., I.B.Balfour s.n. (NY holo, BM).

Heterotypic synonyms:

Acrolejeunea angustispica Steph., in Corbière, Bull.Mus.Hist.Nat.Paris 18: 118 (1912).

Typus: same type as in *Ptychocoleus flagelliferus*!

Ptychocoleus flagelliferus Steph., Spec.Hep. 5: 22 (1912); Jones (1954): 406; VandenBerghen (1948): 43.

Typus: Rep.Congo, Brazzaville, A.Chevalier s.n., VII.1902 (G holo, PC).

Acrolejeunea emergens ssp. *madagascariensis* Gradst. in sched.

Ptychocoleus floribundus Steph., Spec.Hep. 5: 24 (1912); Jones (1954): 405.

Typus: Senegal, Cassamance, Oussouye, Mathieu s.n., 1908 (G holo).

Ptychocoleus grossispicus Steph., Spec.Hep. 5: 34 (1912) syn.nov.

Typus: French Guiana, St.Jean, unknown coll. (G holo).

Ptychocoleus henriquesii Steph., Spec.Hep. 5: 25 (1912) syn.nov.

Typus: Cape Verde Is., Cardoso s.n., 1897 (G holo)

Acrolejeunea pusilla Steph., in Paris, Rev.Bryol. 35: 6 (1908) nom.nud.

Ptychocoleus pusillus Steph., Spec.Hep. 5: 26 (1912).

Typus: Guinea, Timbo. Pobeguin s.n., X.1906 (G holo, PC).

Ptychocoleus renauldii (Steph.) Steph.var.*victoriae* E.W.Jones, Trans.Brit.

Bryol.Soc. 2: 403 (1954); Jones (1957): 197 syn.nov.

Typus: Uganda, Lake Victoria, Karivandi I., S.of Kazi, G.H.S.Wood 1168, II.1950 (Jones holo, K).

Ptychocoleus rupestris Herz., Trans.Brit.Bryol.Soc. 1: 105 (1948); Vanden-Berghen (1965): 153.

Typus: Kenya, Mombasa, H.C.Gilson s.n., I.1934 (JE holo).

Ptychocoleus vanderijstii Steph., Spec.Hep. 5: 21 (1912); VandenBerghen (1948): 41; Jones (1954): 406.

Typus: Zaire, Boko, Vanderijst 511 (G holo, BR).

Misapplied names:

Acrolejeunea aulacophora Auct.quoad plant.afric.(cf.Stephani (1895): 317; VandenBerghen (1948): 49).

Acrolejeunea torulosa Auct.p.p., quoad plant.americ. (cf. Spruce (1884): 117; Lindenberg & Gottsche (1851): 627; Stephani (1897): 14,21).

Plants autoicous or dioicous, small to large in size, 1-3 cm long, 1,0-2,3 mm wide, green when moist, becoming dull yellowish-brown or grayish-brown when dry, irregularly branched; branches short or long, when short of the *Lejeunea*-type and often sexual, occasionally microphyllous or becoming erect and flagelliform (producing caducous leaves), when long and vegetative mostly of the *Frullania*-type.

Stem 0,1-0,2(-0,25) mm in diam.; ventral merophyte 4-8 cells wide, the ventral cortical cells quadrate to rectangular, 30-45(-65) x (20-)24-33(-42) µm, the walls rather thin, colourless to pale-brownish; dorsal cortical cells arranged zig-zag in oblique to almost straight longitudinal rows; stem in transverse section with 10-20 thin-walled cortical cells surrounding 20-40 medullary cells with small to medium-sized trigones, the dorsal cortical cells 30-36(-40) µm high, the ventral cortical cells smaller, (18-) 22-30(-33) µm high, the medullary cells (12-)15-22(-25) µm in diam.

Leaves imbricated, clasping the stem when dry, widely spreading-falcate and convex to squarrose when moist. Lobe asymmetrically suborbicular to ovate-suboblong, (0,5-)0,7-1,2 mm long, 0,4-0,9 mm wide, inserted along the

whole length of the merophyte, the dorsal base not or slightly auriculate, the apex rounded to narrow-subobtusate, the ventral margin plane or upcurved, at an angle of $150-180^{\circ}$ with the keel; keel rounded and smooth, curved near the base, at an angle of $50-60^{\circ}$ with the axis, not decurrent; median leaf cells $25-35 \times 17-24 \mu\text{m}$ in the upper half of the lobe, near leaf base slightly larger, at the margins smaller, subquadrate, $14-18 \mu\text{m}$ high; trigones small to medium-sized, often becoming larger towards the leaf margins, the intermediate thickenings generally scarce but often more frequent along the leaf margins; oil bodies homogeneous, 9-20 in median leaf cells, ellipsoid to fusiform (sphaerical when seen from the side), $2-3 \times 6-8 \mu\text{m}$, more numerous in basal leaf cells, shorter and fewer in marginal leaf cells.

Lobule ovate-triangular with oblique to truncate apex, $0,3-0,6 \text{ mm}$ long, $0,2-0,35 \text{ mm}$ wide, $2/5-1/2 \times$ the length of the lobe, narrowly inflated along the keel, widely flattened above; free margin plane, straight or curved and often sinuate towards apex, with 2-4(-5) teeth, the teeth erect or partially inflexed, often curved outwardly, rarely becoming obsolete, the first tooth 2-3 cells long, the other teeth 1-2 cells long and separated from each other by (2-)3-6 margin cells; hyaline papilla two cells below the proximal base of the first tooth (but attached to free margin when teeth obsolete, Pl.X!).

Underleaves imbricated, transversally-ovate to -obovate, rarely suborbicular, $0,25-0,4 \text{ mm}$ long, $(0,4-)0,5-0,65 \text{ mm}$ wide, plane or \pm gibbous, the apex rounded to shallowly retuse, the margins plane or weakly recurved, the bases cuneate or rounded, rarely auriculate, the line of insertion arched or almost straight; cells rather uniform throughout the underleaf, $(17-)22-30 \times (14-)17-23 \text{ mm}$; rhizoid disc small, consisting of large, almost thin-walled cells.

Androeceia usually intercalary on long *Lejeunea*-type branches, the bracts and bracteoles in 4-13 series, sometimes with a few sterile leaves intercalated, the bracts similar to leaves but slightly smaller, the lobule more strongly inflated, with 1 tooth; antheridia one per bract (VANDENBERGHEN 1972: 2 antheridia!), ovoid, $160 \mu\text{m}$ in diam., the antheridial stalk slightly longer.

Gynoeceium terminating a short or long *Lejeunea*-type, rarely *Frullania*-type (!) branch, frequently with short pseudo-innovations of the *Radula*-type which, by exception, may become floriferous again; bracts and bracteoles in 2-3(-4) series, the inner bract suberect and sharply keeled when enveloping a flattened perianth, spreading-squarrose with a widely rounded keel when surrounding an inflated perianth, \pm unequally bifid to $1/3$, the lobe widely obovate, $1-1,4 \times 0,8-1 \text{ mm}$, the apex rounded, the lobule narrowly oblong, $0,9-1,1 \times 0,4-0,5 \text{ mm}$, the apex rounded to slightly notched, rarely narrow-subobtusate; inner bracteole obovate-oblong to suborbicular, plane, \pm as long as the bracts, the

apex widely rounded, not recurved. Perianth immersed or, when stalked, emergent to 1/3 of its length, obovate-cylindrical to obpyriform, 0.8-1.4 mm long, bilaterally compressed to nearly wholly inflated, \pm anisoplicate with (5-)7-8(-10) narrow and smooth plicae (2 lateral, 2-5 ventral, 1-3 dorsal); beak 3-8 cells long.

Sporophyte: as in *A. torulosa*.

Vegetative propagation by means of caducous leaves produced on upright flagelliform shoots, which arise without torsion from leafy or male branches; flagellae short or long, up to 5 mm long, solitary or clustered, sometimes pinnately branched, the underleaves appressed to spreading-squarrose, but not folded outwardly; caducous leaves three to five times smaller than branch leaves, the lobule up to half the size of the lobe, with 2-3 teeth; short rhizoids arising from cells along the keel.

Chromosomes: $n = 9$ (BERRIE 1958).

Distribution (Pl.XXI): tropical AMERICA and tropical AFRICA.

Previously only known from Africa (VANDENBERGHEN 1972). In America the species is confined to lowland areas. Only few American collections have become available so far. In tropical Africa the species is apparently very common and wide-spread, occurring from sea-level up to 1500 m.

Ecology: on stems and twigs of trees or shrubs in open, xerophytic to mesophytic, primary or secondary forests, in savanna-woodlands, and in narrow wood belts along rivers; apparently common in the central African *Brachystegia* woodlands (Angola through Tanzania); also on road-side trees; rarely on (granite) rocks. The species often grows together with other common xerophytic species, e.g. *Frullania borgenii*, *Fr. squarrosa*, *Schiffneriolejeunea polycarpa*, *S. pappeana* and *Mastigolejeunea carinata*.

Differentiation: *A. emergens* is closely related to *A. torulosa*, from which it differs mainly by the lobule, which has 2-4 teeth, and by the more simple caducous leaves, which resemble small branch leaves. Differences are also observed in the angle between the ventral margin of the lobe and the keel (when the leaf is spread out), which is usually $140-160^\circ$ in *A. torulosa* and c. 180° in *A. emergens*, and in the number of series of female bracts and bracteoles: 2-3(-4) in *A. emergens* and (3-)4-5(-6) in *A. torulosa*. The recent discovery of intermediate specimens calls for a reconsideration of the delimitation of both species (see under *A. torulosa*).

Variation: *A. emergens* is in its present circumscription a rather polymorphic species, especially in Africa. Morphological variation is particularly observed in 1) the denticulation of the lobule (Pl.X), 2) the number and size of the plicae of the perianth, 3) the shape of the underleaf, 4) the width of the ventral merophyte, and 5) the length and arrangement of the flagellae. In Africa the morphological variation is correlated to some degree with geography and altitude. Three broad geographical races can be distinguished. As these races are by no means sharply defined, they have not been given nomenclatural status.

1. Tropical West Africa (Guinea - Zaire).

Relatively small plants from lower altitudes, which are always autoicous and usually fertile. The lobule has 2-3 short, erect teeth, and the underleaves are slightly wider than long, with a weakly curved insertion line. *Frullania*-type branches and pseudo-innovations are rarely present.

Plants from this region were variously named *Ptychocoleus pusillus* and *Pt. vanderijstii* bij STEPHANI. Along the coasts of Nigeria and the Cameroun a form with a deviating perianth occurs, which is known as *Ptychocoleus confertissimus* (JONES 1954). I have kept this form as a separate variety (see below). A sterile form of *A. emergens* from Brazzaville with numerous long flagellae was described by STEPHANI as *Ptychocoleus flagelliferus*.

2. Angola and tropical East Africa (especially Kenya, Uganda and Tanzania).

This race includes mountain forms occurring at altitudes up to 1500 m. The plants differ from the tropical West African lowland plants by one or more of the following characters: 1) Plants robust: up to 2,3 mm wide, the stem up to 280 μ m in diam., the ventral merophyte up to 8 cells wide (e.g. Angola, Welwitsch 249 & Mendez 3405). 2) *Frullania*-type branches and pseudo-innovations frequently present. 3) Lobule with 3-4(-5) teeth, which are sometimes reduced to a single cell. In moist habitats the teeth may become entirely reduced, resulting in the apical hyaline papilla to protrude from the free margin (Pl.X: 10,11,12). By the simple lobule teeth the plants resemble *A. aulacophora* (= *Ptychocoleus renauldii*). *Pt. renauldii* var. *victoriae* Jones belongs here. 4) Underleaves \pm auriculate (Pl.IX: 13). 5) Flagellae short and clustered, or long and pinnately branched (Pl.VI: 2,3). 6) Plants often dioicous. In male plants the leaves are sometimes difficult to distinguish from male bracts (e.g. Uganda, Entebbe, Jones s.n.).

3. Madagascar and Reunion

Relatively robust plants, which in contrast with the East African mountain race occur almost exclusively at sea-level. They are usually dioicous and the lobule has 2-3 teeth as in the West-African populations, but the teeth are

usually very different in shape. The first tooth is 2-3 cells long and usually curved outwardly, the second tooth is either short and erect or longer and curved, and the third tooth is usually rudimentary. The lobule tends to become longer, up to two times longer than wide, and the dorsal leaf-base becomes auriculate in larger stem leaves. I annotated several collections of *A. emergens* from these islands as "*A. emergens* ssp. *madagascariensis* ssp. nov.". Considering the overall morphological variation of the species in Africa, it now appears to me that describing a new subspecies to accomodate these plants is not justified and I therefore refrain from validating my herbarium name.

Note: the epithet "*emergens*" is derived from the perianth which is emergent in the type and several other collections. It should be noted, however, that in this species (and in most other species of *Acrolejeunea*) the perianth protrudes beyond the bracts only, when a stalk is developed at the base of the perianth. Normally the perianth remains more or less hidden between the bracts.

Key to the varieties of *A. emergens*:

- Perianth more or less inflated, with (5-)6-10 smooth plicae.....
4a. var. *emergens*
 Perianth compressed, with 4 large plicae and 1-2 small plicae, the large
 plicae rudimentary winged.....4b. var. *confertissima*

4a. *A. emergens* var. *emergens*

see under the species

4b. *A. emergens* var. *confertissima* (Steph.) Gradst. comb. nov. (Pl. IX)

Lejeunea (subg. *Acrolejeunea*) *confertissima* Steph., Hedwigia 31: 165 (1892).

Ptychocoleus confertissimus (Steph.) Steph., Spec. Hep. 5: 23 (1912); Vanden-Berghen (1948): 40 p.p.; Jones (1954): 405.

Acrolejeunea confertissima (Steph.) Bonner, Index Hep. 1,2: 16 (1962).

Type: Cameroun, prope Ekumbi-Liongo pagum, in truncis Borassi, P. Dusen 446, X.1891 (G holo, H.NY, S, UPS).

Differing from var. *emergens* only in the perianth, which has 4 large, sharp plicae (2 lateral and 2 ventral) and 1-2 small, subsidiary ventral plicae. The large plicae are usually rudimentary alate, bearing up to 3 cells wide wing-like appendages on their backs. The variety is also somewhat different from var. *emergens* in the shape of the perianth, which is usually obpyriform, compressed, and widely truncate at apex. The perianth is not emergent.

Distribution: S. NIGERIA and W. CAMEROUN. Occurring from sea-level to c. 600 m in a rather small area around the Gulf of Guinea.

Ecology: mainly on stems and twigs of shrubs in exposed sites.

Note: VANDENBERGHEN (1948, 1972) treated *Ptychocoleus confertissimus* as a synonym of *A. emergens*, whereas JONES (1954) treated both taxa as separate species. The differences between both taxa were discussed by JONES (l.c.). After careful examination of a great number of fertile collections with perianths, I found that the perianth in *Pt. confertissimus* is sufficiently distinct to keep both taxa separate. Since the perianth characters are not correlated with other differences, I have treated the taxa here as varieties. The var. *confertissima* is not widespread as JONES suggested, but apparently restricted to a small area within the range of var. *emergens*. According to JONES, both taxa may grow together in the field.

Specimens seen (*A. emergens*):

a. var. *emergens*

MEXICO. Oaxaca: between Tuxtepec and Chiltepec, Clayton B483, III.1953 (F).

PANAMA. Madden Dam and near Alahuela, Dodge 16872, XI.1934 (Fulford ex MO).

VENEZUELA. Guarico: Calabozo, Goodland s.n., 1965 (US).

SURINAME. Paramaribo, Kegel s.n. (BM,U,W).

FRENCH GUIANA. Cayenne, Broadway 843, VII.1921 (FH,NY,U,US,YU); St.Jean, unknown coll. (G).

BRAZIL. Pará: Obidos, Spruce s.n., 1849 (MANCH); Maypures, Spruce s.n. (MANCH); Amazonas: road Manaus-Itacoatiara, Griffin 212 p.p., VII.1974 (FLAS,U); road Manaus-Caracarai, Campina forest, Griffin et al. 48 p.p., VII.1974 (FLAS,U); Rio Negro, Sao Gabriel, Spruce s.n. (MANCH); Rio Cururu, Sioli 40 p.p., VI.1942 (GRO); Sao Paulo: Res.Biol.de Mogi-Guacu, Vital 2647 & 2666, X.1973 (SP,U); Nova Independencia near Andradino, Vital 2088, V.1972 (NICH,SP,U); Matto Grosso: Sao Joao, in "Poaia", Lindman 5441, IV(XI?). 1894 (M,S).

CAPE VERDE IS. without loc., Cardoso s.n., 1897 (G).

GUINEA. Iles de Los, Pobeguín s.n., V.1905 (G); Kindia, Pobeguín s.n., 1905 (L,PC); Timbo, Pobeguín s.n., X.1906 (G,PC); Fouta-Djallon, Sangarave, Normand s.n., IV.1901 (G,PC).

SIERRA LEONE. Freetown, Mt.Oriel, Arnell 2304,2305,2308,2434,2506, XII.1951 (UPU).

SENEGAL. Oussouye, Casamance, Mathieu s.n., 1908, (G).

CHANA. Eastern Region: Kade agr.res.stat., Jones s.n., I.1971 (Jones); Aburi Bot.Gard., Jones & Hall s.n., I.1971 (Jones).

NIGERIA. Western Region: Ibadan, Jones 1166 p.p., VII.1956 (Jones); Ibid., Brenan & Jones 22, XII.1947 (K); Olokomeji, Jones 1156, VII.1958 (K);

- Abuja, Jones s.n., X.1955 (Jones); Bonu, Jones 1063, VI.1958 (TNS); Jemaa, Jones 1024, 1033, 1045, V.1958 (K); Eastern Region: Enugu, Milliken Hill, Jones 837, X.1955 (K); *ibid.* 838b (Jones); Calabar, Jones 211, III.1948 (K).
- REPUBLIC CONGO. Brazzaville, Chevalier s.n., VII.1902 (G,PC); *idem*, Mansimou, Degelius s.n., III.1960 (S,UPS).
- ZAIRE. Boko, Vanderijst 511 (G,BR); Bumba, Vanderijst 14059, I.1925 (BR); Haute Nsele, Vanderijst 14102, 14799, 14801, I.1925 (BR); Kisantu, Vanderijst 14475, 15042a, 37104 & 37853 (BR); Mpese, Vanderijst 14013, 14009 & 14025, I.1925 (BR); Bao, Vanderijst 17933 & 18500, VII.1926 (BR); Kipako Sanda, Vanderijst 37110, IV.1933 (BR); Mobekia, Bequart 7106, III.1915 (BR); Yangambi, Plateau de l'Isalowe, Louis 9034, IV.1938 (BR); Yangambi, Jones 808 p.p., IX.1955 (Jones); Stanleyville, Jones 816, IX.1955 (K).
- KATANGA. Haut Lomami, Kaniama, Mullenders 28,65,425,426,427,431 & 1501, 1947 (BR); *ibid.*, Kasenji, Mullenders 532, V.1947 (BR); Fatuma, S. of Albertville, Symoens 2885b, IX.1956 (BR); Pola, S. of Albertville, Symoens 2886, IX.1956 (BR); Elisabethville, Kipopo, Symoens 3413b, III.1957 (BR); Kasenga, Kisamamba, Symoens 6773, XII.1959 (BR); Mulando, Symoens 11064, XI.1964 (BR); Kabiashia, Symoens 11762, XII.1965 (BR); Lupembe, Symoens 12013 & 12015b, I.1966 (BR); Lukubi, Symoens 12463, IV.1966 (BR).
- ZAMBIA. Chibando, Moha, Symoens 6831, XII.1959 (BR); Chipili, Symoens 6846, XII.1959 (BR); Nsakaluba, Symoens 7532, IV.1960 (BR); Kangolesa, Symoens 7570 & 9184, IV.1960 (BR); Mulongo, Symoens 9944b, XII.1962 (BR); Matanda, Symoens 10202a, IV.1963 (BR); Chisunka, Symoens 10227, IV.1963 (BR); Shiwa Ngandu, Symoens 10498a, IV.1963 (BR); Chinsali, Symoens 10528, VI.1963 (BR); Mwamfuli, Symoens 10585 & 11304, VII.1963 (BR); Kalasa Mukosa, Symoens 10590, VII.1963 (BR); Chimupati, Symoens 10654a, XII.1963 (BR); Chembe, Symoens 11339, I.1965 (BR); Lusaka, near Rufunza, Pocs & Kornas 6620/D, I.1972 (EGR,U).
- ANGOLA. Luanda: Ambriz, Welwitsch 261, XI.1853 (BM); Malanje: Pungo Adongo, Dadumba, Welwitsch 231, IV.1857 (BM,G); *ibid.*, Cazella, Welwitsch 249, II.1857 (BM); Bie/Cuando-Cubango: Menonque Cuchi, Mendes 3405, IV.1960 (UPP); Moxico: Lucusse, Degelius s.n., II.1960 (S).
- UGANDA. Entebbe, Jones 574, VIII.1955 (BM,Jones,K,NY,TNS); *ibid.*, Sittins, VI.1956 (Jones); Lake Victoria, Karivandi I., Wood 1168, II.1950 (Jones, K).
- KENYA. Malindi, Jones 655 & 6740, VIII.1955 (BM,EGR,Jones); Mombasa, Wilson s.n., I.1934 (JE); Nairobi, Mau Hills, Agnew 255, XI.1965 (PRC).
- TANZANIA. Usambara, Fischer 52 & 54, 1891-92 (BM,FH); Usagara Mts., Hanning-ton s.n. (NY); Mbudya corall I., E. of Dar es Salaam, Pocs & Harris 6558/0, IV.1972 (EGR,U); Nguru Mts., Kwamanga, Pocs & Mabblerley 6396/I, II.1971 (EGR,U); Unzungwa Mts., Kitonga gorge, Pocs & Jones 6316/T, XII.1970 (EGR, U); Bukoba, Möller s.n., V.1953 (UPS).
- BURUNDI. Rutana, Butetsi, Symoens 2780, IV.1956 (BR).
- MALAWI. Mlanje, Crundwell 408, VII.1969 (Jones).
- COMORE IS. without loc., Hildebrandt s.n. (JE).
- ALDABRA IS. Middle I., Gionnet Channel, Fosberg 49580, II.1968 (BM).
- MADAGASCAR. Nossi-Bé I., Lokobe, Onraedt 71.M.5118 (Grolle, Onraedt); Antalaha, Onraedt 71.M.5661 (Onraedt, U); Andevoranto, Borgen s.n., 1882 (O); Mahanoto, Cremers 2230, 1972 (Grolle, Onraedt); Fort Dauphin, Onraedt 71.M.5579 & 5589 (Grolle, Onraedt, U).
- REUNION. without loc., Renauld 46 (G); *ibid.*, Lepervanche s.n. (BM).

MAURITIUS, without loc., de l'Isle s.n. (BM).

RODRIGUEZ I. without loc., Balfour s.n. (BM, NY).

SEYCHELLES. Mahé I.: Victoria, Onraedt 74.S.006 (Onraedt, U); Praslin I.: Bay St. Anne, Onraedt 74.S.212 & 74.S.484 (Grolle, Onraedt, U); ibid., de l'Isle s.n., XII.1885 (M, MANCH, PC).

b. var. *confertissima*:

NIGERIA. Idanre, Jones 101A, I.1948 (K); Nikrowa, Jones 458, II.1948 (K); Calabar, Jones 215A, II.1948 (K).

CAMEROUN. Ekumbi-Liongo, Dusen 446, X.1891 (G, H.M, NY, S.U, UPS).

5. *ACROLEJEUNEA RECURVATA* Gradst. spec. nov. (Pl. XI)

Ab *A. emergenti* cui affinis est, differt foliis inferioribus recurvis-retusis, lobulis foliorum (3-)4-6 denticulatis, inflorescentia dioica, plicis perianthium undulatis, flagellis subnudis foliis inferioribus minutis adpressis constrictis.

Typus: Thailand, Nakhon Sawan, "near Karen village of Sop Aep", A. Touw 9464, XII.1965 (L holotype, U).

Plants dioicous, small or large, up to 3 cm long, 1,25-2,0 mm wide, dull yellowish- or grayish-brown when dry, irregularly branched; branches short or long, usually of the *Lejeunea*-type, frequently becoming erect and flagelliform (producing caducous leaves), rarely of the *Frullania*-type, microphyllous branches not seen.

Stem 0,15 mm in diam.; ventral merophyte 4-10(!) cells wide, the ventral cortical cells quadrate to narrow rectangular, 26-39 μ m to 45-65 μ m (coll. from Laos) long, (15-)20-27 μ m wide, the walls moderately thickened; dorsal cortical cells larger, arranged zig-zag in oblique rows; stem in transverse section with 15-22 cortical cells surrounding 25-35 medullary cells, the dorsal cortical cells c. 30 μ m high, the ventral cortical cells c. 18 μ m high, the medullary cells 15-20 μ m in diam.; medullary cells and ventral cortical cells thicker-walled than the lateral and dorsal cortical cells, the walls uniformly yellowish.

Leaves closely imbricated, in small fertile plants rather irregularly wrapped around the stem when dry, with the dorsal leaf margin more or less recurved, in larger sterile plants more regularly clasping the stem with the leaf margins plane, when moist widely spreading and strongly convex to squarrose. Lobe orbicular-ovate, 0,9-1,6 x 0,6-1,4 mm, inserted along the whole length of the merophyte, the dorsal base straight to slightly auriculate, the margin often undulate near apex, the apex rounded, plane, the

ventral margin plane or upcurved forming an angle of $150-180^{\circ}$ with the keel; keel weakly curved at base, otherwise straight, at an angle of 60° with the axis, not decurrent; median leaf cells rather variable in size, $(25-30-40 (-45) \times 20-28 \mu\text{m})$, at leaf-base slightly larger, at the margins not forming a continuing row of small cells: cells sometimes longer and wider (up to $25 \times 20 \mu\text{m}$); trigones medium-sized, sometimes larger along the dorsal margin of the leaf, intermediate thickenings scarce; oil bodies unknown.

Lobule ovate-triangular to rectangular with an oblique to straight apex, $0,35-0,6 \text{ mm}$ long, $0,2-0,3 \text{ mm}$ wide, narrowly inflated along the keel, the flattened part wide but usually invisible in situ; free margin more or less recurved in the lower half, sometimes auriculate at base, gradually curved towards apex and shortly continuing into the incurved postical margin of the lobe, with 3-6 variable, erect or inflexed teeth, the teeth 1-2(-3) cells long, separated from each other by 2-5 margin cells; hyaline papilla + three cells below the base of the apical tooth.

Underleaves imbricated, transversally ovate, $0,2-0,3 \text{ mm}$ long, $(0,35-0,6-0,8(-1,1 !)) \text{ mm}$ wide, gibbous, the apex truncate and recurved, rarely plane, when recurved becoming deeply retuse, the bases wide and rounded or weakly auriculate, the line of insertion shallowly curved, c. $30 \mu\text{m}$ deep; cells rather uniform throughout the underleaf, $23-28 \times 18-22 \mu\text{m}$. Rhizoids in short bundles from an orbicular rhizoid disc made up of a few large, bulging cells.

Androecia in terminal or intercalary spikes, the bracts and bracteoles in 4-8 series, slightly smaller than leaves and underleaves, the lobe obliquely spreading, the lobule conspicuously inflated, the free margin with 1-2 teeth, the cells at the keel distinctly protuberant; bracts monandrous.

Gynoecium terminating a short *Lejeunea*-type branch, without pseudo-innovations; bracts and bracteoles in 2 series, becoming much larger than the leaves and underleaves; inner bract unequally bifid to 1/2, the lobe sub-orbicular, c. $1,5 \text{ mm}$ long, erect to widely spreading and squarrose above, the apex widely rounded, the margins undulate near apex, the lobule erect, variable in length, $0,8-1,4 \times 0,4 \text{ mm}$, with rounded apex, inner bracteole erect, suborbicular, plane or gibbous, as long as the perianth, $1,3 \times 1,2 \text{ mm}$, the apex rounded, the margins flat to slightly undulate. Perianth when mature not emergent, obovate-obtriangular, c. $1,2 \text{ mm}$ long, weakly compressed in the upper half, anisoplicate, with 5-8 narrow and more or less undulate plicae: 2 lateral, 2-3 ventral, 1-3 dorsal, often a few additional rudimentary plicae present; beak c. 3 cells long.

Sporophyte: valves c. $0,6 \text{ mm}$ long; spores $45-60 \mu\text{m}$ long; elaters averaging $300 \times 12 \mu\text{m}$, with one yellowish-brown, $4 \mu\text{m}$ wide spiral.

Vegetative reproduction by means of caducous leaves produced on ascending

flagelliform shoots, which arise abruptly from short leafy branches or (more often) gradually from microphyllous or male branches; flagellae up to 3 mm long, rather stiff, the apex often broken, with very small, concave underleaves which are appressed to the axis or weakly spreading (never squarrose); caducous leaves c. 2-4 x smaller than stem leaves, the lobe averaging 0,3 mm in length, the lobule very small, less than 1/3 x the length of the lobe, with 1 tooth.

Distribution: INDO-CHINA (W.Bengal, Thailand, Laos). Apparently not uncommon in lower mountain areas ranging from 350 to 1500 m. Only recent collections available!

Ecology: on stems of trees or on rocks in rather open, xerophytic, deciduous or evergreen forests; also on exposed stone walls or on roadside trees; in dense mats or creeping loosely between pleurocarpous mosses.

Differentiation: *A. recurvata* is an apparently undescribed species, which is reported here from quite a number of localities in Indo-China. All collections result from recent explorations in the area.

The species is easily recognised as a member of the subgenus *Acrolejeunea* by its upright flagellae, which often appear to be barren because the underleaves are + narrower than the axis and more or less appressed. The tip of the flagella is often broken.

A. recurvata is most closely related to certain E.African forms of *A. emergens*, from which it differs by 1) almost barren flagellae, 2) recurved-retuse underleaves, 3) the lobule, which has (3-)4-6 short teeth, and 4) the perianth, which has more or less undulate plicae. Small forms of *A. recurvata*, however, are difficult to distinguish from *A. emergens* (see below).

Sterile plants can be confused with *Trocholejeunea infusca* which occurs in the same area. The latter species is easily recognised by 1) the different lobule (resembling the lobule in *A. tjiibodensis* .), 2) large, orbicular underleaves, and 3) predominantly *Frullania*-type branching.

Variation: *A. recurvata* is strongly variable in size. Like in *A. emergens* and *A. pycnolada*, the size of the plants increases with altitude. Large mountain forms have + undulate leaf margins, auriculate dorsal leaf bases, and somewhat larger cells. The underleaves are wider and the apex is more strongly recurved-retuse. The lobule is longer and more abruptly flattened towards the free margin, and there are more numerous (5-6) teeth which are more widely spatiated (Pl.XII:4,11).

The ventral merophyte in these mountain forms may become up to 10 cells wide (Laos, Tuyama s.n.)

Small lowland forms with almost flat underleaves and lobules with 3-4 teeth (Warncke 2893 & 2895) resemble *A. emergens* very closely. Both species have very different areas of distribution, but it is possible that intermediate forms will turn up from the intermediate geographical areas, e.g. southern India and Ceylon. These areas are hepaticologically still very poorly known and deserve more intensive exploration.

Specimens seen (*A. recurvata*):

INDIA. West Bengal: between Darjeeling and Teesta Bridge, Iwatsuki & Sharp 7802 & 7958a, IV.1965 (NICH); Darjeeling area, Iwatsuki & Sharp 10690 & 10780a, IV.1965 (NICH,U).

THAILAND. Northern: Mae Hong Son, Kitagawa 12270 & 72294, IX.1967 (G, Kitagawa, U); Chiangrai, Kitagawa 12494, IX.1967 (Kitagawa, U); Chiangmai, Mt.Doi Inthanon, Kitagawa & Tagawa 2547 & 2550, XII.1965 (G, Kitagawa, U); Mt.Doi Chiengdao, Touw 9087, XII.1965 (L); Doi Chieng Dao, Pong Pho, Warncke 2893, 2895 & 3005, VII-VIII.1968 (AAU); Central: Nakhon Sawan, Touw 9464, XII.1965 (L,U); *ibid.*, Touw 9468 (L); Phitsanulok, Tung Salaeng Luang, Larsen et al. 752 & 871, VII.1966 (AAU,NICH,U); Udawn, Ban Na Luang, Touw 10372, I.1966 (L).

LAOS. Phonsavanh, Ban Hang, Tuyama s.n., I.1958 (NICH).

Subg. 2. *ISOLEJEUNEA* Gradst. subg. nov.

Folia caduca desunt. Perianthia plerumque omnino inflata, isoplicata vel anisoplicata.

For synonyms see under sect. *Isolejeunea*.

Type species: *Acrolejeunea pycnoclada* (Tayl.) Schiffn.

Plants without vegetative reproduction by means of caducous leaves. Perianth usually entirely inflated, isoplicate or, more rarely, anisoplicate. Outer cells of the seta evenly or unevenly tiered.

Distribution: (Pl.XXI): PALAEOTROPICS, but rare in continental Africa.

Sect. 3. *Regulares* (Verd.) Gradst. comb. nov.

Ptychocoleus Trev. sect. *Regulares* Verd., Ann. Bryol. suppl. 4: 143 (1934).

Type species: *Acrolejeunea aulacophora* (Mont.) Steph.

Stem in transverse section with 20-30 medullary cells, mostly symmetric with the ventral cortical cells as large as the dorsal cortical cells. Leaves often squarrose. Lobule $2\frac{5}{8}$ x the length of the lobe, with (1-)2-9 teeth. Perianth with 5-10 plicae.

Distribution: East African Is., Indo-Malesia, Australasia, Pacific. One collection from Sikkim (*A. sikkimensis*) and one from Tanzania (*A. aulacophora*).

6. *ACROLEJEUNEA SIKKIMENSIS* (Mizut.) Gradst. comb. nov. (Pl.XII).

Ptychocoleus sikkimensis Mizut., in Hara, Flora of Eastern Himalaya: 532 (1966).

Typus: Sikkim, Migothang-Nayathang, 3300-3900 m., hanging from a twig with *Frullania muscicola* and *Metzgeria* sp., M.Togashi s.n., I.VI.1960 (NICH holo, U).

Plants autoicous, medium-sized, up to 2 cm long, c. 1,5 mm wide, becoming wider on female branches, dull dark-brown when dry, irregularly pinnate with many sexual *Lejeunea*-type branches and a few longer, vegetative *Frullania*-type branches; microphyllous branches absent.

Stem 0,15 mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells subrectangular, 40-60 x 30 μ m; stem in transverse section with 13-14 cortical cells surrounding c. 20 medullary cells, the dorsal cortical cells 27-30 μ m high, the ventral cortical cells 23-25 μ m high, the medullary cells

18-22(-24) μm in diam., all cell walls slightly thickened, yellowish.

Leaves laxly inserted, barely overlapping, when dry irregularly appressed to the stem, when moist widely spreading and strongly squarrose in a very irregular fashion, not incurved, brittle, older stems often denuded. Lobe ovate-obovate, 1,4 x 0,8 mm when well developed, otherwise smaller, inserted along 1/2-2/3 of the length of the merophyte, the dorsal base not auriculate, the margins plane, the apex widely rounded, the ventral margin forming an angle of 150-170° with the keel; keel slightly curved, at an angle of c. 60° with the axis, + decurrent, the cells not protuberant; leaf areolation rather dense, the median cells 33-40 x 20-25 μm , longer at leaf base, at the margins smaller, quadrate; cell walls brownish, with small cordate trigones and with frequent, minute intermediate thickenings, c. 1(-2) on each longer cell wall; oil bodies unknown.

Lobule ovate with an oblique apex, c. 0,5 x 0,3 mm, inflated along the keel, the inflated part gradually to abruptly (in larger leaves) flattened, the flattened part about of the same size as the inflated part; free margin plane, gradually curved, not continuing into the ventral margin of the lobe, with (3-)4-5 regularly spatiate, erect teeth, the first tooth 2 cells long, the other teeth 1 cell long and inserted on 2 free margin cells; hyaline papilla not seen.

Underleaves widely spatiate to barely overlapping, longer than wide, c. 0,6 mm long and 0,5 mm wide, the apex rounded to truncate, the margins plane or slightly recurved, the bases subcuneate, the line of insertion almost straight.

Androecia in short spikes becoming intercalary on separate branch systems, the bracts in 4-5 series, much smaller and more densely imbricated than leaves, the lobule more strongly inflated, monandrous; bracteoles smaller than underleaves, orbicular, imbricated.

Gynoecium large, terminating a *Lejeunea*-type branch, without innovations or pseudo-innovations; bracts and bracteoles in 2-3 series, the bracts much larger than the leaves, widely spatiate and strongly squarrose, with a rounded keel in the lower half; lobe of the inner bract obovate, c. 2 mm long and 1,5 mm wide, the apex widely rounded, the lobule small and inconspicuous, less than half the length of the lobe and hardly elongated beyond the keel, the apex narrow and rounded; inner bracteole erect, narrowly obovate-oblong, c. 1,5 mm long, slightly gibbous, the apex rounded, the

margins sometimes recurved. Perianth emergent up to 1/3 of its length, narrowly obpyriform, ventrally inflated, 1,5-1,75 mm long, 0,7 mm wide, in the upper half with 5 unequal, sharp plicae: 2 lateral plicae, 2 ventral plicae (inserted on the edges of a widely rounded ventral keel) and 1 dorsal plica; beak 3-4 cells long; cells of the perianth with bulging, almost orbicular trigones.

Sporophyte: seta after elongation hardly longer than the perianth, the outer cells almost evenly tiered, the valves widely spreading, reddish-brown; elaters erect, stiff, with one brownish spiral.

Distribution: only known from the type.

Differentiation: the position of this species in the sect. *Regulares* is somewhat doubtful because the stem in transverse section is slightly asymmetric and there are only c. 20 medullary cells. It is also the only species of the genus with a pendulous habit, which is possibly an adaptation to growth in cloud forest vegetation (see p. 46). Yet, the species appears to be closely related to *A. fertilis*, from which it differs, apart from the stem cortex, by 1) the more ovate leaf lobule which has only 3-5 small teeth (but compare Ceylon collections of "*A. fertilis*"), 2) the very short lobule of the inner female bract, and 3) the underleaves, which are longer than wide. The brittleness of the plant, the rather widely distant leaves and underleaves, and the irregularly-squarrose fashion of spreading of the leaves and underleaves when moist indicate that a modification is at hand. Further collections are needed for a better understanding of this intriguing, geographically isolated taxon.

7. *ACROLEJEUNEA FERTILIS* (Reinw., Blume & Nees) Schiffn. (Pl.XIII).

- in Engl. & Prantl, Nat.Pfl.-fam. I, 3 (1): 128 (1893); Schiffner (1894): 184, (1898): 284; Gradstein (1974a) 132.
Jungemannia fertilis Reinw., Blume & Nees, Hep.Jav., Nova Acta.... 12 (1): 211 (1824).
Lejeunea fertilis Dum., Rec.d'Obs.: 12 (1835) nom.nud.
Phragmicosma fertilis (Reinw., Blume & Nees) Nees, Syn.Hep.: 299 (1845); Sande Lacoste (1856): 56; Stephani (1889): 166, (1890): 8.
Lejeunea fertilis (Reinw., Blume & Nees) Mitt., J.Proc.Linn.Soc.Bot. 5: 111 (1861); Spruce (1884): 116; Stephani (1890): 133.
Ptychocoleus fertilis (Reinw., Blume & Nees) Trev., Mem.Reale Ist.Lomb.Sci. Mat.Nat., Ser.3,4: 405 (1877); Stephani (1912): 42; Verdoorn (1934c): 144; Mizutani (1961): 283, (1969): 136.
Marchesinia fertilis (Reinw., Blume & Nees) Kuntz, Rev.Gen.Pl. 2: 837 (1891).
 Typus: Java, Lebak Mts., Reinwardt s.n. (STR holo, G 15597 & 15604, NY, W).

Heterotypic synonyms:

Ptychocoleus integribracteatus Steph., Spec.Hep. 5: 45 (1912); Verdoorn (1934c): 145.

Acrolejeunea integribracteata Schiffn., Hedwigia 39: 206 (1900) nom.nud.
Lectotypus (nov.): Sumatra, Kampong Sungei-Beramei, ad truncos, Massart s.n., III.1895 (FH-Schiffn. holo, G, W).

Ptychocoleus spongiosus Steph., Spec.Hep. 5: 55 (1912); Verdoorn (1934c): 139; Bischler (1965): 431 syn.nov.

Typus: Philippines, Guimaras I., E.D.Merrill 6727 p.p.maj. (p.p.min. = *Schiffneriolejeunea tumida* (Nees) Gradst.), III.1910 (G 15807 holo, M, MANCH, PC).

Ptychocoleus tener Steph., Spec.Hep. 5: 56 (1912); Verdoorn (1934b): 2.

Typus: Moluccas, Selaru, Micholitz s.n., XI.1898 (G 15812 holo (female), G 15811 (male)).

Acrolejeunea ustulata (Tayl.) Schiffn., Hedwigia 33: 182 (1894) syn.nov.

Phragmicoma ustulata Tayl.Lond.J.Bot. 5: 388 (1846); Syn.Hep.: 744 (1847); Stephani (1890): 7.

Ptychocoleus ustulatus (Tayl.) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 405 (1877); Stephani (1912): 58; Verdoorn (1934c): 146; Hattori (1951): 54; Bischler (1965): 431.

Lejeunea (subg. *Brachiolejeunea*) *ustulata* (Tayl.) Steph., Hedwigia 29: 134 (1890).

Marchesia ustulata (Tayl.) Kuntz, Rev.Gen.Pl. 2: 837 (1891).

Typus: Philippines, Cuming s.n., 1841 (FH-Tayl.holo, BM, FH-Schiffn., G, MANCH, NY, PC, S, U, W).

Acrolejeunea wichurae Schiffn., Hedwigia 33: 187 (1894); Schiffner (1898): 289.

Ptychocoleus wichurae (Schiffn.) Steph., Spec.Hep. 5: 58 (1912); Verdoorn (1934c): 145.

Lectotypus (nov.): Java, "aus der Bot.Garten zu Buitenzorg", Wichura s.n., 5.II.1861 (FH-Schiffn.holo, G).

Paratypus: ibidem, 6.XI.1861 (FH-Schiffn., G).

Brachiolejeunea micholitzii Steph., Hedwigia 34: 64 (1895); Stephani (1912): 137.

Typus: Philippines, Luzon, Micholitz s.n. (G holo not found, MANCH!).

Brachiolejeunea tortifolia Steph., Spec.Hep. 5: 56 (1912) fide Verdoorn (1934b): 2.

Mastigolejeunea malaccensis Steph., Spec.Hep. 6: 563 (1924) fide Verdoorn (1933b): 84.

Plants autoicous or seemingly dioicous, medium-sized, up to 4 cm long, 1-1,6 mm wide, green, becoming brownish(grayish-brown to blackish-brown) when dry; branches of the *Lejeunea*-type or (frequently!) of the *Frullania*-type, microphyllous branches present.

Stem 0,10-0,17 mm in diam; ventral merophyte 4-6(-8) cells wide, the ventral cortical cells subquadrate to rectangular, 30-75 x 18-27 μ m, the cells almost thin-walled; dorsal cortical cells slightly wider, arranged in straight longitudinal rows; stem in transverse section with 14-17 cortical cells surrounding 24-28 medullary cells, the cortical cells almost uniform in size, c. 30 μ m high, thin-walled, the medullary cells much smaller, 14-20 μ m in

diam., with medium-sized trigones, the cell walls yellowish.

Leaves laxly or densely imbricated, when dry strongly flattened and + clasping the stem, suberect, when moist widely spreading and becoming squarrose, often strongly so, the apical portion of the leaf slightly curving inwards towards the stem-apex. Lobe asymmetrically ovate-orbicular, (0,7-) 0,8-1,2 mm long, (0,45-)0,6-0,9 mm wide, inserted along $\frac{3}{4}$ to + the entire length of the merophyte, the dorsal base not auriculate, the dorsal margin gradually curved, the apex rounded to almost obtuse, the ventral margin plane or upcurved, forming an almost straight line with the keel; keel slightly curved, at an angle of $45-60^\circ$ with the axis, not decurrent, the cells not protuberant; median leaf cells rather variable in size, (26-)30-36(-45) \times 18-25(-30) μm , larger at leaf base, smaller and subquadrate at the margins; trigones small to medium-sized, sometimes almost confluent, intermediate thickenings usually scarce, but locally frequent on longer cell walls; oil bodies present in all cells, homogeneous, in median leaf cells 9-15 per cell, narrowly ellipsoid, 6-10 \times 2-3 μm (sphaerical when seen from the side!), at leaf base up to 25 per cell, in marginal leaf cells fewer, often minute and sphaerical, in stem cells very small and numerous, up to 50 per cell.

Lobule large, (ovate-) semiorbicular, (0,3-)0,35-0,5 mm long, 0,25-0,35 mm wide, c. $\frac{1}{2}$ \times the length of the lobe, narrowly inflated along the keel, widely flattened towards the free margin; free margin plane, typically semi-circular in outline, at apex not or shortly continuing into the ventral margin of the lobe, with (4-)5-9 conspicuous, regularly spatiated, subequal, erect to partially inflexed teeth (3-4 teeth in the anormal Ceylon coll.), the teeth 1-3 cells long, at base 2-3 cells wide, separated from each other by 1-4 margin cells; hyaline papilla at the proximal base of the apical tooth or one cell below it.

Underleaves imbricated, transversally ovate, (0,35-)0,4-0,6(-0,75) mm wide, 0,25-0,4(-0,5) mm long, plane, the apex rounded to truncate, the bases rounded, the line of insertion curved to arched, 30-60(-100) μm high; cells c. 23-28 \times 15-20 μm ; rhizoid disc of few larger cells at the base of the underleaf.

Androecia on short *Lejeunea*-type branches close to a gynoeceium, with up to 10 series of bracts, or on separate branch systems in long spikes of up to 50 series of bracts; bracts slightly smaller than leaves, the lobule with reduced teeth, monandrous.

Gynoeceium terminating a short or long *Lejeunea*-type branch, without true innovations but frequently with pseudo-innovations of the *Radula*-type: bracts and bracteoles in (1-)2-5 series, when in 4-5 series the bracts densely crowded and becoming shallowly bifid towards the inner series with subequal

lobe and lobule ("*integribracteata*"); inner bract suberect and sharply keeled when young, widely spreading with a rounded keel when mature, bifid to 1/5, the sinus wide and rounded, the lobe widely ovate, 0,9-1,3 mm long, the apex widely rounded to more narrowly obtuse, the lobule narrower, shorter or as long as the lobe, (0,6-)0,8-1,1 mm long, the apex narrowly obtuse to apiculate, more rarely rounded; inner bracteole suberect, obovate-obspathulate, 0,8-1 x 0,6 mm, in the median line gibbous from base to near apex, the apex rounded or truncate, rarely almost retuse (*Pt. spongiosus*) the margins plane or slightly recurved. Perianth immersed to emergent up to 1/2 of its length, obovate-cylindrical to obpyriform, 1-1,3 mm long, the base often stalk-like elongated, inflated or slightly compressed above, anisplicate or isoplicate, in the upper 1/2 - 2/3 with 5-10(-11) plicae; beak 3-5(-8) cells long.

Sporophyte: seta after elongation up to 4 mm long, the outer cells evenly or unevenly tiered.

Distribution (Pl.XXII): INDO-MALESIA (Ceylon (?) to New Guinea). In the Malesian archipelago this is a common lowland species, ranging in altitude from sea level up to 250 m. (Bogor). Pacific collections named *A. fertilis* (VERDOORN 1934c) belong to *A. aulacophora* or *A. securifolia*.

Ecology: on trees (e.g. *Cocos*) in open habitats: villages, plantations, gardens, along road-sides, beaches, etc.

Differentiation: the most outstanding character of *A. fertilis* is the large leaf lobule, which has a semi-circular free margin with (4-)5-9 conspicuous, 2-3 cells long teeth. Furthermore the species is characterised by its leaves, which are flattened when dry (often hardly clasping the stem) and usually strongly squarrose when moist. *A. fertilis* is most closely related to *A. aulacophora*, which differs by 1) its less squarrose leaves, 2) the plane female bracteole, and 3) its lobule, which has 3-5 teeth consisting of only one cell. Both species have very different geographical distributions.

Habitually *A. fertilis* resembles the species of the sect. *Acrolejeunea*, from which it differs essentially by the absence of caducous leaves.

Variation: *A. fertilis* most notably varies in the number of lobule teeth and in the morphology of the gynoecium. This variation is apparently not correlated with geographical distribution.

VERDOORN (1932, 1934c) discussed the variation in the gynoecium. In plants with 1-3 series of female bracts (*Ptychocoleus wichurae*, Pl.XIII:2,3) the

inner bract has a relatively short lobule with a narrow apex. The perianth is usually anisoplicate and has only 5-7 plicae. In plants with 4-5 series of female bracts (*Pt. integribracteata*, *Pt. tener*, Pl.XIII:4) the lobule of the inner bract is almost as large as the lobe and the apex of the lobule is rather wide. The perianth is usually isoplicate and has 8-10 plicae. Intergradation of both forms is often seen.

The number of lobule teeth varies somewhat in relation to the size of the plant: small plants have fewer teeth than large plants. In poor collections of *A. fertilis* the leaves are hardly squarrose, especially on younger stems and branches. These plants are usually almost blackish in colour and rather brittle, whereas the cells are collapsed and have strongly flexuose walls. The type material of *Ptychocoleus ustulatus* (Tayl.) Steph. belongs here.

Three aberrant forms are placed in *A. fertilis* with some doubt:

- a. a form with almost purely *Frullania*-type branching, large underleaves (0,75 x 0,5 mm), and heavy stems with the ventral merophyte up to 8 cells wide. Plants belonging here were collected on Java (Nyman s.n.) and on the Andaman Is. (Man s.n.), together with the typical form of *A. fertilis*. The form closely resembles *Trocholejeunea sandvicensis* (Gott.) Mizut. When sterile, the latter species differs mainly by 1) the lobule, which is ovate in outline and has only 4 small teeth, 2) the blackish or whitish colour of the plant when dry, 3) the large, orbicular underleaves, which often have recurved margins, and 4) the leaves, which are not or weakly squarrose.
- b. specimens from Ceylon. The lobule in these plants is more ovate and has only 3-4 teeth. In this respect the plants resemble *A. securifolia* ssp. *hartmannii* from eastern Malesia. Further Ceylonese collections are needed to determine their proper affinity.
- c. sterile plants from Bali (Sipman 7027). They resemble *A. aulacophora* by the lobule, which has 4-5 teeth consisting of a single, more or less inflexed cell. The strongly squarrose leaves are more typical for *A. fertilis*. As gametoecea are absent the proper affinity of these plants is difficult to determine. I believe that they represent a habitat modification of *A. fertilis*, because reduction of the lobule teeth is known to occur in other species of the genus as a response to habitat conditions (e.g. *A. emergens*, *A. securifolia*). Moreover, *A. aulacophora* is not yet known from Indo-Malesia.

Specimens seen (*A. fertilis*):

CEYLON. Thwaites s.n. (NY); Peradeniya, Beccari 61, V.1865 (GRO, U).

ANDAMAN IS. Litt.Cocos, Prain s.n. (BM, G); Port Blair, Man s.n., X.1898 (BM, G, H, PC, JE, W).

NICOBAR IS. Tillangschong, Jelinek 54 (FH-Schiffn., W); Camorta, Kurz 3883 & 3887, II.1875 (BM, G, W).

BURMA. Schmidt 21 (G).

SOUTH VIETNAM. Hué, Eberhardt, s.n. 1908-09 (G).

MALAYA. Allen 986 & 987, (GRO); Taiping, Fleischer s.n., II.1909 (S).

SINGAPORE. Bot.Garden, Schiffner s.n., XI.1893, Hep.Sel.Crit. Verdoorn 279 (C, FH, G, GRO, H, JE, K, L, M, MANCH, NY, O, S, U, YU); *ibid.* Fleischer s.n., III.1898 (G); *ibid.* Ridley 1408 (G); Airport, Togashi 33, XII.1961 (NICH); Bukit Timah Rd., Togashi 8d, XII.1961 (NICH); Mus.Tiger Jade house, Sipman 6883, X.1974 (Sipman, U); *div.loc.*, Ridley 305, 367, 697 & 732, 1897-98 (NY).

RIAU. Bantam, Djantan 2, 5, 6, 8 & 9, IX.1949 (GRO); Sei Menjin, Tonang 37, 1949 (GRO); Dapur Tiga, Dahlan 35 & 36, IX.1949 (G, GRO, L).

BANGKA. Nyman s.n. (G); between Kp.Mayang and Kp.Baroe, Kurz 20, VIII.1858 (L).

SUMATRA. Medan, Staal 106, IX.1949 (L); Padang, Schild 44, 50, 55, 95, 97, 101, 103, 111 & 112 (JE, W); *ibid.*, Schiffner 5, VII.1894 (FH); *ibid.*, Apenberg, VanderWijk 1158 & 1166, V.1952 (L); Kp.sungei-Beramei, Massart s.n., III.1895 (FH-Schiffn., G, W); Kp.Gau, Massart s.n., III.1895 (FH-Schiffn., G); Vlakke Hoek, Ernst 5 & 8, IV.1906 (FH-Schiffn., G); Telukbetung, Fleischer s.n., VIII. 1899 (FH, G).

SELAT SUNDA. Lang I., Docters van Leeuwen 11854, VI.1928 (GRO, L).

JAVA. Djakarta, Edam I., Fleischer s.n., III.1899 (FH, G); *ibid.*, Zaneveld 1204, IV.1949 (GRO); Duizend Eilanden, Zaneveld 1185, IV.1949 (GRO); Zandbaai, Nyman s.n., XI.1897 (G, L, S); Zippelius s.n. (L); Lebak Mts., Reinwardt s.n. (G, NY, STR, W); Bogor, Tjiliwong, Kurz 360 p.p., I.1861 (L); Bogor, Bot.Garden, Wichura s.n., XI.1861 (FH-Schiffn., G); *ibid.*, Schiffner s.n., Hep.Sel.Crit.Verdoorn 278 (C, FH, G, H, GRO, JE, K, L, M, MANCH, NY, O, S, W, YU); *ibid.*, Schiffner s.n., several collections (FH); *ibid.*, Fleischer s.n., XI.1898 (G); *ibid.*, Docters van Leeuwen 11732, IV.1928 (GRO, L); G.Salak, Nyman s.n. (G); G.Merapi, Fleischer s.n. (G).

BALI. Tampaksiring, Sipman 7027, XI.1974 (Sipman, U).

TIMOR. unknown coll., (G).

BORNEO. Kalimantan: Pulau Laut, Meijer B3265, VIII.1952 (L); Serawei, Winkler 3029a, XI.1924 (JE); Singawang, Ledru s.n., 1897 (G, JE); Sabah: Labuan I., Micholitz s.n., X.1899 (G); Jesselton, Mizutani 3329, 3330, & 3331, VI.1963 (NICH); Kota Kinabalu, Kodama 41149, III.1970 (U); Lahad Datu, Iwatsuki 5702a, VI.1963 (NICH); Sandakan, Elton s.n., 1899 (L); *ibid.*, Sepilok For.Res., Iwatsuki 4677b & 4678, VI.1963 (NICH); Sandakan Radio Station, Mizutani 3392, VI.1963 (NICH).

PHILIPPINES. without loc., Cuming s.n., 1841 (BM, FH, G, MANCH, NY, PC, S, U, W), Palawan: Taytay, Merrill 9000, IV.1913 (FH); Luzon: Micholitz s.n. (G, MANCH); *ibid.*, Zambales Mts., Eballo 6, IX.1935 (YU); Guimaras: Merrill 6727, III.1910 (G, M, MANCH, PC); Negros: Merrill 6782, IV.1910 (G, JE, K, MANCH, PC, YU); Mindanao: Dapitan, Micholitz s.n. (FH, G, GRO).

MOLUCCAS. Ambon: Zippelius s.n. (L); Micholitz 1491 (G); Banda: Visser, V. 1881 (L); Micholitz s.n., 1891 (G); Nyman s.n., X.1898 (GRO); Weber van Bosse s.n., XI.1899 (G); Selaru: Micholitz s.n., XI.1898 (G).

NEW GUINEA. Irian Barat: Sorong, Doom I., Westenberg s.n., IX.1949 (GRO); ibid., Zaneveld s.n., 1949 (JE); Misoöl I., Zaneveld s.n., XI.1949 (JE); Tanah Merah, van Zanten 182c, V.1959 (L); Papua: Berlinhafen, Fleischer 738b, III.1903 (FH); Konstantinshafen, Nyman s.n., 1899 (G,S).

8. *ACROLEJEUNEA AULACOPHORA* (Mont.) Steph. (Pl.XIV)

Bot.Jahrb. 20: 317 (1895); Gradstein (1974a): 332.

Phragmicoma aulacophora Mont., Ann.Sci.Nat.Bot. 2, 19: 259 (1843); Syn.Hep.: 743 (1847); Stephani (1889): 166, (1890): 7.

Lejeunea (subg. *Acrolejeunea*) *aulacophora* (Mont.) Steph., Hedwigia 29: 133 (1890).

Marchesia aulacophora (Mont.) Kuntz, Rev.Gen.Pl. 2: 836 (1891).

Ptychocoleus aulacophorus (Mont.) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 405 (1877); Evans (1908): 161; Stephani (1912): 38; Verdoorn (1934c): 147.

Typus: S. Pacific, Gambier Is., Mangarêva, "cum *Frullania deloti* N. et M. et *Calymperes molluensis* promiscue ad radices arborum crescit", Hombron s.n. (PC-Mont.holo, G,PC,S,W,YU).

Heterotypic synonyms:

Acrolejeunea caledonica Steph., in Thériot, Musci et Hep.Nov.Caled.Exsicc. 166 nom.nud.

Ptychocoleus caledonicus Verd., Blumea 1: 235 (1934) comb.illeg., non Steph. (1912); Bischler (1965): 431.

Typus: New Caledonia, Nouméa, Ouen-Toro, on *Ficus*, Franc s.n., XI.1909 (G 15510, 15540, & 15544, H,L,M,O,PC,PRC,W).

Acrolejeunea renauldii (Steph.) Bonner, Index Hep. 1, 2: 21 (1962).

Lejeunea (subg. *Acrolejeunea*) *renauldii* Steph., Hedwigia 27: 7 (1888).

Ptychocoleus renauldii (Steph.) Steph., Spec.Hep. 5: 26 (1912); Jones (1954): 402; Bischler (1965): 431.

Lectotypus (nov.): Réunion, Rodriguez s.n., 1887(?), ex hb.Renaud 63 (G holo). Paratypus: ibidem, Renaud 42, 60, 62, & s.n. (G); ibidem, Renaud s.n. (BM,L,O,PC).

Plants autoicous, usually small, up to 2 cm long, 1.0-1.4 mm wide, green, becoming pale yellowish- or whitish-green (rarely brownish) when dry, irregularly branched with *Lejeunea*-type branches and a few longer, vegetative *Frullania*-type branches, microphyllous branches absent.

Stem 0,12-0,15(-0,17) mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells quadrate to subrectangular, 27-40(-50) x 23-30 μ m, the walls thin or slightly thickened, colourless; dorsal cortical cells arranged in straight rows, slightly wider than the ventral cortical cells, 27-33(-38) μ m wide; stem in transverse section with 14-16 cortical cells surrounding 22-27 smaller medullary cells, the cortical cells almost uniform in size, 27-34 μ m high, the medullary cells 20-27 μ m in diam.; all cell walls thin or slightly thickened, colourless.

Leaves imbricated, when dry suberect-convoluted, when moist widely spreading and convex to more or less squarrose, the apex almost falcate, not incurved. Lobe ovate-orbicular, 0,7-0,8(-1,1) mm long, 0,55-0,65(-0,8) mm wide, inserted along + the whole length of the merophyte, the dorsal base not auriculate, the margins plane, the apex rounded to subobtuse, the ventral margin forming an angle of 120-150° with the keel; keel curved, sometimes with distinctly protuberant cells, in the lower half at right angle with the axis, not decurrent; median leaf cells (27-)30-38(-45) x 24-30(-33) μm, cells at leaf base slightly longer, at the margins small, subquadrate, c. 15 μm; cell walls with small cordate trigones and few intermediate thickenings; oil bodies homogeneous, (10-)15-25 in median leaf cells, narrowly ellipsoid (seemingly sphaerical when seen from the side!), small, 4-7 x 1,5-2 μm.

Lobule relatively large, (ovate-)semiorbicular, 0,3-0,4(-0,5) mm long, 0,25-0,3(-0,35) mm wide, c. 2/5-1/2 the length of the lobe, distinctly inflated along the keel and gradually flattened towards the free margin; free margin plane, semi-circular in outline, rarely + straight, at apex not continuing into the ventral margin of the lobe, with (3-)4-5 inconspicuous, partially to wholly inflexed teeth consisting of only one large, sphaerical cell, the first tooth sometimes 2 cells long, the teeth attached to 1-3 margin cells and separated from each other by (1-)2-3 free margin cells; hyaline papilla two cells below the proximal base of the first tooth.

Underleaves barely overlapping, suborbicular to transversally ovate, 0,25-0,4 mm long, 0,3-0,5(-0,6) mm wide, plane, the apex rounded, rarely truncate and slightly recurved, the bases rounded, the line of insertion shallowly curved; cells rather uniform in size, 23-30 x 16-21 μm, not becoming longer towards the base of the underleaf; rhizoid disc made up of few larger cells at the base of the underleaf.

Androecia on *Lejeunea*-type branches usually close to the gynoeceium, the bracts in 5-15(-40) series, slightly smaller than the leaves, the lobule without teeth, monandrous; bracteoles similar to underleaves, often bearing rhizoids.

Gynoeceium terminating a short or long *Lejeunea*-type branch, without pseudo-innovations; bracts and bracteoles in 2(-3) series, the inner bract only slightly larger than the leaves, obliquely spreading, subequally bifid to 1/4, the sinus wide and rounded, the keel widely rounded, the lobe c. 1 x 0,6 mm, the margin tapering to a relatively narrow, rounded to obtuse apex, the lobule c. 0,9 x 0,4 mm, the apex as in the lobe or narrower; inner bracteoles suberect, orbicular to obovate, c. 0,9 mm long, plane, the apex rounded to truncate.

Perianth slightly or conspicuously emergent up to 1/2 of its length, ovate-obovate, 1,0-1,3 mm long, strongly inflated, isoplicate, with 9-10 rather narrow, rounded plicae in the upper 1/2-2/3, sometimes slightly anisoplicate with only 7-8 rather weakly developed plicae; beak c. 4-5 cells long, persistent; cell walls as in the leaves thin, with small trigones.

Sporophyte: seta of 16 outer rows of cells and 4 inner rows of cells, after elongation 1 - 2,5 mm long, the outer cells almost evenly tiered; elaters with one yellowish spiral.

Distribution (Pl.XXII): PACIFIC (southern), AUSTRALASIA, tropical S.E. AFRICA (especially Madagascar and Réunion). This is a remarkably disjunct Afro-Austral-Pacific species. From Australasia the species is at present only known by single collections from Norfolk I. and Tasmania, but collections from New Zealand and Australia are to be expected. The species occurs at altitudes ranging from sea level to 800 m. In Tahiti and Samoa the species is more common at sea level, whereas in New Caledonia and Africa the species was usually collected between 300 and 800 m.

Ecology: on trees in mesophytic or xerophytic, secondary or primary forests; also along road-sides, rivers and beaches. Rarely occurring on calcareous soil (New Caledonia) or on wet rocks (Tahiti).

Differentiation: *A. aulacophora* is mainly characterised by the leaf lobule, which has a semi-circular free margin with 3-5 inconspicuous teeth. Each tooth consists of a single, inflexed, sphaerical cell, which is attached to the inner side of the free margin. Similar teeth are found in the otherwise very different American species *A. heterophylla*. *A. aulacophora* might be confused with certain modifications of *A. emergens* (e.g. *Ptychocoleus renauldii* var. *victoriae* Jones), *A. fertilis* and *A. securifolia* (e.g. *Ptychocoleus wildii* Steph.), in which the lobule-teeth have become reduced due to growth in relatively humid atmosphere. Differences are discussed under the latter species.

Variation: in contrast with the closely related *A. securifolia*, *A. aulacophora* is morphologically very stable throughout its vast range. Plants from E. African islands, usually named *Ptychocoleus renauldii* (Steph.) Steph., are very similar to pacific populations. Some variation is observed in the perianth, in the position of the leaves and in the keel. Well-developed perianths are regularly 10-plicate and distinctly emergent beyond the bracts.

Sometimes more or less anomalous perianths are observed which remain hidden between the bracts, having only 7-8 weakly developed plicae. When moist, the leaves in *A. aulacophora* are either convex or weakly squarrose. Like in *A. securifolia*, this variation in the leaves is to be observed on a single stem. Sometimes the keel is rough due to projecting cells, but plants with smooth keels are also observed.

Notes:

1. The species has consistently been misinterpreted since its original publication in 1844. Pacific collections belonging to this species were variously named *Ptychocoleus securifolius*, *Pt. pycnocladus*, or *Pt. fertilis*. Most of the collections cited by VERDOORN (1934c) as *Ptychocoleus aulacophorus*, actually belong to *Acrolejeunea securifolia* ssp. *hartmannii*. Malesian collections named *A. aulacophora* - identifications mostly by STEPHANI - belong to *A. fertilis* or *A. pycnoclada*, as VERDOORN (l.c.) has shown. Collections of *A. aulacophora* from the E. African islands have always been named *Ptychocoleus renauldii*, a species which is reduced here to synonymy. In several herbaria there are duplicates of collections from Tanzania, Usambara (leg. Fischer), which STEPHANI identified as *A. aulacophora*. These collections represent a depauperate modification of *A. emergens*. All previous reports of *A. aulacophora* from continental Africa were based on these collections and therefore are incorrect. However, among the recently collected unidentified specimens of *Acrolejeunea* from Tanzania which Dr. POCS sent me, I found a true specimen of *A. aulacophora*. Therefore, it can be stated without doubt here that *A. aulacophora* does occur in continental Africa.

2. The type-material of *Lejeunea renauldii* Steph. was collected on Réunion by RODRIGUEZ and sent to STEPHANI by RENAULD. In the STEPHANI herbarium there are at least 5 different authentic collections: Renault 46, 60, 62, 63, and Renault s.n. I have chosen Renault 63 as the lectotype because this is the only fertile collection which is not a mixture of several species. STEPHANI's original description of *Lejeunea renauldii* is somewhat confusing since it is stated erroneously that the plant is "dioicous". It is notable however, that none of the collections named *Ptychocoleus renauldii* by STEPHANI were misidentified!

Specimens seen (*A. aulacophora*):

GAMBIER IS. Mangaréva: Hombron s.n. (G, PC, PC-Mont., S, W, YU).

TUAMOTU. Raroia At.: Doty & Newhouse 11651 & 11658, VIII.1952 (G, NY).

- SOCIETY IS. Tahiti: Papeete, Fautaua valley, Hürlimann T1116, II.1952 (Hürlimann, U); *ibid.*, road Fare Rau Ape-Aorai, Hürlimann T1214, II.1952 (Hürlimann, U); without loc., Jardin s.n., 1855 (BM,MANCH), Tilden s.n. (BP).
- TONGA. Tongatapu: Hürlimann T805, X.1951 (Hürlimann, U); Lifuka: Hürlimann T869a, XI.1951 (Hürlimann, U).
- SAMOA. without loc., Powell s.n. (NY), Reinecke 1006 (G); Savaii: Matantu, Reinecke 24a, IX.1894 (FH-Schiffn., G,U); Asau, Rechinger 1495, VII.1905 (G,W); new vulcano, Rechinger 3719, VIII.1905 (G,W); Manono: Schultze-Motel 3936b & 3938c, V.1972 (B,Grolle,U); Upolu: Apia, Schultze-Motel 3118, 3921, & 3926b, V.1972 (B,Grolle,U).
- NEW CALEDONIA. Nouméa, Ouen-Toro, Franc s.n., XI.1909 (G,H,L,M,O.PC,PRC,W); *Ibid.*, Hürlimann 2037 & 2047, VIII-X.1950 (Hürlimann, U); Ermitage, Mt. Koghi, Däniker X219, II.1926 (Hürlimann, U).
- NORFOLK I. Anson Bay, Hoogland 11131, X.1967 (JE).
- TASMANIA. Archer s.n., 1876, commun. Kiaer 203 (O).
- MASCARENE IS. Mauritius: Curepipe, unkn. coll., VII.1906 (L); without loc., Lepervanche s.n., Marie s.n., Rodriguez s.n. (BM); Reunion: without loc., Rodriguez s.n., several coll. ex hb. Renaud (BM,G,L,M,O,PC); St. Benoit, de l'Isle 253 (BM,FH-Schiffn.,G,O,PC); St. Francois, Onraedt 69.R.02 & 74.R.8093 (Onraedt, U); Terre carrère, road St.Pierre-St.Benoit, Onraedt 71.R.9281 (Grolle,Onraedt,U).
- MADAGASCAR. without loc., Campenon s.n. (BM);
- COMORE IS. Mayotte, Hildebrandt s.n. (BM)
- TANZANIA. Uluguru Mts., Kikundi, Pocs et al. 6217/G, VII.1970 (EGR,U).

9. *ACROLEJEUNEA SECURIFOLIA* (Endl.) Watts ex Steph. (Pl.XIV,XV)

Proc.Linn.Soc.New South Wales 26: 215 (1901); Gradstein, J.Hattori Bot.Lab. 38: 333 (1974).

For synonyms, literature and type specimens see under the subspecies.

Distribution (Pl.XXII): E.MALESIA, AUSTRALASIA, PACIFIC. Rather unevenly distributed throughout this area. Mostly a lowland and coastal species except in New Guinea, where the species was collected in the mountains at altitudes up to 1500 m.

Ecology: usually epiphytic, rarely on soil or on rocks.

Differentiation: the distinguishing characters of *A. securifolia* are 1) the ovate to rectangular lobule, which has 1-3(-4) more or less erect teeth of variable size and length, 2) the female bracts, which are shallowly bifid with a subequal lobe and lobule separated from each other by a wide sinus, 3) the perianth, which is emergent to 1/2 or more of its length and regularly 8-10-plicate.

Intermediate thickenings occur frequently: one or two on each longer cell-wall. The species is most closely related to *A. aulacophora* (see ssp. *securifolia*).

Variation: in its present circumscription *A. securifolia* is rather polymorphic species, especially with respect to lobule morphology. Four morphologically distinct geographic races are distinguished:

Key to the subspecies of *A. securifolia*:

1. Lobule rectangular with sharply truncate apex and 1-2 large, prominent teeth.
 2. Underleaves 0,6-0,9 mm wide, with deeply arched insertion-line and + recurved apex. Dioicous. Perianth emergent to 1/2 of its length..... c. ssp. *caledonica* (N.Caledonia)
 2. Underleaves 0,5-0,6 mm wide, with almost straight insertion-line and + flat apex. Autoicous. Perianth emergent to 2/3 of its length..... d. ssp. *pallida* (S.C.Pacific)
1. Lobule ovate with oblique apex and 2-4 short teeth.
 3. Leaves distinctly squarrose. Inner female bracteole gibbous. Dioicous..... b. ssp. *hartmannii* (E.Malesia)
 3. Leaves not or weakly squarrose. Inner female bracteole not gibbous. Usually autoicous..... a. ssp. *securifolia* (Australasia)

9a. *A. securifolia* ssp. *securifolia* (Pl.XIV,XV)

Jungermannia securifolia Nees, in Endl., Prodr.Fl.Norfolk: 5 (1833).
Phragmicoma securifolia (Nees) Nees, Syn.Hep.: 300 (1845); Stephani (1889): 166, (1890): 9.
Ptychocoleus securifolius (Nees) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 405 (1877); Stephani (1912): 59; Verdoorn (1934c): 133.
Lejeunea (subg. *Acrolejeunea*) *securifolia* (Nees) Steph., Hedwigia 29: 133 (1890).
Marchesia securifolia (Nees) Kuntz, Rev.Gen.Pl. 2: 837 (1891).
Acrolejeunea securifolia Steph., Hedwigia 34: 59 (1895) nom.nud.
 Typus: Norfolk I., F.Bayer s.n. (W holo, FH, G 15790 & 15791, S, STR).

Heterotypic synonyms:

Ptychocoleus parvus Steph., Spec.Hep. 5: 50 (1912); Verdoorn (1934a): 236.
 Typus: Australia, N.S.Wales, Richmond River, North Creek, in arbore, W. Watts 226, III.1901 (G 9848 holo, FH).
Acrolejeunea wildii (Steph.) Watts, Proc.Linn.Soc.New South Wales 26: 215 (1901) syn.nov.
Lejeunea ("Acrolejeunea") *wildii* Steph., Hedwigia 28: 165 (1889).
Ptychocoleus wildii (Steph.) Steph., Spec. Hep. 5: 60 (1912); Verdoorn (1934c): 237.

Typus: Australia, Queensland, Hamilton near Brisbane, C.Wild 20, VIII.1887 (G 15847 holo, BM, MANCH).

Plants autoicous or dioicous, small to medium-sized, up to 2 cm long, 1,2-1,6 mm wide, pale whitish-green to grayish-brown when dry, irregularly branched with both *Lejeunea*-type and *Frullania*-type branches; microphyllous branches absent.

Stem 0,13-0,18 mm in diam; ventral merophyte 4 cells wide, the ventral cortical cells quadrate to subrectangular, 30-50(-60) μ m long, 30-40 μ m wide (!), the dorsal cortical cells slightly wider, 35-42 μ m, arranged in straight to slightly oblique longitudinal rows; stem in transverse section with 14-16 almost thin-walled cortical cells surrounding 25-30 smaller, thicker-walled medullary cells, the dorsal cortical cells (27-)30-35 μ m high, the ventral cortical cells 23-28(-30) μ m high, the medullary cells 15-25 μ m in diam., the cell walls yellowish.

Leaves imbricated, when dry appressed and slightly clasping the stem, when moist widely spreading and convex, sometimes weakly squarrose (not regularly so), the apex not incurved. Lobe ovate-suborbicular, (0,6-)0,7-1 (-1,4) mm long, 0,5-0,7(-1) mm wide, inserted along \pm the whole length of the merophyte, the dorsal base not auriculate, the apex rounded, the ventral margin plane or upcurved, when spread out forming an angle of (130-)150-180° with the keel; keel curved or almost straight, at an angle of c. 60° with the axis, not decurrent, usually with protuberant cells; median cells (27-)33-39(-45) x (21-)24-30 μ m, cells at leaf base slightly longer, at the margins small, subquadrate; trigones small, intermediate thickenings usually frequent on longer cellwalls, 1-2 on each wall; oil bodies unknown.

Lobule ovate with oblique apex, 0,35-0,5(-0,6) mm long, 0,3-0,4 mm wide, 2/5-1/2x the length of the lobe, gradually flattened towards the free margin;

margin plane or (in small lobules) incurved, gradually curved, \pm not continuing into the ventral margin of the lobe, sinuate-dentate with 2-4(-5) erect or partially inflexed teeth of variable length; the first tooth 2-3

s long, 2 cells wide at base, the second tooth 1-2 cells long, the other teeth of 1 cell only or rudimentary; hyaline papilla not seen.

Underleaves barely overlapping, obovate-suborbicular or transversally ovate, 0,3-0,5(-0,6) mm wide, 0,2-0,4 mm long, plane, the apex rounded, rarely truncate and slightly recurved, the bases rounded to cuneate, the line of insertion almost straight; cells variable in size, (18-)23-30(-35) x (15-)18-24 μ m, not becoming larger towards the base of the underleaf.

Androecia in short or long spikes, usually on separate branch systems, the bracts in 5-25 series, becoming gradually smaller than leaves, the

lobules becoming more strongly inflated, without teeth, monandrous; antheridia ovoid when young, globose when mature, 170 μm in largest diam., the stalk uniseriate, 135 μm long.

Gynoecium terminating a short or long *Lejeunea*-type branch, occasionally with pseudo-innovations of the *Radula*-type; bracts and bracteoles in 2-3 series, becoming larger and more widely spreading towards the inner series; inner bract unequally to subequally bifid to 1/4, the sinus narrowly to widely rounded, the lobe 1-1,3 x 0,6-0,9 mm, the apex widely rounded, the lobule 1-1,1 x 0,5-0,7 mm, the apex rounded; inner bracteole erect, obovate-suborbicular, 1-1,2 x 0,9 mm, plane, the apex rounded, plane. Perianth emergent to 1/2 of its length, cylindrical-obpyriform, 1,5-1,8 mm long, isoplicate with 8-10 plicae in the upperhalf; beak 3-7 cells long.

Sporophyte: the outer cells of the seta arranged in even tiers.

Distribution: AUSTRALASIA (E.Australia, N.New Zealand, Norfolk I.), occurring mainly along the coast at sea-level.

Ecology: usually on trees, but in New Zealand collected amongst grass in sandy soil.

Differentiation: *A. securifolia* ssp. *securifolia* is closely related to *A. aulacophora*. The latter species differs essentially by its lobule, which is semi-circular in outline and has (3-)4-5 inflexed teeth consisting of only cell. Furthermore the ventral cortical cells in *A. aulacophora* appear to be narrower (23-30 μm), intermediate thickenings are scarcer, and the perianth is shorter and more widely obovate.

Notes:

1. All *Acrolejeunea* specimens seen from Australia were collected by WATTS in the beginning of this century in the surroundings of Ballina, N.S.Wales, except for the type of *A. wildii*. STEPHANI variously named these specimens *A. parva*, *A. securifolia*, and *A. wildii*. In my opinion they all belong to *A. securifolia* ssp. *securifolia*, but plants from humid habitats with poorly developed lobules are sometimes difficult to identify. They resemble *A. aulacophora* very closely. It is likely that *A. aulacophora* also occurs in Australia, but I have not yet seen good specimens to support this assumption.
2. All New Zealand specimens labelled *Ptychocoleus securifolius* belong to *A. mollis* (Hook. & Tayl.) Schiffn. or *A. allisonii* sp.nov. *A. securifolia*

was in fact discovered in New Zealand only quite recently (leg. Hamlin, III.1970).

9b. *A. securifolia* ssp. *hartmannii* (Steph.) Gradst. comb.nov. (Pl.XIV, XV)

Lejeunea ("*Acrolejeunea*") *hartmannii* Steph., Hedwigia 28: 164 (1889).

Phragmicoma hartmannii (Steph.) Steph., Hedwigia 28: 166 (1889).

Acrolejeunea hartmannii (Steph.) Bonner, Index Hep. 1,2: 21 (1962).

Ptychocoleus hartmannii (Steph.) Steph., Spec.Hep. 5: 44 (1912); Verdoorn (1934c): 147.

Typus: New Guinea, Papua, Owen Stanley Range, C.Hartmann s.n. (G holo).

Heterotypic synonyms:

Acrolejeunea micholitzii Steph., Hedwigia 34: 58 (1895).

Ptychocoleus micholitzii (Steph.) Steph., Spec.Hep. 5: 48 (1912); Verdoorn (1934c): 147.

Typus: Philippines, Luzon, Micholitz s.n. (G 15674 holo, BM).

? *Ptychocoleus papulosus* Steph., Spec.Hep. 5: 50 (1912); Verdoorn (1934c): 147.

Typus: Solomons Is., Parkinson s.n. (G holo).

Dioicous, male and female plants often growing closely together; small to medium-sized, olive-green to brownish when dry, with long, often parallel *Lejeunea*- or *Frullania*-type branches; ventral cortical cells narrower than in ssp. *securifolia*, 25-30 μ m wide. Leaves when moist very regularly squarrose, the lobe 0,8-0,9 mm long, 0,6-0,7 mm wide, plane; lobule ovate-subrectangular with an oblique apex, the free margin with (1-)2(-3) straight or outwardly curved teeth, the teeth 1-2 cells long. Underleaves suborbicular to transversally (ob)ovate, 0,35-0,5 mm wide, the apex narrowly recurved or plane, the bases rounded to cuneate, the line of insertion slightly curved.

Androecia in long spikes of 15-25 series of bracts, occasionally on *Frullania*-type branches (!). Gynoecium with widely concave and very shallowly bifid inner bracts, the lobe and lobule of almost similar length, separated by a widely rounded sinus, the lobe rounded at apex, the apex of the lobule variable: rounded, obtuse, subapiculate or narrowly retuse; inner bracteole narrowly oblong-obspathulate or wider, obovate, gibbous from base to near apex (as in *Acrolej. fertilis*), the margins narrowly recurved or plane; perianth as in ssp. *securifolia*.

Distribution: E.MALESIA (Philippines, Ambon, E.New Guinea), ranging in altitude from sea-level up to 1500 m.

Ecology: epiphytic in (rain) forests and mangrove swamps.

Differentiation: *A. securifolia* ssp. *hartmannii* is particularly characterised by 1) the strongly squarrose leaves, 2) the lobule, which as a rule has only 2 short teeth, and 3) the gynoeceum: especially by the rather narrow, gibbous inner bracteole. In habit and in the gynoeceum this subspecies resembles *A. fertilis*.

Notes:

1. VERDOORN (1934c) treated this subspecies as a synonym of *Acrolejeunea aulacophora*.
2. The authentic material of *A. micholitzii* Steph. (Luzon, Micholitz s.n.) consists of two packets, one of them containing male plants only (G 15674), the other one containing female plants with sporophytes (G 15673). Since STEPHANI in his original description described only male plants, I consider G 15674 the holotype.
3. *Ptychocoleus papulosus* Steph. from the Solomons Is. is a depauperate modification, characterised by the leaves remaining more or less wrapped around the stem when moist (as in *Ptychocoleus ustulatus* (Tayl.) Steph.). Better collections of the Solomons Is. are wanting.

9c. *A. securifolia* ssp. *caledonica* (Steph.) Gradst. comb. nov. (Pl. XV)

Ptychocoleus caledonicus Steph., Spec. Hep. 5: 39 (1912).

Phragmicosma caledonica Gott. in sched.

Acrolejeunea caledonica Steph. in sched.

Type: New Caledonia, Balade, Vieillard 1771 (G holo, PC).

Autoicous or dioicous, relatively large in size. Ventral merophyte 4-6 cells wide. Leaves not or weakly squarrose when moist, the lobe 1-1,3 mm long, 0,9-1 mm wide, the apex in stem leaves slightly recurved; lobule \pm rectangular with a truncate apex, the free margin near apex usually bifid with 2 very prominent teeth of subequal size and separated by a v-shaped sinus, the teeth several cells wide at base and with a uniseriate apex of 1-2 cells, more rarely 3 teeth or only 1 short tooth present (in type!). Underleaves large, wider than long, 0,6-0,9 x 0,4-0,5 mm, the apex usually recurved, the line of insertion arched, 60-75 μ m deep, the bases cuneate to weakly auriculate.

Gametoecia as in ssp. *securifolia*

Distribution: NEW CALEDONIA, 0-700 m.

Ecology: On stems and twigs of trees and on rocks in mesophytic forests.

Differentiation: *A. securifolia* ssp. *caledonica* is particularly characterised by the shape of the underleaves and by the peculiar shape of the lobule teeth. In other respects ssp. *caledonica* is quite similar to ssp. *securifolia*.

Note: in STEPHANI's herbarium there are two different taxa from New Caledonia named "*Acrolej. caledonica* St. n.sp.". One of them is the plant described here (Balade, Vieillard 1771). This plant was depicted by STEPHANI in his *Iconed Ined.* and described in the *Species Hepaticarum* as *Ptychocoleus caledonicus*.

The other taxon, which was distributed by THÉRIOT in his "Musci et Hep. Novae Caledonicae Exsicc. nr. 116" (Nouméa, Franc s.n.), belongs to *A. aulacophora*. This plant is not depicted in the *Icones Ined.* Later authors (e.g. VERDOORN 1934c, BISCHLER 1965) have erroneously treated this collection of *A. aulacophora* as the type of *Ptychocoleus caledonicus* Steph.

9d. *A. securifolia* ssp. *pallida* (Aongstr.) Gradst. comb.nov. (Pl.XIV,XV)

Phragmicoma pallida Aongstr., *Ofvers.Förh.Kongl.Svenska Vetensk.-Akad.* 5: 132 (1873).

Ptychocoleus pallidus (Aongstr.) Trev., *Mem.Reale Ist.Lomb.Sci.Mat.Nat.*, Ser. 3,4: 405 (1877); Stephani (1912): 50.

Lejeunea (subg. *Acrolejeunea*) *pallida* (Aongstr.) Steph., in *Bescherelle, J. Bot.(Morot)* 12: 4 (1898).

Typus: Tahiti, "inter muscos", N.J.Andersson 17, IX.1852 (S hol., G).

Autoicous (rarely parautoicous : Cook I., Palmer s.n.), pale brownish to whitish-green when dry, with relatively long stems and long male spikes. Leaves not squarrose when moist, the lobe 0,9-1,2 mm long, 0,7-0,9 mm wide, plane; lobule ovate-subrectangular with a truncate apex, the free margin 1-2(-3) dentate, with a very prominent first tooth, which is ca. 3-5 cells wide at base and has a uniseriate apex of 1-2 cells, the second and third teeth small or absent. Underleaves suborbicular to transversally ovate, 0,5-0,6 mm wide, the apex plane, the line of insertion slightly curved.

Androecia in long spikes of up to 40 series of bracts, the bracteole often larger than the underleaves. Gynoecium as in ssp. *securifolia* except for the inner bracteole which is orbicular, and the perianth which is more longly emergent: up to 2/3 of its length.

Distribution: Southern Central PACIFIC (Cook Is., Tahiti), occurring mainly at sea-level.

Ecology: epiphytic on tree trunks.

Differentiation: this subspecies is distinguished by the prominent apical tooth of the lobule and by the longly emergent perianth. The plants are larger and slenderer than in ssp. *securifolia*, and they are always monoicous.

Specimens seen (*A. securifolia*):

a. ssp. *securifolia*:

AUSTRALIA. New South Wales: Ballina & Richmond River, Watts 38 collections (FH,G,M,O,PC,U); Queensland: Brisbane, Wild 20, VIII.1887 (BM,G,MANCH).

NEW ZEALAND. N.Island: East Cape, Omuruiti Point, Hamlin 2168, III.1970 (WELT).

NORFOLK I. Bauer s.n. (FH,G,S,STR,W).

b. ssp. *hartmannii*:

PHILIPPINES. Luzon: Micholitz s.n. (BM,G); Catanduanes: Micholitz s.n. (BM,GRO); Mindanao: Dapitan, Micholitz s.n. (BM).

MOLUCCAS. Ambon: Karsten s.n. (BM).

NEW GUINEA Papua: Bogadjim, Kärnbach 35, VIII.1881 (BM,FH-Schiffn., W); Wau, Kunei Cr., Schuster 67-5856, V.1967 (JE); Morobe, Bulolo, Kurokawa 18763, XI.1965 (TNS); Owen Stanley Range, Hartmann s.n. (G); Cape Vogel, Menapi, Brass 2174 & 2175, III.1953 (FH,JE); Fergusson I., Brass 27286, VI.1956 (GRO,JE).

SOLOMONS IS. without loc., Parkinson s.n. (G).

c. ssp. *caledoniae*:

NEW CALEDONIA. Balade, Vieillard 1771 (G,PC); Yehoué, Franc s.n., III.1909 (G); Dumbéa, vallée de l'Ermitage, Hürlimann 2061, XI.1950 (Hürlimann, U); Kalouéholia, Hürlimann 2714, VI.1951 (Hürlimann, U); Oui Pouen, Guillaumin & Baumann 761, XI.1950 (Hürlimann, U); Mé Améri, Guillaumin & Baumann 8852b, XI.1950 (Hürlimann, U).

d. ssp. *pallida*:

COOK IS. Rarotonga: unkn. coll., X.1934 (CHR); Aitutaki: Palmer s.n., IX.1933 (NY).

SOCIETY IS. Tahiti: without loc., Andersson 17. IX.1852 (G,S), Jardin s.n., 1855 (BM,PC), Setchell & Parks 5239, 1922 (FH); Papeete, Fautaua valley, Hürlimann T1130, II.1952 (Hürlimann, U); Hitiaa, Hürlimann T1137, II.1952 (Hürlimann, U).

Sect. 4. *Isolejeunea*

Ptychocoleus Trev.sect. *Minores* Verd., Ann.Bryol.Suppl. 4: 132 (1934).

Heterotypic synonym:

Ptychocoleus Trev.sect. *Arcuatae* Verd., Ann.Bryol.Suppl. 4: 128 (1934).

Type species: *Acrolejeunea arcuata* (Nees) Grolle & Gradst.

Stem in transverse section with 10-20 medullary cells, the ventral cortical cells smaller than the dorsal cortical cells. Leaves + not squarrose.

Lobule (2/5-)1/2-2/3 x the length of the lobe, with 1-3 teeth.

Distribution: Tropical Africa, Indo-Malesia, New Zealand, and the Pacific.

10. *ACROLEJEUNEA ALLISONII* Gradst. spec.nov. (PL.XII)

Ab *A. molle* cui affinis est, differt foliis inferioribus latioribus, bracteis femineis inequaliter bifidis usque ad 1/2, bracteolis femineis margine recurvo, perianthio conspicue emergenti a basi ad 1/3 alt. laevi, dein ad apicem usque alte 10-plicato.

Typus: New Zealand, N.Island, Rotorua Co., Below Atiamuri, in shrubs along Waikato river, on bark, c. 900 ft., K.W.Allison H 362 (=H2807), 24.IX.1929 (CHR holo,JE,U).

Plants parocious, c. 2 mm long, 1-1.5 mm wide, dull brownish when dry, usually fertile; vegetative and sexual branches of the *Lejeunea*-type or *Frullania*-type, the sexual branches often originating on sexual stems just below the lowest male or female bracts; microphyllous branches occasionally present.

Stem c. 0,15 mm in diam.; ventral merophyte 4 cells wide, the ventral cells subquadrate to rectangular, 35-70 x 25 μ m, the walls slightly thickened, the dorsal cortical cells wider, quadrate, arranged in straight to slightly oblique, longitudinal zig-zag rows; stem in transverse section with c. 15 cortical cells surrounding c. 18 medullary cells, the dorsal cortical cells 30-35 μ m high, the ventral cortical cells much smaller, 18-22 μ m high, the medullary cells relatively large, 18-35 (!) μ m in diam., all cell-walls thin to slightly thickened, colourless.

Leaves imbricated, when dry strongly wrapped around the stem, when moist obliquely spreading and strongly convex with the antical margin becoming subvertical in position, not falcate. Lobe asymmetrically ovate-suborbicular, 0,9-1 x 0,6-0,85 mm, inserted along 2/3-3/4 x the length of the merophyte, the dorsal base not auriculate, the antical margin widely arched, the apex

rounded and weakly incurved, the ventral margin upcurved, when spread out forming an angle of $120-150^{\circ}$ with the keel; keel curved near its base, otherwise + straight, at an angle of $45-60^{\circ}$ with the axis, weakly decurrent, the cells of the keel not or weakly protuberant; median cells $35-45 \times 21-28 \mu\text{m}$, with small to moderately large trigones and 1(-2) intermediate thickenings on longer cell walls; oil bodies unknown.

Lobule subrectangular with a sharply truncate apex, $0,35-0,4 \times 0,25 \text{ mm}$ inflated along the keel, gradually flattened and becoming slightly concave towards the free margin; free margin almost straight, with one prominent tooth, the tooth 1-2(-3) cells wide at base, with a uniseriate tip of 2-3 cells, separated from the free margin by a widely rounded to rather sharp sinus; hyaline papilla (proximal) 2-3 cells below the base of the tooth.

Underleaves transversally ovate-obovate, $0,6-0,8 \text{ mm}$ wide, $0,4-0,5 \text{ mm}$ long, plane or concave, the apex rounded to truncate, the margins plane or weakly recurved, the bases cuneate to rounded, the line of insertion shallowly curved; cells $27-34 \times 21-24 \mu\text{m}$, becoming increasingly longer towards the base of the underleaf, the longer walls with 1-2 intermediate thickenings; cell walls along the margins regularly undulate.

Androecia on female branches a few leaf cycles below the gynoecium; the bracts and bracteoles in 2-4 series, essentially similar to those in *A. mollis*.

Gynoecium terminating a *Lejeunea*-type or *Frullania*-type (!) branch, without (pseudo-)innovations; bracts and bracteoles in 2 series, the stem within the gynoecium sometimes swollen like in *A. mollis*; inner bracts larger than leaves, suberect, + clasping the perianth, bifid to $1/2-2/3$, the lobule usually small; lobe widely ovate, $1,2 \times 1 \text{ mm}$, the antical margin widely arched below and tapering to a rounded apex, the lobule variable in length, often hardly elongated beyond the keel, $0,4-0,9 \times 0,2-0,4 \text{ mm}$, the apex rounded; inner bracteole + obspathulate, $0,9-1 \text{ mm}$ long, $0,8-0,9 \text{ mm}$ wide above, the apex rounded, the apex and margins distinctly recurved, the lower portion abruptly narrowed into the base. Perianth upon maturity distinctly emergent up to $1/2$ of its length, obpyriform, $1,5-1,8 \text{ mm}$ long, c. 1 mm in diam. above, almost entirely inflated, at base with a $0,2-0,4 \text{ mm}$ long stalk, deeply plicate with 10 rounded, (sub)equal plicae extending over $1/2-2/3$ of its length, not constricted below the plicae like in *A. mollis*, truncate at apex, with a 3-4 cells long beak.

Sporophyte: capsule valves obliquely spreading after dehiscence, $0,6 \times 0,35 \text{ mm}$, the inner surface of the valve with c. 5 ridges, the layer of thickening coarsely fenestrate: + monofenestrate in the upper half of the valve and

almost plurifenestrate in the lower half; elaters bispiralled, the spirals sometimes developed rudimentarily.

Distribution: NEW ZEALAND, 250-750 m. Most collections are from the Rotorua region in the North Island, but surprisingly the species has turned up from the northern part of the South Island as well (Nelson State Park, on Nothofagus along lake Roto-iti). Together with the Tasmanian record of *A. aulacophora*, this is the southernmost record of the genus.

Ecology: on bark of trees, and on stems of *Leptospermum* sp. in dry bush.

Differentiation: *A. allisonii* is an apparently undescribed New Zealandian species, represented by six different collections in the herbarium of K.W. ALLISON, which just moved to the Botany Division of D.S.I.R., Christchurch. The species is closely related to *A. mollis*, from which it differs by 1) the wider, 0,6-0,8 mm wide underleaves, which have + recurved margins, at least in the gynoeceum, 2) the more deeply (up to 1/2) bifid female bracts, which usually have relatively short lobules, 3) the distinctly emergent perianth, which is truncate at apex and plicate over at least 1/2(-2/3) of its length, 4) the leaves, which have the apex and ventral margin of the lobe more or less incurved, and 5) the lobule, which has a narrower tooth. *A. allisonii* was previously identified as *Ptychocoleus securifolius*, which it does resemble by its emergent perianth. *A. mollis* and *A. allisonii* differ from New Zealandian specimens of *A. securifolia* (= ssp. *securifolia*) by 1) the paroicous inflorescence (autoicous or dioicous in ssp. *securifolia*), and 2) the lobule, which has only one tooth (2-4 teeth in ssp. *securifolia*). In transverse section the stems are different too, which is the main reason why the species are placed in different sections.

Variation: the species varies most notably in the length of the lobule of the female bracts. In the type material the margin of the lobe of the female bract is more widely arched in the lower half than it is in other collections.

Specimens seen (*A. allisonii*):

NEW ZEALAND. North Island: Waiotapu Forest, Allison s.n., V.1934 (CHR); Kaingaroa Forest, Allison 2804, VII.1935, (CHR); Reporoa, Allison 2802, X.1936 (CHR); Atiamuri, Allison 362 (= 2807), IX.1929 (CHR,JE,U); Taupo, Allison 2809, I.1935 (CHR,U); South Island: Nelson, Lake Roto-iti, Sainsbury s.n., XII.1947 (CHR,U).

11. *ACROLEJEUNEA MOLLIS* (Hook. & Tayl.) Schiffn. (Pl.XII)

Hedwigia 33: 178 (1894).

Ptychanthus mollis Hook. & Tayl., London J.Bot. 5: 384 (1846); Syn.Hep.: 739 (1847).

Lejeunea mollis (Hook. & Tayl.) Mitt., Fl.Nov.Zel. 2: 156 (1855).

Ptychocoleus mollis (Hook. & Tayl.) Steph., Spec.Hep. 5: 59 (1912); Verdoorn (1934a): 236.

Typus: New Zealand, "among lichens...with a *Monoclea*", J.D. Hooker s.n., X.1844 (FH-Tayl. holo).

Plants parocious, rather small, 2-3 cm long, 1-1,3 mm wide, green, becoming yellowish-brown when dry, usually fertile; vegetative branches almost invariably of the *Frullania*-type, the sexual branches being of the *Lejeunea*-type; microphyllous branches absent.

Stem c. 0,15 mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells quadrate-rectangular, 30-45(-55) x 30 μ m, the walls thin, the dorsal cortical cells larger, quadrate, arranged in straight longitudinal rows; stem in transverse section with 14-15 cortical cells surrounding c. 20 medullary cells, the dorsal cortical cells 28-33 μ m high, the ventral cortical cells smaller, similar in size to the medullary cells, 17-23 μ m; all cell walls thin, colourless to yellowish.

Leaves imbricated, when dry strongly wrapped around the stem, when moist obliquely spreading and becoming convex to more or less squarrose (as in *A. securifolia*), not falcate, the apex not incurved. Lobe asymmetrically ovate-oblong, 0,8-0,9 mm long, 0,5-0,7 mm wide, inserted along 3/4 to almost the entire length of the merophyte, the dorsal base not auriculate, the apex rounded, the ventral margin plane or slightly upcurved, forming an angle of 120-150° with the keel; keel curved near base, otherwise \pm straight, at an angle of 45°-60° with the axis, not decurrent, with protuberant cells; median cells 30-40 x 24-28 μ m, with small cordate trigones and usually one intermediate thickening on each longer cell wall; oil bodies unknown.

Lobule ovate-subrectangular, 0,35-0,4 mm long, 0,2-0,25 mm wide, c. 2/5 x the length of the lobe, narrowly inflated along the keel, deeply concave above and \pm appressed to the lobe; free margin almost straight, with a big, erect apical tooth and a rudimentary second tooth, the teeth separated from each other by a deep sinus; apical tooth at base up to 4 cells wide, the uniseriate tip 1-3 cells long; hyaline papilla proximal 2 cells below the uniseriate tip of the apical tooth.

Underleaves barely overlapping, transversally obovate to suborbicular, c. 0,5 mm wide, 0,35 mm long, plane, the apex rounded to truncate, the bases rounded to cuneate, the line of insertion shallowly curved; cells uniform in

size, 24-30 x 21-24 μm .

Androecia on female branches just below the lowest female bract, the bracts in 2-3 series, in size similar to leaves or slightly larger, the lobe more erect and the lobule more strongly inflated, the free margin curved towards the truncate apex, without teeth; bracts monandrous; bracteoles slightly larger than underleaves, becoming gradually larger towards the female bracteoles.

Gynoecium terminating a stem, without (pseudo-)innovations but usually with a branch originating just below the androecia; bracts and bracteoles in 2-3 series, the stem within the gynoecium strongly swollen, up to 2x the diameter of the vegetative axis; inner bract much larger than leaves, (sub-)erect and concave with the margins enveloping the perianth, unequally bifid to 1/5, the sinus rather narrow, rounded, the keel widely rounded; lobe widely obovate, 1,2 x 0,8 mm, the apex rounded, the lobule shorter and much narrower, 0,9-1,0 x 0,3-0,4 mm, the apex rounded; inner bracteole large, almost entirely covering the perianth, obtrapezoid, up to 1,1 mm wide, the apex truncate, plane. Perianth at maturity not or slightly emergent, obpyriform-cylindrical, c. 1,4 mm long, entirely inflated, isoplicate with 10 plicae in the upper 1/4-1/3, the plicae rounded, the perianth constricted below the plicae, at apex tapering into a 7-8 cells long beak.

Sporophyte: seta with 16 outer cells and 4 inner cells, the outer cells after elongation almost evenly tiered; valves 0,6 mm long, widely spreading after dehiscence of the capsule; spores 60-75 x 40-45 μm , the spore coat c. 6 μm thick, covered with relatively few short bluntish papillae and with 4-5 rosettes; elaters 36 per capsule (9 on each valve), 250-350 μm long, with two pale-brownish spirals, the spirals 6 μm wide, sometimes developed rudimentary.

Distribution: NEW ZEALAND (North Island), 0 - 800 m.

Ecology: on bark of trees, and on stems of *Leptospermum* sp. in dry bush.

Differentiation: the New Zealandian endemics *A. mollis* and *A. allisonii* differ essentially from the other species of the genus *Acrolejeunea* by their paroicous inflorescence. The presence on the lobule of one, prominent tooth, which is separated from the free margin by a rather deep sinus, is another character of these two species. Differences between *A. mollis* and *A. allisonii* are discussed under the latter species. Like *A. allisonii*, *A. mollis* was previously identified as *Ptychocoleus securifolius* and all

existing herbarium collections (except the type) were stored under that name. *A. mollis* resembles *A. pycnoclada* by the shape of the leaf and by the perianth, which is tapering into the beak, plicate only in the upper 1/4-1/3, and constricted below the plicae.

Variation: the specimens seen are morphologically very stable.

Note: STEPHANI (1912) and VERDOORN (1934b) reported that the type specimen of *Acrolejeunea mollis* could not be detected. I found portions of authentic material labelled "*Ptychanthus mollis* Tayl., New Zealand, Hooker", in the herbarium of Thomas TAYLOR at Farlow, in the British Museum and at Stockholm (LEHMANN collections). The authentic material was apparently an incredible mixture, containing at least 8 different species of bryophytes. The Farlow material contains fragments of a *Lejeunea* sp., *Archilejeunea* sp. (?), and three stem fragments of the plant which was depicted on the collection label by TAYLOR and described by him as *Ptychanthus mollis* Hook. & Tayl. These fragments represent the holotype of *Acrolejeunea mollis*. Portions of authentic material kept at the British Museum and in Stockholm do not contain *A. mollis*. The material in the British Museum consists of on large specimen of *Ptychanthus striatus*, whereas the convolute in Stockholm contains a poor mixture of *Ptychanthus striatus*, *Lejeunea* sp., *Metageria* sp., *Plagiochila* sp., and three species of mosses!

Specimens seen (*A. mollis*):

NEW ZEALAND. North Island: Hooker s.n., X.1844 (FH-Tayl.); Coromandel, Whangamata, Hamlin 2459a, III.1970 (WELT); Bay of Plenty, Rongakawa valley, Allison 2812, XI.1940 (CHR); Kaingaroa Forest, Allison 2803, XII.1938 (CHR); Taupo, Allison 2810, V.1934 (CHR); Wairoa, Kiwi, Hodgson several collections, 1929-1943 (CHR,F,FH,G,U); ibid., Morere, Hodgson 1362, 1945 (NICH,S).

12. *ACROLEJEUNEA PYCNOCLADA* (Tayl.) Schiffn. (Pl.XVI)

in Engl. & Prantl, Nat.Pfl.-fam. I, 3 (1): 128 (1893); Schiffner (1894): 178, (1898): 287; Gradstein (1974): 333.
Ptychanthus pycnocladus Tayl., London J.Bot. 5: 385 (1846); Syn.Hep.: 740 (1847); Stephani (1890): 6.
Lejeunea pycnoclada (Tayl.) Mitt., J.Proc.Linn.Soc.Bot. 5: 111 (1861); Stephani (1889): 259, (1890): 140.
Ptychocoleus pycnocladus (Tayl.) Steph., Spec.Hep. 5: 52 (1912); Verdoorn (1934c): 132; Miller et al. (1963): 46; Bischler (1965): 431; Mizutani (1969): 136.
 Typus: Malacca, Cantor s.n. (FH-Tayl.holo,G,MANCH,NY,S,U,W).

Heterotypic synonyms:

- Ptychocoleus brunneus* Steph., Spec.Hep. 5: 38 (1912); Verdoorn (1933b): 86.
 Typus: Ambon, Nyman s.n. (G holo).
- Ptychocoleus cucullatus* Steph., Spec.Hep. 5: 41 (1912); Verdoorn (1933b): 86; Bischler et al. (1962): 460.
- Phragmicoma cucullata* Gott.in sched.; Stephani (1889): 166 nom.nud., (1890): 10 nom.nud.
- Lejeunea* (Subg. *Acrolejeunea*) *cucullata* Steph., non Nees (1845), Hedwigia 29: 133 (1890) nom.nud.
- Acrolejeunea cucullata* Steph., Denkschr.Akad.Wiss.Wien 81: 295 (1907) nom.nud.
 Typus: Java, Bogor, Bot.Gard., Kurz 781, I.1862 (G 15566 holo, BM,G 15563, W).
- Ptychocoleus gomphocalyx* Herz., Mitt.Inst.Allg.Bot.Hamburg 7: 200 (1931); Verdoorn (1934c): 133.
 Typus: West Borneo, "am Dorfzaun bei Djotta am Serawei", c. 100 m., H.Winkler 3029, 22.XI.1924 (JE holo).
- Acrolejeunea pycnoclada* var. *rostrata* (Schiffn.) Schiffn., Hedwigia 33: 184 (1894); Schiffner (1898): 288.
- Lejeunea* (subg. *Acrolejeunea*) *rostrata* var. *minor* Schiffn., Forschungsr. "Gazelle" 4, 4: 27 (1890).
- Acrolejeunea rostrata* (Schiffn.) Bonner var. *minor* (Schiffn.) Bonner, Index Hep. 1,2: 22 (1962).
 Typus: Ambon, Naumann s.n., 7.VI.1875 (FH-Schiffn.holo).
- Acrolejeunea subinnovans* Steph., Hedwigia 34: 59 (1895) "*subinuovans*"
- Ptychocoleus subinnovans* (Steph.) Steph., Spec.Hep. 5: 56 (1912); Verdoorn (1934c): 133.
 Typus: Solomons Is. ("Nova Guinea"), Buka I., Kärbach 5 (G 15810 holo, G 15809, M).
- Acrolejeunea terminalis* (Spruce) Schiffn., Hedwigia 33: 178 (1894); Schiffner (1898): 288.
- Lejeunea* (subg. *Acrolejeunea*) *terminalis* Spruce, Trans. & Proc.Bot.Soc. Edinburgh 15: 116 (1884); Stephani (1889): 166.
- Ptychocoleus terminalis* (Spruce) Steph., Spec.Hep. 5: 57 (1912); Verdoorn (1934c): 133.
 Typus: "Ins.Malayanis.Sub nom. *Phragmicoma oiliaris* Nees in herb. Lindbergii visa a qua tamen valde diversa" (type not seen; syn.fide Verdoorn l.c.).

Plants autoicous, in size varying from very small (size of *A. parvula*) to large (size of *A. tjibodensis*), the stems usually long and slender, up to 4 cm long, (0,7-)0,9 - 1,2(-1,5) mm wide, green, becoming pale- to dark-brown when dry; branches usually of the *Lejeunea*-type and sexual, occasionally a few longer, vegetative *Frullania*-type branches also present; microphyllous branches present in small plants.

Stem 0,075-0,1(-0,13) mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells subrectangular, 30-40 x 25 µm, the dorsal cortical cells slightly wider, arranged in straight longitudinal rows; stem in

transverse section with 13-17 almost thin-walled cortical cells surrounding 15-20 smaller and slightly thicker-walled medullary cells, the dorsal cortical cells c. 25 μm , high, the ventral cortical cells c. 20 μm high, the medullary cells 12-18 μm in diam., all cell walls yellowish or almost colourless.

Leaves imbricated, sometimes laxly so, clasping the stem when dry, when moist widely spreading and convex, not becoming squarrose, the apex ventrally curving inwards, rarely plane. Lobe asymmetrically ovate-oblong, 0,5-1,2 mm long, 0,3-0,9 mm wide, suborbicular in large plants, inserted along the entire length of the merophyte, the dorsal base not auriculate, the apex rounded, incurved or (rarely) plane, the ventral margin short and \pm incurved, when spread out forming a sharp angle of 90-120(-150) $^{\circ}$ with the keel; keel curved, at an angle of (30-)45-60 $^{\circ}$ with the axis, \pm not decurrent, the cells not or weakly protuberant; median leaf cells (27-)30-35(-40) \times 21-26 μm , cells at leaf base 45-50 \times 30-33 μm , at the margins small and subquadrate, c. 15 μm ; trigones medium-sized, intermediate thickenings scarce or locally frequent; oil bodies homogeneous, 8-15 in median leaf cells, 3-7 \times 2-3 μm , fusiform to subsphaerical (sphaerical when seen from the side).

Lobule narrowly ovate-rectangular, with an oblique apex, 1,5-2,5 \times longer than wide, 0,3-0,6(-0,65) mm long, 0,15-0,25(-0,3) mm wide, 1/2-2/3 \times the length of the lobe, widely inflated along the keel and gradually flattened towards the free margin; free margin not incurved, almost straight, not or shortly continuing into the ventral margin of the lobe, (sinuate-)dentate with 2-3 teeth, the teeth 1-2(-3) cells long, erect or outwardly curved, or (especially when long) more or less inflexed, the first tooth situated at the extreme end of the free margin; hyaline papilla at the proximal base of the second tooth (=apical tooth!).

Underleaves barely overlapping, orbicular-quadrate to transversally ovate, 0,25-0,35(-0,45) mm long, 0,25-0,45(0,6) mm wide, 3-4 \times the width of the stem, plane or slightly concave, the apex rounded, plane or weakly recurved, the bases rounded, the line of insertion straight to curved, up to 60 μm deep; cells rather uniform throughout the underleaf, 20-30 \times 12-20 μm , \pm not elongated at base; rhizoid disc small.

Androecia in rather short spikes terminal or intercalary on short branches, usually close to the gynoecia, the bracts in 3-10 series, becoming smaller and more erect than the leaves, the lobule more strongly inflated; bracts monandrous; bracteoles similar to the underleaves.

Gynoecium terminating a stem or branch, without (pseudo-)innovations, often with a *Lejeunea*-type branch originating just below the lowest bract; bracts

and bracteoles in 2-3 series, the inner bracts much larger than the leaves, when young strongly involuted, erect and sometimes longly emerging beyond the subinvolucral bracts; inner bract when mature obliquely spreading, strongly concave with the apices incurved-cucullate or weakly concave with the apices erect and almost plane, when explanate (+ impossible without rupturing the bract!) suborbicular, 1-1,5(-2) x 0,8-1,2(-1,5) mm, unequally bifid to 1/4, the sinus narrow, the lobule almost as long as the lobe, the lobe widely rounded to obtuse-apiculate at apex, the lobule at apex rounded to acute or apiculate; inner bracteole + suborbicular, 1-1,5 mm long, the apex rounded, incurved-cucullate, the margins widely involuted; subinvolucral bracteoles often recurved at apex! Perianth not emergent, 1-1,5 mm long, + cylindrical, entirely inflated, isoplicate, with 10 narrowly rounded plicae in the upper 1/3-2/3, the perianth constricted below the plicae, at apex rather gradually narrowed into a 7-12 cells long beak.

Sporophyte: seta 16: 4, the outer cells after elongation unevenly to + evenly tiered: capsule split over 4/5 of its length into 4 valves, the valves widely spreading, rarely suberect, 0,35-0,5 mm long, 0,25-0,35 mm wide; spores 50-60 μ m long, angular-roundish, covered with numerous short bluntish papillae and a few rosettes; elaters 36 (9 per valve), 250-350 μ m long, 12 μ m wide, with one yellowish-brown, c. 4 μ m wide spiral.

Distribution (Pl.XXII): tropical AFRICA, INDO-MALESIA, PACIFIC. A vastly distributed species, which is apparently common in lowland and lower mountain areas, especially in tropical south-east Asia. In Indo-Malesia the species was collected from sea-level up to 1500 m. Eastwards the species reaches as far as Tahiti, and it is apparently common on Samoa and some islands in Micronesia. Ceylon has long been considered its western limit of distribution (VERDOORN 1934c), but surprisingly the species has now turned up from several localities in tropical Africa: Seychelles, Reunion, Madagascar, Zaire, and Chana. The continental African localities are somewhat disjunct, but additional African records are to be expected because the species grows preferably in anthropogenic habitats.

Ecology: always epiphytic, on stems or bases of trees; in mesophytic secondary forests and shrubs, on road-side trees, in plantations, and in gardens.

Differentiation: *A. pycnolada* differs from all other species of *Acrolejeunea* by the presence of an "extra" tooth on the leaf-lobule, which is situated at the extreme end of the free margin near the junction of the lobule and the lobe.

When inflexed, this tooth is easily overlooked. The second tooth is in fact the apical tooth, because it has the hyaline papilla at its proximal base. Further diagnostic characters include the cucullate female bracteole and the immersed perianth which is + gradually contracted into a long beak (7-12 cells long).

A. pycnoclada shares many characters with other species of the sect. *Isolejeunea*. It resembles *A. arcuata* and *A. mollis* in the shape of the leaf. *A. mollis* has a similar perianth, except for its shorter beak. Small phases of *A. pycnoclada* very much resemble *A. parvula*.

Variation: *A. pycnoclada* varies considerably in size, in the shape of the leaf and the teeth on the leaf lobule, in the width of the underleaf, and in the shape of the female bracts and the perianth (see descr.) The variation in size correlates significantly with altitude and growth conditions (VERDOORN 1934c).

Very small plants of the size of *A. parvula* grow exposed on trees in lowland areas. Numerous collections of this form have been made in the botanical garden at Bogor, Java. This form was described as *Lejeunea rostrata* var. MINOR Schiffn. In shade habitats the plants become larger according to VERDOORN (l.c.), who was able to study the variation of the species in the field. Most of the synonyms of the species represent small to medium-sized plants.

The type of *A. pycnoclada* is a more robust mountain plant with leafy stems of c. 1,5 mm wide. Similar mountain forms have been collected in Borneo, Java, Malaya and Ceylon at altitudes of 1000 - 1500 m. The leaves and underleaves in these mountain forms tend to become wider and the underleaves become more or less recurved at apex. A very interesting mountain form of *A. pycnoclada* was recently collected in New Guinea. This form is sufficiently distinct to describe it as a new subspecies.

Key to the subspecies of *A. pycnoclada* :

- a. Plants small or large: 0,7-1,5 mm wide; underleaves (on stems) 1-1,5 x wider than long, 0,4-0,6 mm wide; autoicous ssp. *pycnoclada*
(Pacific islands, Indo-Malesia, tropical Africa).
- b. Plants large and turgid: 1,2-1,5 mm wide; underleaves (on stems) 1,5-2 x wider than long, usually 0,7-1 mm wide; dioicous.....ssp. *latistipula*
(mountains of New Guinea).

12a. *A. pycnoclada* ssp. *pycnoclada*:

see under the species

12b. *A. pycnoclada* ssp. *latistipula* Gradst. ssp. nov.

A typo differt statura majore, foliis inferioribus latioribus, inflorescentia dioica.

Typus: New Guinea, Irian Barat, Star Mts., Ok Sibil, on stem of *Arcauaria*, exposed to sun, 1260 m., VAN ZANTEN 564, 14.VIII.1959 (GRO holotype, JE, L, U).

Plants dioicous, rather large and turgid, 1,2-1,5 mm wide, when dry (golden-) brownish, or pale-greenish (sterile plants). Stem rather rigid, 1,5-1,7 mm in diam., the ventral merophyte 4-6 cells wide, the ventral cortical cells 40-75 x 27-35 μ m, moderately thick-walled.

Leaves closely imbricated, when moist strongly convex, the apex widely incurved and sometimes (female plants) almost touching the underleaves; lobe asymmetrically ovate-orbicular, 0,9-1,1 mm long (from keel base to lobe apex, but 1,4 mm long when measured from dorsal lobe base to lobe apex!), 0,75-0,9 mm wide, the dorsal base subauriculate, the lobe very wide in the lower half and almost arching beyond the stem, the apex widely rounded, the ventral margin curved to sharply hooked at the transition to the keel; cells as in ssp. *pycnoclada*, but \pm protuberant at the keel. Lobule 1/3-1/2 x the length of the lobe, 0,35-0,5 mm long, 0,17-0,2 mm wide, the teeth as in ssp. *pycnoclada*.

Underleaves relatively large and wide, 1,5-2 x wider than long, 0,7-1 mm wide, 0,4-0,6 mm long, on branches usually smaller, the apex usually incurved, rounded, the bases widely rounded.

Gametoecia as in ssp. *pycnoclada*: the female bracts and bracteoles large and strongly cucullate; male plants somewhat smaller than female plants, with longer, and less turgid stems and branches, the spikes becoming intercalary with 6-12 series of monandrous bracts.

Distribution: NEW GUINEA, at altitudes of 1200-1600 m. A few recent collections only.

Ecology: on trees in open, mesophytic mountain forests.

Note: *A. pycnoclada* ssp. *latistipula* is habitually rather similar to *A. tjibodensis*. Both taxa grow together in the field near Ok Sibil, New Guinea. Differences are discussed under *A. tjibodensis*.

Specimens seen (*A. pycnoclada*):

a. ssp. *pycnoclada*:

- GHANA. Kade, Aoyala Forest Res., Jones & Hall 1232, I. 1971 (Jones).
- ZAIRE. Stanleyville, near airfield, Jones 816, IX.1955 (K).
- MADAGASCAR. Andapa, Onraedt 71.M.5017 (Grolle, Onraedt, U); Antalaha, Onraedt 71.M.5671 (Onraedt,U); Tamatave, Beforona, Cremers 3050, III.1974 (Onraedt); road Fort Dauphin - St.Luce, Onraedt 70.M.2015b (Grolle, Onraedt).
- MASCARENE IS. Réunion: Terre carrère, road St.Pierre - St.Benoît, Onraedt 71. R.9276 (Grolle, Onraedt,U); Ravine de Tremblet, Onraedt 73.R.1227 (Onraedt, U).
- SEYCHELLES. Praslin I: Vallée de Mai, Onraedt 74.S.172 (Grolle, Onraedt).
- CEYLON. Beccari 24, V.1865 (GRO), Dew s.n., 1895 (MANCH).
- ANDAMAN IS. Port Blair, Man s.n., 5 collections, 1890-1898 (BM,G,H,JE).
- THAILAND. Southern: Phangnga, Kitagawa 15291 & 15305, VIII.1967 (Kitagawa, U); Phuket I., Mt.Kluay, Touw 11182, I.1966 (L); Nakhonsithammarat, Mt. Luang, Touw 11362 & 11387, II.1966 (L).
- MALAYA. without loc., Cantor s.n. (FH-Tayl., G,MANCH,NY,S,U,W).
- SINGAPORE. without loc., Kurz 1201 (G,M); Bot.Garden, Ridley 325, 1894 (BM, FH-Schiffn.G); University, Togashi 14a, XII.1961 (NICH); Bukit Timah Rd., Togashi 6a & 8b, XII.1961 (NICH,U).
- BANGKA. Kp. Baroe, Kurz s.n., VIII.1858 (L).
- SUMATRA. without loc., Korthals s.n. (L); Kloof van Haran, Reuver 306a, 1931 (JE); Prapat, Reuver 323, 1931 (JE); Bukittinggi, Sisipang, VanderWijk 1319a, VI.1952 (L); Padang, Schild 99 & 103 (S,W).
- JAVA. without loc., Junghung s.n. (L), Karsten s.n. (BM), Stahl s.n. (BM); West Java: Bogor, Tjiliwong, Kurz 360, I.1861 (G,L); Bogor, Kp.Bauter Djatti, Schiffner s.n., Hep.Sel.Crit.Verdoorn 276 (C,FH,GRO,BM,L,JE,M, MANCH,NY,O,S,U,W,YU); Bogor, Kebun Raya, Meijer 83d, XII.1951 (S); Bogor, Bot.Garden, Kurz 781, I.1862 (BM,G,W); *ibid.*, Schiffner s.n., 1893-94, Hep.Sel.Crit.Verdoorn 275 (BM,C,FH,G.GRO,JE,H,L,M,MANCH,NY,O,S,U,YU); *ibid.* Massart 749, XI.1894 (W); *ibid.*, Nyman s.n., IV.1897 (G,S,W); *ibid.*, Docters van Leeuwen 11733m IV.1928 (L); *ibid.*, Verdoorn 134, 1930 (MANCH); *ibid.*, Borssum Waalkes 113 & 133, II.1951 (L); *ibid.*, Meijer 78b, XII.1951 (L), Meijer 3839, IV.1953 (G,GRO,L,NICH,S); *ibid.*, Sipman 6922, X.1974 (Sipman,U); Tjibodas, Reuver 117 & 129, 1931 (JE); East Java: Tretes, Mt.Ardjuno, Sipman 6991 & 7006, XI.1974 (Sipman,U).
- BORNEO. without loc., Korthals s.n. (L); Kalimantan: Serawei, Winkler 3029 (JE); Singawang, Ledru s.n., III.1897 (G); Sarawak: Everett s.n. (NY); Brunei: between Seria and Badas, Richards 5721, VII.1963 (NICH); Sabah: Labuan, Elton s.n., 1899 (G); between Panau and Poring, Kodama 40853, III.1970 (NICH); Jesselton, Iwatsuki 82, V.1963 (NICH); Mt.Kinabalu, Mizutani 2110e, V.1963 (NICH); *ibid.*, Kodama 41071, III.1970 (Kitagawa,NICH,U); Sandakan, Mizutani 3336, VI.1963 (NICH).
- PHILIPPINES. without loc., Micholitz s.n., 1884 (G,MANCH); Palawan: Taytay, Merrill 8997, IV.1913 (G,GRO,L,NY,YU); Luzon: Mt.Bulusan, Iwatsuki & Sharp 13768a, V.1965 (NICH).
- MOLUCCAS. Ambon: Naumann s.n., VI.1875 (FH-Schiffn.), Nyman s.n. (G)
- NEW GUINEA. without loc., Micholitz s.n. (G), Kärnbach 96 (GRO); Irian Barat: Tanah Merah, van Zanten 182c, V.1959 (GRO,L); Papua: Lae, Weber B-32185, VI.1968 (JE).
- SOLOMONS IS. Buka I.: Kärnbach 5 (G,M)

CAROLINE IS. Truk (fide Mizutani 1964).

MARSHALL IS. Arno Atoll: Horwitz 9429, VIII.1951 (F,PC,U); *ibid.*, Stone 1041a (TNS).

SAMOA. without loc., Powell s.n. (NY); Upolu: Rechinger 2984, 3108, 3204, 3213, 3217 & 3245 (EM,G,W); Schultze-Motel 3153b, 3631, 3750, 3932, 3965b & 3967, IV-V.1972 (B,Grolle,U); Tutuila: Fagatogo, Schultze-Motel 4404, VI.1972 (B,Grolle,U).

FIJI. Viti Levu: Mt. Victoria, Hürlimann T-1071a, I.1952 (Hürlimann,U).

SOCIETY IS. Tahiti: Nadeaux s.n. (G).

b. *A. pycnocolada* ssp. *latistipula*

NEW GUINEA. Irian Barat: Star Mts., Ok Sibil, van Zanten 564, VIII.1959 (GRO,JE,L,U); Papua: Wau, Kunei Cr., Schuster 5861, 5862, 5865 & 5880, III.1967 (JE,U); Central Highlands, Watabunga, Schuster 5947, VI.1967 (JE); Owen Stanley Range, Efogi-2, van Zanten 3743/m², 1968 (GRO,JE).

13. *ACROLEJEUNEA PARVULA* (Mizut.) Gradst. comb. nov. (Pl. XVII)

Ptychocolaenus parvulus Mizut., Dansk. Bot. Ark. 27(1): 97 (1969).

Typus: Thailand, Chantaburi, Koh Chang I., 1 km S. of Ban Khlong Nonsi, epixylic on Cocos, E. Warncke 1799, 25.VIII.1966 (AAU holotype, NICH, U).

Plants dioicous, (very) small, up to 1 cm long, 0.5-1 mm wide, often almost dark brown when dry; branches usually long and slender, and numerous, always of the *Lejeunea*-type, sometimes microphyllous.

Stems fragile, 60-90 μ m in diam.; ventral merophyte 2-4 cells wide, the ventral cortical cells quadrate to rectangular, 20-45 x 16-21 μ m, thin-walled; stem in transverse section with 11-15 thin-walled cortical cells surrounding 10-14 smaller medullary cells with small trigones; dorsal cortical cells 20-24 μ m high, ventral cortical cells 16-19 μ m high, medullary cells 12-18 μ m in diam., all cell walls colourless.

Leaves (laxly) imbricated, when dry flattened, weakly clasping the stem, when moist obliquely to widely spreading and convex, sometimes weakly squarrose, the apex plane or (in larger plants) slightly incurved. Lobe ovate-suborbicular to oblong, (0.4-)0.5-0.8 mm long, 0.3-0.5 mm wide, inserted along 1/2-3/4 x the length of the merophyte, the dorsal base not auriculate, the apex rounded, the ventral margin plane or slightly upcurved, forming an angle of c. 150° with the keel; keel gradually curved, at an angle of c. 60° with the axis, not decurrent, the cells protuberant; median leaf cells 25-33 x 19-25 μ m, slightly longer at leaf base, at the margins smaller and subquadrate; trigones medium-sized to large(!), intermediate thickenings locally frequent; oil bodies unknown.

Lobule very conspicuous in situ, ovate-subrectangular, 0,25-0,3 mm long, 1,5 mm wide, $1/2-2/3$ x the length of the lobe, strongly inflated, gradually flattened towards the free margin; free margin plane, almost straight or gradually curved towards the almost truncate apex, with one small, erect tooth of 1(-2) cells; hyaline papilla not seen.

Underleaves barely overlapping, orbicular-subquadrate to wider than long, 0,25-0,35(-0,5) mm wide, 0,2-0,35 mm long, flat, the apex rounded to truncate the bases rounded to cuneate, the line of insertion shallowly curved; cells uniform in size, (18-)20-25(-30) x 15-20 μ m; rhizoid disc inconspicuous, made up of a few large, bulging cells.

Androecia terminal becoming intercalary on long branches, the bracts in up to 10 series, becoming gradually smaller towards the apex of the spike, monandrous. Gynoecium terminating a long stem or branch, without pseudo-innovations, often with a *Lejeunea*-type branch originating below the lowest bract and becoming floriferous again; bracts and bracteoles in 2-3(-4) series, larger than leaves and underleaves, not incurved; inner bract sub-erect to obliquely spreading, unequally bifid to $1/5$, the lobe 0,8-1 x 0,4-0,5 mm, the apex rounded to obtuse, the lobule erect, weakly elongated beyond the keel, 0,7-0,8 x 0,3 mm, the apex narrowly rounded, obtuse, or apiculate; inner bracteole oblong to suborbicular, 0,8-0,9 mm long, gibbous from base to apex, the apex rounded, the margins plane. Perianth immersed or emergent to $1/3$, obpyriform-cylindrical, 1-1,2 mm long, compressed or inflated ventrally, anisoplicate with 5-10 unequal, straight to undulate, sharp plicae in the upper half: 2 wide lateral plicae, 2-5 smaller ventral plicae (inserted on a large ventral keel), and 1-3 small dorsal plicae; beak 4-6 cells long.

Sporophyte: capsule wall with a + mono-fenestrate sheath of thickening on the inner layer of cells; elaters averaging 260 x 12 μ m, monospiralled or bispiralled, the spirals 3-4 μ m wide.

Sporeling of the *Lopholejeunea*-type, the protonema globose, made up of c. 12 cells.

Distribution (Pl.XXII): ANDAMAN IS., THAILAND. Ranging in altitude from sea-level in southeastern Thailand to 1800 m. in northern Thailand.

Ecology: on stems of trees, usually in moist evergreen forests.

Differentiation: the distinguishing characters of *A. parvula* include 1) its small size (with *A. pusilla* from Japan this is the smallest species of the genus), 2) the fragile stem, 3) the ventral merophyte, which is only 2 cells

wide in small plants or on branches of larger plants, 4) the leaf lobule, which has only one tooth, and 5) the dioicous inflorescence. I agree with MIZUTANI (1969) that *A. parvula* is most closely related to *A. pycnoclada*. The two species have very different female bracteoles and perianths. By its gynoeceum *A. parvula* is in fact rather similar to *A. fertilis*.

Variation: *A. parvula* varies particularly in size and in the morphology of the perianth. Very small plants occur at sea-level in the Andaman Is. and southeastern Thailand. The ventral merophyte in these plants is only 2 cells wide, the leaves are plane and the underleaves are orbicular. Plants with larger stems (up to 1 mm wide) occur in the mountains of northern Thailand. They have the ventral merophyte 4 cells wide as usual, stem leaves with the apex incurved like in *A. pycnoclada* and underleaves which are wider than long. Branches of these plants have the characters of the smaller plants from lower altitudes.

It is not certain whether the species is always dioicous. In some collections (e.g. Andaman I., Balu Ghat, Man s.n.) I found male and female plants in the same patch. A connection between the male and female stems could not be traced.

Note: the species was previously only known from the type. Collections from the Andaman Is. belonging here were variously identified by STEPHANI as *Ptychocoleus fertilis*, *Pt. ustulatus* and *Pt. securifolius*!

Specimens seen (*A. parvula*):

ANDAMAN IS. Port Blair, Man s.n., X.1898 (FH,G,H,U); Balu Ghat, Man s.n., IX.1894 (EM,G,H,PC); Harriet Mts., Man s.n., VI.1894 (G,H,PC); without loc., Man s.n. (JE).

THAILAND. Southeastern: Koh Chang I., Warncke 1799, VIII.1966 (AAU,NICH,U); Central: Phetchabun, Mt. Phu Miang, Kitagawa 12543, X.1967 (G,Kitagawa,U); Northern: Lamphun, Doi Khun Tan, Tagawa & Kitagawa 12085 & 12036, IX.1967 (G,Kitagawa,U); Doi Pha Dam, Warncke 2179 & 2181, VII.1968 (AAU); Doi Chiang Dao, Warncke 3005, VIII.1968 (AAU); Chiangrai, Doi Suthep, Warncke 2510, 2517 & 2811, VII.1968 (AAU); *ibid.*, Kitagawa 3311 & 12141 (G); Doi Tung, Kitagawa 12407 & 12408, IX.1967 (G,Kitagawa,U); Doi Pahompok, Kitagawa 12165, 12177, 12178 & 15319, IX.1967 (G,Kitagawa,U); Doi Pachon, Kitagawa 3580 & 3698, XII.1965 (G).

14. *ACROLEJEUNEA TJIBODENSIS* (Verd.) Grolle & Gradst. (Pl.XVIII)

in Gradst., J.Hattori Bot.Lab. 38: 333 (1974).

Ptychocoleus tjibodensis Verd., Rec.Trav.Bot.Neerl. 30: 227 (1933); Verdoorn

(1934c): 135.

Typus: West Java, "In Decl.austral.montis Pangerango; in horto montano "Tjibodas" ad arborum truncos; regio nubium, alt. 1420 m.", V. Schiffner s.n., 8.V.1894 (FH Verdoorn 21388 holo).

Plants dioicous, medium-sized to large, up to 4 cm long, 1,2-1,6 mm wide, yellowish-brown to dark brown when dry; branches usually of the *Lejeunea*-type, often long and more or less parallel, occasionally of the *Frullania*-type, microphyllous branches rare.

Stem c. 0,15 mm in diam.; ventral merophyte 4 cells wide, the ventral cortical cells quadrate to rectangular, 35-60 x 30-35 μm , the walls thickened; stem in transverse section with c. 14 cortical cells surrounding c. 20 medullary cells, the dorsal cortical cells 27-30 μm high, the ventral cortical cells 18-22 μm high, the medullary cells 15-22 μm in diam., all cell walls yellowish, moderately thickened but cell walls in the ventral merophyte more strongly thickened.

Leaves imbricated, when dry wrapped around the stem with the leaf-surface more or less undulate, when moist widely spreading and convex, not squarrose, the apex curving inwards as in *A. pycnoclada*. Lobe ovate-orbicular, (0,7-) 0,9 - 1,2 mm long, 0,6-0,9 mm wide, inserted along almost the entire length of the merophyte, the dorsal base (sub)auriculate, widely arched, the apex widely rounded, the apex and the ventral margin in situ curving inwards, the ventral margin when spread out forming a very wide curvature with the keel in large leaves, in smaller leaves forming a rather sharp angle of 90-130°; keel almost straight, at an angle of 45° with the axis, decurrent, the cells not or slightly protuberant; median leaf cells c. 30-35 x 20 μm , longer at leaf base, at the margins smaller, subquadrate; trigones small to medium-sized, intermediate thickenings frequently present, one on each longer wall; oil bodies (INOUE 1967) 7-13 in median and basal leaf cells, fewer in cells along the margins, homogeneous, ellipsoid to globose, up to 9 μm long.

Lobule hidden behind large underleaves, ovate-subrectangular with a truncate apex, 0,3-0,6 mm long, 0,2-0,35 mm wide, narrowly inflated along the keel, widely flattened above; free margin + straight, at base + recurved, at apex not continuing into the ventral margin of the lobe, with 2(-3) teeth, the first tooth short and erect, 1-2 cells long, the second tooth usually longer and slightly curved, (1-)2-4 cells long and 2-3 cells wide at base, in small plants shorter and sometimes almost reduced, a third teeth present in larger stem leaves, 1-2 cells long, separated from the second tooth by c. 10 free margin cells; hyaline papilla 2 cells below the proximal base of the first tooth.

Underleaves imbricated, transversally obovate, 0,35-0,5 mm long, 0,5-0,75 mm wide, 4-5 times wider than the stem, concave and not gibbous, the apex rounded and recurved especially on female branches, the bases cuneate to subauriculate, the line of insertion arched, 50-100 μ m deep; cells narrowly elongated, 25-30 x 12-15(-18) μ m; rhizoid disc small, made up of a few large bulging cells.

Androeceia occurring on separate plants close to the female plants, the spikes terminal or intercalary, the bracts in 4-12 series, \pm similar to leaves but the lobule more strongly inflated, monandrous; bracteoles similar to underleaves.

Gynoeceium terminating a stem or a *Lejeunea*-type branch (rarely *Frullania*-type branch!), occasionally with pseudo-innovations; bracts and bracteoles in 2(-3) series, much enlarged towards the inner series; inner bracts obliquely spreading, rarely becoming squarrose, not involuted, unequally bifid to 1/4, the lobe 1,4-1,6 x 0,9-1,2 mm, the margins tapering to an obtuse or subacute apex, the lobule erect, oblanceolate, weakly elongated beyond the keel, 1-1,2 x 0,4-0,5 mm, the margins plane, the apex acute and sometimes twisted, or rounded to truncate, usually crowned with a short tooth; inner bracteole erect, obovate to narrowly oblong, 1,2-1,4 x 0,7-1,1 mm, \pm gibbous, the apex rounded to shallowly retuse, plane or recurved, the apex of the subinvolucral bracteoles more strongly recurved. Perianth emergent, sometimes longly so due to stalk-like elongation of the base, obovate to cylindrical, 1,3-1,8 x 0,8 mm, isoplicate, with 10 prominent, rounded plicae in the upper 1/2-2/3; the perianth not constricted below the plicae; at apex gradually narrowed into a 3-8 cells long beak.

Distribution: MALESIA (Malaya, Sumatra, Java, New Guinea). Most collections are from West Java where the species was collected between 1100 and 2650 m. In other areas records are from 1300-1600 m.

Ecology: on stems of trees in primary mountain forests.

Differentiation: *A. tjibodensis* is mainly distinguished by 1) its large size, 2) the dioicous inflorescence, 3) the leaves, which are auriculate at the dorsal base and not squarrose when moist, 4) the lobule, which has 2(-3) teeth, and 5) the recurved apex of the underleaf. The female involucre is large and spreads widely around the regularly 10-plicate perianth.

The species is most closely related to *A. pycnoclada*, especially to the ssp. *latistipula* from New Guinea with which it occurs together in the field.

When dry the two taxa are distinguished habitually by the undulate leaf-surfaces in *A. tjibodensis* and the + smooth leaf-surfaces in *A. pycnolada* ssp. *latistipula*. *A. pycnolada* differs further by its tooth at the extreme end of the free margin, and by the more or less cucullate female involucre.

A. arcuata, which also occurs in the same localities as *A. tjibodensis*, differs in quite a number of characters, e.g. 1) the reddish brown colour, 2) the smaller leaf cells with larger trigones, 3) the narrower leaf and longer lobule, and 4) the very different female bracts.

Sterile *A. tjibodensis* is strikingly similar to *Trocholejeunea infusata* from continental East Asia. Apart from their different areas of distribution, the two species differ when sterile by the more orbicular underleaves and the predominantly *Frullania*-type branching in *T. infusata*. Their gametophytic similarity is a good example of morphological parallelism in Lejeuneaceae.

Variation: the species most notably varies in the lobule of the female bract, which is acute to acuminate (with twisted apex), or widely rounded. In collections from Tjibodas (Verdoorn s.n.) this variation is present within single plants. Variation is also observed in the width of the underleaves and female bracteoles, and in the recurvature of leaves and underleaves. In plants from Malaya (Inoue 11195) the apex of leaves (and underleaves) is very widely recurved so that the leaf apex touches the underleaf (similarly as in the type of *A. pycnolada* ssp. *latistipula*!).

The size of the plants varies in correlation with the lobule teeth: large plants have 2-3 teeth with the second tooth long and curved. Small plants have only (1-)2 short teeth.

Note: the oil bodies were described and beautifully illustrated by INOUE (1967) from Malayan plants identified as *Ptychocoleus sarawakensis*.

Specimens seen (*A. tjibodensis*):

MALAYA. Panang, Cameron Highlands, Inoue 11195, IX.1965 (TNS,JE,U).

SUMATRA. Pajakumbuh, Mt. Sago, Meijer 6246 & 6689, 1955 (L,U).

JAVA. G.Gede, Tjibodas, Schiffner s.n., 1894 (FH,U), Nyman s.n. (G), Verdoorn 2108 & 2140, 1930 (FH); G.Gede, Artja, Schiffner s.n., IV.1894 (FH); Lembang, Butot s.n. VII.1949 (GRO); G.Kawi, Docters van Leeuwen s.n., IV. 1929 (FH); G.Lawoe, Verdoorn 827, VI.1930 (FH).

NEW GUINEA. Irian Barat: Star Mts., Ok Sibil, van Zanten 28 & 559, 1959 (GRO, L).

15. *ACROLEJEUNEA ARCUATA* (Nees) Grolle & Gradst. (Pl.XIX)

in Gradst., J.Hattori Bot.Lab. 38: 332 (1974).

Jungermannia arcuata Nees, Enum.Plant.Crypt.Javae 1: 38 (1830).

Phragmicoma arcuata (Nees) Nees, Syn.Hep.: 300 (1845); Sande Lacoste (1856): 57; Stephani (1890): 9.

Ptychocoleus arcuatus (Nees) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 405 (1877); Stephani (1912): 37; Verdoorn (1934c): 128; Bischler (1965): 431.

Lejeunea (subg. *Mastigolejeunea*) *arcuata* (Nees) Steph., Hedwigia 29: 130 (1890).

Mastigolejeunea arcuata (Nees) Schiffn., Hedwigia 33: 183 (1894); Schiffner (1898): 297.

Jungermannia fertilis *beta tenerior* Lindenb. in sched.

Typus: Java, Blume s.n. (STR holo,G,L,NY,PC-Mont.,W).

Heterotypic synonyms:

Ptychocoleus hians Steph., Spec.Hep. 5: 45 (1912); Verdoorn (1934): 129 syn. nov.

Typus: Java, Giesenhagen s.n. (G holo).

Ptychocoleus coroniformis Kodama & Kitagawa, J.Hattori Bot.Lab. 38: 443 (1974) syn. nov.

Typus: Borneo, Sabah, Mt.Kinabalu, near Carson's Camp, in mossy forest, c. 2600 m., Kokawa & Hotta 3884bis, 14.I.1969 (OSA holo,NICH,U).

Plants dioicous, small to medium-sized, the stems slender, up to 3 cm long, 0,7-1,2 mm wide, reddish-brown when dry, more rarely pale brownish; branches usually of the *Lejeunea*-type, often long and arranged parallel, occasionally of the *Frullania*-type, microphyllous branches absent.

Stem rather rigid (!), 75-130 μ m in diam.; ventral merophyte 4 cells wide, the ventral cortical cells narrowly rectangular, 25-45 x 12-20(-25) μ m, moderately thick-walled, the dorsal cortical cells shorter and wider, c. 30 x 18-22 μ m, arranged in straight longitudinal rows; stem in transverse section with 15-17 cortical cells surrounding 14-15 medullary cells, the dorsal cortical cells 25-30 μ m high, the ventral cortical cells 20-25 μ m high, the medullary cells 16-25(-27) μ m in diam., all cells with \pm thickened, yellowish walls, the medullary cells distinctly thicker-walled than the cortical cells.

Leaves (laxly) imbricated, clasping the stem when dry, when moist obliquely spreading and convex, not squarrose. Lobe asymmetrically obovate-oblong, falcate, 0,5-0,9 mm long, 0,35-0,55 mm wide, inserted along $3/4$ x the length of the merophyte, the dorsal base sharply angled, the margins tapering to a rounded or almost obtuse apex, the apex and the ventral margin curving inwards, the ventral margin when spread out forming an angle of 140-180° with the keel; keel long and almost straight, at an angle of 30(-45)° with the axis, decurrent, the cells not protuberant; median leaf cells arranged in

diverging rows, small, 18-27(-33) x 12-16(-21) μm , at leaf base slightly longer, at the margins smaller and subquadrate, c. 12 x 15 μm ; trigones medium-sized to large, yellowish, cordate, becoming orbicular and almost confluent when large; intermediate thickenings usually scarce, locally present on longer walls; oil bodies unknown.

Lobule very long and rectangular, usually c. three times longer than wide, $(1/2-2/3)$ x the length of the lobe, 0,3-0,6 mm long, 0,12-0,2 mm wide, in situ longly decurrent along the axis, narrowly inflated along the keel; free margin plane, straight, shortly continuing into the ventral margin of the lobe, near apex with 2 closely inserted, erect to inflexed teeth, the first tooth 2-3 cells long, pointing towards leaf apex, the second tooth usually shorter, but sometimes longer: up to 4 cells long and curved outwardly, slenderer than the first tooth; hyaline papilla at the proximal base of the first tooth.

Underleaves imbricated to barely overlapping, quadrate-suborbicular, 0,25-0,5 mm in diam., 3,5-5 times wider than the stem, not gibbous, the apex rounded to truncate, sometimes weakly recurved, the margins plane, the bases subauriculate, the line of insertion almost straight; cells relatively narrow and thick-walled, 18-28 x 12-15 μm , smaller at the margins, not enlarged at base; rhizoid disc small, made up of 8-15 thick-walled cells which are not larger than underleaf cells.

Androecia in short spikes, terminal or intercalary on long stems or branches, the bracts in 4-6 series, + similar to leaves but the lobule more strongly inflated and the keel arched; bracts monandrous.

Gynoecium terminating a stem or branch, without pseudo-innovations; bracts and bracteoles in 2-3(-4) series, usually much larger than leaves and underleaves, and spreading to form a "flower-like" involucre around the perianth; inner bract squarrose above, the tips sometimes strongly recurved, subequally bifid to $1/2$, with a rather narrow sinus and lanceolate-oblong lobe and lobule, the lobe 1-2 mm long, 0,5-0,9 mm wide, the margins tapering to a narrowly obtuse-acute apex, the lobule 0,9-1,5 mm long, 0,2-0,5 mm wide, the apex obtuse-acute, sometimes reflexed; inner bracteole erect, or obliquely spreading, ligulate-(ob)ovate, 1-1,7 mm long, 0,5-1 mm wide, plane or laterally involute, the apex rounded to almost retuse, + recurved. Perianth emergent, sometimes longly so due to stalk-like elongation of the base, cylindrical, 1,5-1,8 x 0,6 mm, inflated, 5-10 plicate, in the upper $1/2$ (-2/3) isoplicate or anisoplicate, the plicate narrow or widely inflated; beak c. 7 cells long.

Sporophyte: seta hardly longer than the perianth, the outer cells evenly tiered; capsule valves 0,5 x 0,3 mm; elaters averaging 300 x 15-18 μm with

one brownish, c. 4 μm wide spiral.

Distribution: MALESIA (Sumatra, Java, Borneo, Philippines, New Guinea), 1500-3500 m.

Ecology: on stems of trees, preferably in primary mountain forests (mossy forestst).

Differentiation: *A. arcuata* is a very distinct species. Its distinguishing characters are 1) the relatively long and narrow lobule, which always has two teeth near the apex, 2) the long and straight keel, which makes a sharp angle of 30(-45) $^{\circ}$ with the axis and is distinctly decurrent at base, 3) the small median leaf-cells, 12-20 μm wide, 4) the relatively large trigones, and 5) the inner female bract, which is subequally divided up to 1/2 of its length into a narrowly lanceolate-oblong lobe and lobule. The inner bract resembles a leaf of *Herbertus*!

Typical specimens of *A. arcuata* are reddish-brown in colour, distinguishing the species from any other species of the genus. When pale-brownish, the species is somewhat like *A. pycnoclada*, which it also resembles in the long and slender habit and in the shape of the leaves.

Variation: notable variation is observed in the size of the plant, in the width of the lobe and lobule of the inner female bract, in the shape of the lobule teeth, and in the shape and number of the plicae on the perianth. Male plants tend to be smaller than female plants.

In the mountains of Java and New Guinea large female plants occur which have perianths with c. 10 narrow, sharp plicae. Plants from Borneo (Mt. Kinabalu) have perianths with only 5-7 plicae, which are sometimes strongly inflated and widely rounded (e.g. *Ptychocoleus coroniformis* Kodama & Kitagawa).

The second tooth of the lobule varies in length like in *A. tjibodensis*. In the type-collection of *Ptychocoleus hians* it is longer than the first tooth and conspicuously curved outwardly, whereas in the type of *A. arcuata* it is much shorter. VERDOORN (1934c) therefore considered *Pt. hians* to be different from *A. arcuata* on the species level. Having been able to study a considerably larger amount of material than was available to Dr. VERDOORN, I found intergradations between *A. arcuata* and *Pt. hians* with respect to lobule teeth. Consequently the latter species is reduced to synonymy here. I found no evidence to support VERDOORN's statement that *Pt. arcuatus* is more fragile ("brüchig") than *Pt. hians*.

Note: KODAMA & KITAGAWA (1974) illustrated male bracts with large, hypostatic lobules in *Ptychocoleus coroniformis*. I suspect that this is an error because all species of *Acrolejeunea* have relatively small, epistatic lobules.

Specimens seen (*A. arcuata*):

SUMATRA. Pajakumbuh, Mt.Sago, Meijer 735b, VI.1955 (L); Bukittinggi, summit Mt.Singgalang, Meijer 7303 & 7319, VII.1955 (L,U).

JAVA. without loc., Blume s.n. (G,L,NY,PC-Mont., STR,W), Giesenhagen s.n. (G), Stahl s.n. (G), Treub s.n. (G); Mt.Pangerango, Meijer 797a, III.1953 (L); G.Gede, Kurz s.n. (GRO,L).

BORNEO. Sabah: Penampang, G.Alab, Kokawa & Hotta 2058bis, XII.1968 (NICH); Mt.Kinabalu, Kokawa & Hotta 3884bis, I.1969 (OSA,NICH,U); *ibid.*, Mizutani 2242, 2622, 2625, 2626, 2644, 2828, 2829, 2983, 3522, 3660 & 3711, V.1963 (NICH).

PHILIPPINES. Luzon: Mt.Banahao, Loher s.n., 1906 (G).

NEW GUINEA. Irian Barat: Helwig Mts., Pulle s.n., I.1913 (FH); Papua: Wau, summit Mt.Kaindi, Schuster 67-5828, V.1967 (JE); Mt.Yule., Exp. Roy.Geogr. Soc. s.n. (FH); without loc., Carr 15118, 1935 (JE).

EXCLUDENDA

All taxa listed here were studied from type material.

Three categories of names are treated:

- a. Names published in *Acrolejeunea* (starting point for valid combinations = SCHIFFNER sept. 1893).
- b. Names published in *Lejeunea* subg. *Acrolejeunea* (*Acrolejeunea* combination not available).
- c. Hitherto unrevised names published in *Ptychocoleus* (*Acrolejeunea* combination not available).

Lejeunea (subg. *Acrolejeunea*) *amplectens* (Steph.) Steph., Hedwigia 29: 133 (1890) syn. nov. = *Schiffneriolejeunea polycarpa* (Nees) Gradst., J. Hattori Bot. Lab. 38: 335 (1974).

Acrolejeunea atroviridis (Spruce) Bonner, Index Hep. 1,2: 15 (1962) = *Lopholejeunea atroviridis* (Spruce) Evans, Bryologist 14 (1911)

Acrolejeunea borneensis Steph. ex Bonner, Index Hep. 1,2: 16 (1962) nom. nud. = *Schiffneriolejeunea*

Ptychocoleus boliviensis Steph., in Herzog, Bibl.Bot. 87: 250 (1916) nom. nud. = *Brachiolejeunea cf. densifolia* (Raddi) Evans

Acrolejeunea borgenii (Steph.) Steph., in Engl., Die Pflanzenwelt Ostafrikas, C: 65 (1895) syn.nov. = *Schiffneriolejeunea pappeana* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

Ptychocoleus brachiolejeuneoides Verd., Nova Guinea 18(1): 6 (1934) syn.nov. = *Mastigolejeunea recondita* (Steph.) Mizut., J. Hattori Bot.Lab. 32: 134 (1969)

Because of its pluriplicate perianth *M. recondita* belongs in *Mastigolejeunea* sect. *Nigrae* Schust. 1963. This name is antedated by *Ptychocoleus* sect. *Brachiolejeuneoides* Verd. 1934 (Typus: *Pt. brachiolejeuneoides* Verd.). Therefore the following nomenclatural change should be made: *Mastigolejeunea* sect. *Brachiolejeuneoides* (Verd.) Gradst. comb. nov. (*Ptychocoleus* sect. *Brachiolejeuneoides* Verd., Ann.Bryol.Suppl. 4: 147 1934c); *Mastigolejeunea* sect. *Nigrae* Schust., Nova Hedwigia Beih. 9: 99 (1963) syn.nov.

- Acrolejeunea convexa* Steph., Wiss.Ergebn.Deutsch.Z.Afr.Exp. 2: 128 (1911)
Evansiolejeunea roccatii (Gola) VandenBerghen, Bull.Soc.Bot.Belg. 92: 117 (1960)
- Acrolejeunea cordistipula* Steph., Mem.Soc.Nat.Sci.Nat.Math.Cherbourg 29: 208 (1894) = *Trocholejeunea infuscata* (Mitt.) Verd., Ann.Bryol.Suppl. 4: 190 (1934)
- Acrolejeunea cristiloba* Steph., Hedwigia 34: 56 (1895) = *Caudalejeunea cristiloba* (Steph.) Gradst., Acta Bot.Neerl. 23: 340 (1974)
- Acrolejeunea densifolia* (Schiffn.) Bonner, Index Hep. 1,2: 17 (1962) = *Schiffneriolejeunea pulopenangensis* (Gott.) Gradst., J. Hattori Bot.Lab. 38: 335 (1974).
- Acrolejeunea domingensis* (Tayl.) Bonner, Index Hep. 1,2: 17 (1962) = *Schiffneriolejeunea polycarpa* (Nees) Gradst.
- Ptychocoleus dentilobulus* Steph., in Herzog, Bibl. Bot. 87: 250 (1916) = *Marchesinia*
- Acrolejeunea ferruginea* Steph., Hedwigia 34: 57 (1895) = *Schiffneriolejeunea ferruginea* (Steph.) Gradst., J. Hattori Bot.Lab. 38: 333 (1974)
- Acrolejeunea fuscescens* Gola, Annali di Bot. 6: 275 (1907) syn.nov.(Typus in TO!) = *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans, Torreya 7: 229 (1907)
- Ptychocoleus fuscescens* (Hampe) Trev., Mem.Reale Ist.Lomb.Sci.Mat.Nat., Ser. 3,4: 405 (1877)= *Archilejeunea fuscescens* (Hampe) Fulf., Bryologist 45: 174 (1942)
- Acrolejeunea hasskarliana* (Gott.) Schiffn., in Engl. & Prantl, Nat.Pfl.-fam. I, 3(1): 128 (1893) = *Schiffneriolejeunea*
- Acrolejeunea javanica* Steph. ex Bonner., Index Hep. 1,2: 18 (1962) nom.nud. = *Schiffneriolejeunea cumingiana* (Mont.) Gradst., fide Verdoorn (1934c): 138.
- Acrolejeunea juliformis* (Nees) Schiffn. "Steph.", Hedwigia 33: 183 (1894) =

= *Archilejeunea juliformis* (Nees) Gradst. comb.nov.

(*Jungermannia juliformis* ("*filiformis*") Nees, in Mart.Fl.Bras. 1,1: 351 (1833) = *Phragmicoma juliformis* (Nees) Nees, Syn.Hep.: 298 (1845) = *Ptychocoleus juliformis* (Nees) Trev., Mem.Reale Ist.Lomb. 3,4: 405 (1877) = *Lejeunea* (subg. *Acrolejeunea*) *juliformis* (Nees) Steph., Hedwigia 29: 133 (1890));

Typus: Brazil, "In monte Arara Coara", Martius s.n. (STR holo, FH,M,P,S, W).

Heterotypic synonym:

Archilejeunea rufa (Spruce) Steph., Spec.Hep. 4: 719 (1911) (*Lejeunea* (subg. *Archilejeunea*) *rufa* Spruce, Trans. & Proc.Bot.Soc.Edinburgh 15: 94 (1884)) syn.nov.

Typus: Brazil, Obidos, Spruce s.n. (BM iso?).

Previous authors (e.g. HERZOG 1951: 135) compared *Ptychocoleus juliformis* (Nees) Trev. with *Ptychocoleus polycarpus* (Nees) Trev. (= *Schiffneriolejeunea polycarpa* (Nees) Gradst.). The two species are readily distinguished, however, by the very different leaf areolation: elongate cells with cordate trigones in *Schiffneriolejeunea polycarpa*, versus isodiametric cells with symmetrically-triangular to radiate trigones in *Archilejeunea juliformis*. *Phragmicoma juliformis* var. *bèta* Nees (Syn.Hep.: 298, 1845) is indeed a synonym of *Schiffneriolejeunea polycarpa* (Nees) Gradst. (Typus: Brazil, Serra dos Orgaes, Martius s.n., STR holo !)

Ptychocoleus latus Steph., Spec. Hep. 5: 46 (1912) = *Caudalejeunea* cf. *reniloba* (Gott.) Steph. modif.leptoderma-laxifolia-viridis (cf. Verdoorn (1934a): 235)

Acrolejeunea linguaeifolia (Tayl.) Bonner, Index Hep. 1,2: 19 (1962) = *Brachiolejeunea corticalis* (Lehm. & Lindenb.) Schiffn.

Acrolejeunea luzonensis Steph., Hedwigia 34: 57 (1895) = *Schiffneriolejeunea cumingiana* (Mont.) Gradst., J. Hattori Bot.Lab. 38: 333 (1974) fide Verdoorn (1934c): 138.

Acrolejeunea malaccensis (Tayl.) Bonner, Index Hep. 1,2: 19 (1962) = *Schiffneriolejeunea cumingiana* (Mont.) Gradst. fide Verdoorn (1934c): 137

Acrolejeunea marquesana Steph., Hedwigia 34: 58 (1895) = *Schiffneriolejeunea cumingiana* (Mont.) Gradst., J. Hattori Bot.Lab. 38: 333 (1974) fide Verdoorn (1934a): 217.

Lejeunea (subg. *Acrolejeunea*) *marsupifolia* Spruce, Trans. & Proc.Bot.Soc. Edinburgh 15: 118 (1884) = ?

Typus: Brazil, Rio Negro, S. Gabriel, Spruce s.n. (MANCH holo, FH).

I do not yet know where this species belongs. It is related to *Schiffneriolejeunea*, but differs by 1) the leaf areolation, which is more like in *Archilejeunea*, 2) the lobule, which is distinctly incurved at apex, and 3) the polystratose rhizoid disc, which is elongate and gives rise to a bundle of rhizoids somewhat above the base of the underleaf (as in some spp. of *Frullania* subg. *Chonanthelia*). The species is only known from fragmentary (but fertile!) type material. Better collections are wanted.

Ptychocoleus molleri (Steph.) Steph., Spec.Hep. 5: 29 (1912) syn.nov. = *Schiffneriolejeunea polycarpa* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

Ptychocoleus multiflorus Steph., Spec. Hep. 5: 35 (1912) syn.nov. = *Schiffneriolejeunea polycarpa* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

Acrolejeunea novaequinae (Steph.) Steph., Denkschr.Akad.Wiss.Wien Math.Nat. Kl. 81: 295 (1907) = *Schiffneriolejeunea cumingiana* (Mont.) Gradst., J. Hattori Bot.Lab. 38: 333 (1974) fide Verdoorn (1934a): 236

Acrolejeunea occulta (Steph.) Bonner, Index Hep. 1,2: 20 (1962) = *Schiffneriolejeunea occulta* (Steph.) Gradst., J. Hattori Bot.Lab. 38: 333 (1974)

Acrolejeunea orchidae Pears., Natuurw. Tijdschr. 4: 122 (1922) = *Schiffneriolejeunea polycarpa* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

Acrolejeunea pappeana (Nees) Schiffn., Hedwigia 33: 182 (1894) = *Schiffneriolejeunea pappeana* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

Acrolejeunea parviloba (Steph.) Bonner, Index Hep. 1,2: 20 (1962) =

- Schiffneriolejeunea parviloba* (Steph.) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)
- Acrolejeunea peradeniensis* (Mitt.) Schiffn., Consp.Hep.Arch.Ind.: 286 (1898) = *Schiffneriolejeunea*
- Acrolejeunea polycarpa* (Nees) Schiffn., in Engl. & Prantl, Nat.Pfl.-fam. I, 3(1): 128 (1893) = *Schiffneriolejeunea polycarpa* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)
- Acrolejeunea pulopenangensis* (Gott.) Schiffn., Hedwigia 33: 184 (1894) = *Schiffneriolejeunea pulopenangensis* (Gott.) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)
- Acrolejeunea rechingeri* Steph., Denkschr.Akad.Wiss.Wien Math.Nat.Kl. 85: 195 (1910) = *Schiffneriolejeunea*
- Acrolejeunea roccatii* Gola, Annali di Bot. 6: 275 (1907) = *Evansiolejeunea roccatii* (Gola) VandenBerghen, Bull.Soc.Bot.Belg. 92: 117 (1960) (*Omphalanthus roccatii* (Gola) Schust., Nova Hedwigia Beih. 9: 96 (1963)).
Typus in TO !
- Acrolejeunea rostrata* (Schiffn.) Bonner var. *major* (Schiffn.) Bonner, Index Hep. 1,2: 22 (1962) = *Schiffneriolejeunea pulopenangensis* (Gott.) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)
- Acrolejeunea saccatula* Steph. ex Bonner, Index Hep. 1,2: 22 (1962) nom.nud. = *Trocholejeunea infuscata* (Mitt.) Verd., fide Verdoorn (1934c): 191, 192.
- Ptychocoleus saccatus* (Mitt.) Steph., Spec. Hep. 5: 53 (1912) syn.nov. (Typus in NY!) = *Trocholejeunea infuscata* (Mitt.) Verd., Ann.Bryol.Suppl. 4: 190 (1934)
- Acrolejeunea setacea* Steph., Bot.Jahrb. 23: 311 (1896) = *Schiffneriolejeunea*
- Ptychocoleus torulosus* fo. *parvistipulus* Herz. Rev.Bryol.Lichénol. 20: 135 (1951) = *Brachiolejeunea* (subg. *Plicolejeunea*)
- Acrolejeunea trigona* Steph. ex Bonner, Index Hep. 1,2: 24 (1962) = *Mastigo-*

Lejeunea trigona Steph. = *Mastigolejeunea carinata* (Mitt.) Steph., Spec. Hep. 4: 759 (1912) fide VandenBerghen, Bull.Jard.Bot.Belg. 19: 378 (1949)

Acrolejeunea tumida (Nees) Schiffn., Hedwigia 33: 185 (1894) = *Schiffneriolejeunea tumida* (Nees) Gradst., J. Hattori Bot.Lab. 38: 335 (1974)

TYPES NOT AVAILABLE FOR THIS STUDY

Lejeunea (subg. *Acrolejeunea*) *abnormis* (Gott.) Steph., Bull.Soc.Roy.Bot. Belg. 32: 119 (1894).

Phragmicoma abnormis Gott., Abh.Nat.Ver.Bremen 7: 352 (1882).

Ptychocoleus (?) *abnormis* (Gott.) Steph., Spec.Hep. 5: 32 (1912).

Typus: Madagascar, "Aliis *Lejeunias* inhaerentem legit Dr. Rutenberg stirpem sterilem in silva Ambatondrazaka" (B, destroyed 1945).

Judging from the original description this species (and *L. inflexa*!) should be excluded from *Acrolejeunea*.

Acrolejeunea comptonii Pears., J.Linn.Soc. 46: 33 (1922).

Typus: New Caledonia, Compton 616.

The type material was not available in Manchester (hb. Pearson) or other herbaria. Judging from the original description this might be a species of *Mastigolejeunea*.

Lejeunea (subg. *Acrolejeunea*) *fulva* (Gott.) Steph., Hedwigia 29: 10 (1890) comb.illeg., non Spruce (1884: 237).

Phragmicoma fulva Gott., Abh.Nat.Ver.Bremen 7: 550 (1882).

Ptychocoleus fulvus (Gott.) Steph., Spec.Hep. 5: 29 (1912).

Typus: Madagascar, Rutenberg s.n. (B, destroyed 1945).

Several herbaria have collections from Madagascar (leg. Borgen) labelled "*Phragmicoma fulva* G." and re-determined by STEPHANI as "*Acrolejeunea borgenii* sp. nov.". These plants belong to *Schiffneriolejeunea pappeana* (Nees) Gradst. According to STEPHANI (1890: 10) *Phragmicoma fulva* Gott. is very different from *S. pappeana*. In his original description GOTTSCHKE compared *Phr. fulva* with *Schiffneriolejeunea polycarpa* (Nees) Gradst.

Lejeunea (subg. *Acrolejeunea*) *inflexa* (Gott.) Steph.,
Bull.Soc.Roy.Bot.Belg. 32: 119 (1894) comb.illeg., non Hampe in Lehm.
(1838: 22).

Phragmicoma inflexa Gott., Abh.Nat.Ver.Bremen 7: 351 (1882).

Ptychocoleus inflexus (Gott.) Steph., Spec.Hep. 5: 33 (1912).

Typus: Madagascar, "Aliis *Lejeunias* inhaerentem legit Dr. Rutenberg
sterilem in silva Ambatondrazaka" (B, destroyed 1945).

To be excluded from *Acrolejeunea* (see *L.abnormis*).

Ptychocoleus (?) *planiusculus* (Mitt.) Verd., Ann.Bryol.Suppl. 4: 126 (1934).

Lejeunea planiuscula Mitt., J.Proc.Linn.Soc.Bot. 5: 111 (1861).

Archilejeunea (?) *planiuscula* (Mitt.) Steph., Spec.Hep. 4: 731 (1911).

Typus: Birma, "Pegu ad Rangoon, inter *L. unguatae* et *Meteorii squarrosi*
caespites, M'Clelland" s.n.

The type material was not available in New York (hb. Mitten) or other
herbaria. Judging from the original description this might be *Schiffner-*
iolejeunea tumida (Nees) Gradst.

Ptychocoleus reflexus Winkler, Rev.Bryol.Lichénol. 35: 329 (1968).

Typus: S.Salvador, S.Winkler B/6/d8, 23.V.1962.

The type material was unfortunately not sent on loan. Judging from the
original description this species should be excluded from *Acrolejeunea*.

Ptychocoleus subfalcatus Herz., in Standley, Field Mus.Nat.Hist.Bot. 10:
61 (1931) nom.nud.

= ? Material nowhere available.

II

AN ARRANGEMENT OF THE GENERA OF PTYCHANTHOIDEAE

1. Circumscription of the Ptychanthoideae

This part deals with the taxonomy of a group of genera traditionally named "holostipous Lejeuneaceae". The genus *Acrolejeunea* is one of them.

The concept of holostipous Lejeuneaceae goes back to SPRUCE (1884), who placed his subgenera of *Lejeunea* in two groups: *Holostipae* and *Schizostipae*. *Holostipae* contained species with undivided underleaves, whereas *Schizostipae* contained species with bifid underleaves. EVANS (1935) and SCHUSTER (1955) showed that both groups also differ in the structure of the stem, which in *Holostipae* is usually robust and has 10 or more rows of cortical cells (4 of which constitute the ventral merophyte), whereas in *Schizostipae* the stem is thinner and has only 7 rows of cortical cells (2 of which constitute the ventral merophyte).

Holostipae and *Schizostipae* - variously considered subtribes, tribes, or subfamilies of Lejeuneaceae - were not sharply defined by these characters, and consequently opinions differed as to the position of some genera (see Table II). Of c. 90 genera currently accepted in the family Lejeuneaceae Casares Gil (GROLLE 1973), c. 30 have been attributed to the *Holostipae* in recent reviews (BISCHLER 1965, SCHUSTER 1963, 1966). They are listed in Table II.

The subdivision of Lejeuneaceae was fundamentally improved by MIZUTANI (1961). In contrast with previous authors he laid more emphasis on characters of the sporophyte and showed that *Holostipae* and *Schizostipae* are sharply different by the structure of the seta, the capsule-wall thickenings, and the elaters. He treated the two groups as separate subfamilies, which he more appropriately named Ptychanthoideae Mizut. (= *Holostipae*) and Lejeuneoideae Massal.^x (= *Schizostipae*).

The differences between Ptychanthoideae and Lejeuneoideae are shown in Table III, which is adapted from the key given by MIZUTANI (1961: 135). Characters of the underleaf, the branching type, the inner cells of the capsule wall and the sporeling are added on the basis of descriptions by MIZUTANI and others. The difference in sporeling-pattern given in the table (fide NEHIRA 1974) is tentative, because in many genera the sporeling is still unknown. Probably the most fundamental difference is the structure of the seta, which has 16 outer longitudinal rows of cells in Ptychanthoideae and only 12 rows in Lejeuneoideae. It should be noted that this difference was already discussed in detail by SPRUCE (1884: 69), but was usually ignored by later authors.

(x) author citation follows GROLLE (1964: 225)

BISCHLER (1965) and SCHUSTER (1963, 1966):

Anoplolejeunea (Spruce) Schiffn. 1893
Archilejeunea (Spruce) Schiffn. 1893
Brachiolejeunea (Spruce) Schiffn. 1893
Bryopteris (Nees) Lindenb. 1845
Cardiolejeunea Schust. & Kachroo 1963
Caudalejeunea (Steph.) Schiffn. 1893
Dicranolejeunea (Spruce) Schiffn. 1893
Evansiolejeunea VandenB. 1948 (= Omphalanthus subg. Evansio-
lejeunea (VandenB.) Schust. 1963)
Leucolejeunea Evans 1907
Lopholejeunea (Spruce) Schiffn. 1893
Marchesia S.F. Gray 1821
Mastigolejeunea (Spruce) Schiffn. 1893
Neurolejeunea (Spruce) Schiffn. 1893
Omphalanthus Lindenb. 1845
Peltolejeunea (Spruce) Schiffn. 1893 (= Omphalanthus subg.
Peltolejeunea (Spruce) Schust. 1963)
Phragmolejeunea Schust. 1954 (= Schiffneriolejeunea Verd.
fide Gradstein 1974a)
Ptychanthus Nees 1838
Ptychocoleus auct. non Trev. 1877 (= Acrolejeunea (Spruce)
Schiffn. fide Gradstein 1974 a)
Schiffneriolejeunea Verd. 1933
Spruceanthus Verd. 1934
Stictolejeunea (Spruce) Schiffn. 1893
Symbiezidium Trev. 1877
Thysananthus Lindenb. 1844
Trocholejeunea Schiffn. 1932 (= Brachiolejeunea subg.
Trocholejeunea (Schiffn.) Schust. 1963)
Tuzibeanthus Hatt. 1947

BISCHLER (1965):

Cyclolejeunea Evans 1904 (SCHUSTER 1966: Schizostipae)
Echinolejeunea Schust. 1963 (SCHUSTER 1966: Schizostipae)
Heterolejeunea Schiffn. 1941 ----
Odontolejeunea (Spruce) Schiffn. 1893 (SCHUSTER 1966: Schizostipae)

SCHUSTER (1966):

Blepharolejeunea Arnell 1962 (BISCHLER 1967: Schizostipae)

Genera attributed to Holostipae after 1966:

Acanthocoleus Schust. 1970

Phaeolejeunea Mizut. 1968

TABLE II: Genera attributed to Holostipae in recent publications.

Underlined are the genera which MIZUTANI (1961, 1969) assigned to
Ptychanthoideae.

PTYCHANTHOIDEAE Mizut.

(= *Holostipae* s.str.)

- underleaves undivided
- cortical cells in 10-50 longitudinal rows
- branching *Frullania*-type, *Lejeunea*-type or *Radula*-type
- male bracteoles present throughout the spike (except in *Symbiezidium*)
- seta with at least 16 outer longitudinal rows of cells
- capsule valves + recurved after dehiscence
- outer cells of the capsule wall with nodulose trigones, inner cells covered by an orange-brown fenestrate sheath of thickening
- elaters with 1 or 2 spiral bands
- sporeling globose (*Lopholejeunea*-type) or unistratose (*Stictolejeunea*-type)

LEJEUNEOIDEAE Massal.

(= *Schizostipae* s.str. + *Holostipae* p.p.)

- underleaves bifid or undivided
- cortical cells usually in 7 longitudinal rows; sometimes more numerous
- branching *Lejeunea*-type or *Radula*-type
- male bracteoles limited to the base of the spike or absent
- seta with 12 outer longitudinal rows of cells
- capsule valves not recurved after dehiscence
- outer cells of the capsule wall almost thin-walled, inner cells with pale trigones and intermediate thickenings
- elaters without spiral bands
- sporeling cylindrical (*Leucolejeunea*-type) or unistratose (*Lejeunea*-type)

TABLE III : Differences between Ptychanthoideae Mizut. and Lejeuneoideae Massal. (revised after MIZUTANI 1961).

Since MIZUTANI (l.c.) dealt primarily with Japanese Lejeuneaceae, his study concerns 12 genera of *Holostipae* (underlined in Table II). He placed them all in Ptychanthoideae except for *Leucolejeunea*, which was proved to have a Lejeuneoid sporophyte and was consequently placed in Lejeuneoideae. In a more recent publication (MIZUTANI 1969) he also placed *Caudalejeunea* and *Schiffneriolejeunea* (= *Ptychocoleus* p.p.) in Ptychanthoideae. All genera treated were known by their sporophyte except for *Tuzibeanthus*. The close gametophytic relationship between *Ptychanthus* and *Tuzibeanthus* leaves indeed little doubt about it that the latter genus belongs to Ptychanthoideae.

The present study aims at providing an arrangement of all the genera of Ptychanthoideae presently known. To achieve this, I had to determine the taxonomic

position of those holostipous genera which were not yet attached to MIZUTANI's subfamilies. I have been particularly anxious to get hold of material with sporophytes, but failed in some 10 genera. These genera consequently had to be classified by means of gametophytic characters. The results are the following ("1" etc. refers to notes given below):

a. Ptychanthoid sporophyte (→Ptychanthoideae)

Odontolejeunea

b. Lejeuneoid sporophyte (→Lejeuneoideae)

*Anoplolejeunea*¹⁾, *Omphalanthus*²⁾

c. Frullanioid sporophyte (→Bryopteridoideae)

*Bryopteris*³⁾

d. Sporophyte unknown

1. Ptychanthoideae:

*Acanthocoleus*⁴⁾ (= *Dicranolejeunea* ?), *Heterolejeunea*⁵⁾, (= *Spruceanthus* ?), *Marchesia*, *Neurolejeunea* (?), *Phaeolejeunea*, *Stictolejeunea* (?), *Symbiezidium*.

2. Lejeuneoideae:

*Cardiolejeunea*⁶⁾, *Evansiolejeunea*²⁾, *Peltolejeunea*²⁾, *Cyclolejeunea*⁶⁾, *Echinolejeunea*⁶⁾

3. position doubtful:

Blepharolejeunea

The subfamily Ptychanthoideae Mizut. as presently conceived contains 19 genera (see Table IV). In the Tables I have included the two subgenera of *Brachiolejeunea* as well, because these groups, of which I have started a revision, might prove different enough to be treated as separate genera.

Since the structure of the sporophyte is conclusive for the inclusion of taxa in this subfamily, and effort should be made to detect and describe the sporophyte in those genera in which it is still unknown. This holds in particular for *Stictolejeunea* and *Neurolejeunea*, which by their ocelli and by their almost evenly thickened cell walls stand somewhat isolated in the Ptychanthoideae.

Notes :

1) In fresh material of *Anoplolejeunea conferta* (Meissn.) Evans from Colombia (Florschütz 4485a, I. 1975) I found a Lejeuneoid sporophyte, and 25-50 minute, homogeneous oil bodies per leaf cell, each oil body measuring $3-4 \times 1,5-2$ μ m. Apparently *Anoplolejeunea* has the largest number of oil bodies per cell in the family.

2) *Omphalanthus*, *Evansiolejeunea* and *Peltolejeunea* have generally been considered bona fide members of Holostipae, although SCHUSTER (1963) suggested a close affinity to *Leucolejeunea* (Lejeuneoideae). My study of several fresh collections of *Omphalanthus* sp. from South America, one of them with sporophytes (Brazil, Mt. Itatiaia, Vital s.n., IX. 1974), revealed that this genus has a Lejeuneoid sporophyte and a *Leucolejeunea*-type sporeling, which leaves no doubt about its belonging in the Lejeuneoideae. The oil bodies of *Omphalanthus* are large, 1-4 per leaf cell, and coarsely granulose. By these and other gametophytic characters (nodulose trigones, absence of intermediate thickenings, reduced apical tooth) *Omphalanthus*, with its satellite genera *Evansiolejeunea* and *Peltolejeunea*, indeed closely resembles *Leucolejeunea* and *Cheilolejeunea* s.l.. I believe these genera to form a separate, primitive group within the Lejeuneoideae.

3) In their outstanding monograph of the genus *Bryopteris*, STOTLER & CRANDALL-STOTLER (1974), showed that this genus is fundamentally different from other holostipous Lejeuneaceae. Diagnostic differences are the leaf lobule, which is attached to the stem by only 3-7 cells and has no leaf brace cells, the presence of *Bryopteris*-type branches and the virtual absence of *Lejeunea*-type branches, the heavier seta and foot, and the *Frullania*-type sporeling. In the branching-type, sporophyte, and sporeling the genus closely resembles *Frullania* (Frullaniaceae Lorch). A new family Bryopteridaceae Stotl. was proposed, which was placed more closely to the Frullaniaceae than to the Lejeuneaceae.

The taxonomic position of *Bryopteris* might be compared with the position of *Jubula*. Both genera are more or less intermediate between Frullaniaceae and Lejeuneaceae, and have been connected with either group in the past. Their position depends on the definition of these families. For most authors (e.g. SCHUSTER 1963, GROLLE 1973) the gametophytic differences (lobule!) are conclusive. This would classify *Jubula* with *Frullania*, and *Bryopteris* with the Lejeuneaceae. For some authors (MIZUTANI 1961) the sporophytic differences (seta!) are more essential. This would put *Jubula* in the Lejeuneaceae and

Bryopteris in the Frullaniaceae. Both classifications seem to have merits of their own.

However, if we accept a separate family Bryopteridaceae, a sharp definition of Frullaniaceae and Lejeuneaceae can no longer be given with our present knowledge of these groups. Following the more generally accepted definition of Lejeuneaceae, as characterized by the structure of the lobule, I therefore propose to keep *Bryopteris* within the Lejeuneaceae and to establish a separate subfamily for its accommodation: Bryopteridoideae (Stotl.) Gradst. comb. nov. (Bryopteridaceae Stotl., Bryophyt. Biblioth. 3: 57, 1974; type-genus: *Bryopteris* (Nees) Lindenb.).

It should be noted that *Trocholejeunea sandvicensis* (Gott.) Mizut. apparently bridges the sporophytic differences between Ptychanthoideae and Bryopteridoideae, having a seta similar to the seta reported in *Bryopteris trinitensis* (MIZUTANI 1961: fig. XI, 31; STOTLER & CRANDALL-STOTLER 1974, fig. 71A), and a sporeling which closely resembles the *Frullania*-type sporeling (INOUE 1958).

4) The monotypic genus *Acanthocoleus* Schust. (*A. fulvus* Schust. from Dominica) was placed by its author next to *Lopholejeunea*, from which it was said to differ by 1) presence of *Frullania*-type branching and a subfloral innovation, 2) sharply pointed, fulvous (not fuscous) leaves, 3) (4-) 5-keeled perianth, 4) relatively small female bracts, 5) two lobule teeth, 6) 10-25 segmented oil bodies per leaf cell. Except for the perianth and the oil bodies, the same characters serve to distinguish *Dicranolejeunea* from *Lopholejeunea*.

The similarity of *Acanthocoleus* and *Dicranolejeunea* is further demonstrated by the 2-cells wide ventral merophyte and the sometimes weakly cordate trigones in *Acanthocoleus*. The oil bodies of *Acanthocoleus* are somewhat peculiar, because all genera of Ptychanthoideae with more than 10 oil bodies per cell (including *Lopholejeunea* and *Dicranolejeunea*) have homogeneous oil bodies. A closer study of the type material should reveal whether *Acanthocoleus* should be reduced to synonymy under *Dicranolejeunea* or not.

5) The monotypic genus *Heterolejeunea* Schiffn. (*H. javanica* Schiffn. from Java) was established for a species growing on rocks in rivers in lowland areas of Java. The widely spatiated leaves and underleaves, the rudimentary lobule, the minute trigones, and the recurved apex of the underleaf are typical morphological expressions of hygrophytic plants. Similar modifications are often seen in *Archilejeunea* and *Spruceanthus*. Judging from the original description and

1. Stem leaves when dry suberect-convoluted (+) or widely spreading (-)	
2. Leaf cells elongated (+) or isodiametric (-)	
3. Trigones cordate (+) or simple-triangular to radiate (-)	
4. Plant with blackish secondary pigmentation (+) or without (-)	
5. Dorsal cortical cells larger (+) or not larger (-) than the medullary cells . .	
6. Oil bodies segmented (+) or homogeneous (-)	
7. Perianth with 2-5 ventral plicae (+) or with 0-1(-2) ventral plicae (-)	
8. Branching predominantly <i>Frullania</i> -type (+) or <i>Lejeunea</i> -type (-)	
9. Seta non-articulate (+) or articulate (-)	
10. Male bracts epistatic (+) or hypostatic (-)	
11. Ventral merophyte at least 4 cells wide (+) or 2-4 cells wide (-)	
12. Disciform gemmae present (+) or absent (-)	
13. Ocelli present (+) or absent (-)	
14. Innovations present (+) or absent (-)	
15. Sporeling <i>Lopholejeunea</i> -type (+) or <i>Stictolejeunea</i> -type (-)	

Table IV : Generic classification of Ptychanthoideae

[illegible]

illustration *Heterolejeunea javanica* is indeed very similar to *Archilejeunea subaloba* Herz. from Borneo, which is a synonym of *Spruceanthus marianus* (Gott.) Mizut. (fide VERDOORN 1934c:49). SCHUSTER (1963) and BISCHLER (1965) noted that the type material of *Heterolejeunea* is lost, and SCHUSTER (l.c.: 55) suggested to suppress the genus as inadequately founded. I would rather propose to reduce *Heterolejeunea* to synonymy under *Spruceanthus*, with a question mark.

6) *Cardiolejeunea*, *Cyclolejeunea*, and *Echinolejeunea* most probably belong in the Lejeuneoideae because of their thin stem, which has only 7 rows of cortical cells (BISCHLER 1965).

2. Generic classification

The genera of Ptychanthoideae have been arranged here in 7 genus complexes (see Synopsis). A "genus complex" is an informal taxonomic category, which was introduced in the system of Lejeuneaceae by SCHUSTER (1963) for small, natural groups of genera, which might eventually be given formal names (tribe, series) when knowledge of the taxonomy of the family increases. Considering our present knowledge I believe this category is indeed most suitable for expressing natural relationships between the almost countless number of genera presently distinguished in the family.

I have grouped the genus complexes of Ptychanthoideae in two tribes, which are the main subdivisions of this subfamily: tribe Ptychantheae and tribe Archilejeuneae.

The characters relevant for the delimitation of the groups are shown in Table IV. For a morphological discussion of these characters the reader is referred to Part I of this work. The taxonomic evaluation presented here was primarily based on examination of specimens, but data from relevant literature were incorporated as well, e.g. EVANS (1907-08), MIZUTANI (1961), SCHUSTER (1963) and BISCHLER (1965). Data on sporeling-types were taken from FULFORD (1956) and NEHIRA (1974). Valuable data on branch morphology of the genera were provided by CRANDALL (1969). Some generic characters discussed in Part I are still too poorly known to be included in this evaluation, e.g. the under-leaf base structure and the first leafy appendage of the *Frullania*-type branch.

Future research should focus on these characters.

The tribes are distinguished by three correlated characters: 1) trigone shape, 2) cell shape and arrangement, and 3) leaf position.

The importance of trigone shape for the taxonomy of liverworts was convincingly demonstrated in *Plagiochila* by CARL (1931). He distinguished 6 different trigone types, which served to delimit the sections of this notoriously difficult genus. In Lejeuneaceae variation in trigone shape was noted by EVANS (1907-08), BENEDIX (1953), JONES (1958), SCHUSTER (1963) and VANDENBERGHEN (1972), but in classifications this character was used only in a very limited way. SCHUSTER (l.c.) employed it to circumscribe some of his genus complexes.

In a very early phase of my work on *Acrolejeunea* I was struck by the fact that species of this genus have distinctly cordate or semicordate trigones in their leaves (Pl. I). Scrutinizing the genera of Lejeuneaceae for their trigones, I found that cordate (and semicordate) trigones occur in leaves of *Acrolejeunea*, *Trocholejeunea*, *Brachiolejeunea*, *Caudalejeunea*, *Schiffneriolejeunea*, *Mastigolejeunea*, *Thysananthus* and *Ptychanthus* (Pl. XXIII: 1-8). These genera presently constitute the tribe Ptychantheae.

In *Schiffneriolejeunea*, *Mastigolejeunea*, *Thysananthus* and *Ptychanthus* (*Ptychanthus*-complex) the trigones sometimes become large and almost confluent, but the original heart-shape is usually still visible in younger leaves or locally in older leaves (Pl. XXIII:1,2,5). Asiatic collections of *Ptychanthus striatus* usually have almost orbicular and somewhat radiate trigones (cf. MIZUTANI 1961: fig. V,5), but in African collections of the same species I found smaller, distinctly cordate trigones (cf. VANDENBERGHEN 1972: 92).

In *Caudalejeunea* (*Caudalejeunea*-complex) two types of cells and trigones are found: 1) large leaf cells, which have 2-4 intermediate thickenings on longer walls and trigones with 2 convex sides and 1 straight side; 2) small leaf cells, which have only one intermediate thickening on longer walls and more or less distinctly cordate trigones. In *C. cristiloba* both types of cells and trigones occur in different kinds of leaves: specialized gemmiferous leaves have the large cell type, whereas the unspecialized leaves and bracts have the small cell type (GRADSTEIN 1974b). This is probably also true in *C. dusenii* and *C. yangambiensis*.

All other genera of Ptychanthoideae, constituting the tribe Archilejeuneae, have trigones which are basically triangular with straight or equally bulging sides (Pl. XXIII:9-19). Often the trigones are elongated along the adjacent cell walls ("radiate"). The tribe has four genus complexes, which somewhat

differ by their trigones. The *Archilejeunea*-complex has simple to radiate trigones with rather short and wide rays, whereas in the *Lopholejeunea*-complex the rays, if present, are long and narrow. In the *Dicranolejeunea*-complex the trigones are never radiate, but sometimes they are weakly cordate, which is the reason why I first tentatively placed *Dicranolejeunea* in the Ptychantheae (GRADSTEIN 1974c). I now believe that this genus is better placed in Archilejeuneae next to *Odontolejeunea* because of its leaves, which are spreading when dry, and because of its isodiametric cells (see below). In the *Stictolejeunea*-complex, finally, the cell walls tend to become evenly thickened, obscuring the trigones.

In Ptychanthoideae trigone shape is apparently correlated with cell shape, cell arrangement and leaf position. Leaves with cordate trigones (Ptychantheae) are suberect and more or less convoluted when dry, but when wetted they spread out widely and become squarrose in several genera (*Acrolejeunea*, *Mastigolejeunea*, e.o.). They have cells which are longer than wide in the lobe and arranged in more or less diverging rows. The diverging pattern is particularly distinct in leaves with strongly elongated lobe cells, as in *Mastigolejeunea* and *Thysananthus*.

Leaves which do not have cordate trigones (Archilejeuneae) are usually spreading both in the dry and in the wet state. They may be somewhat involuted when dry, though, particularly in *Dicranolejeunea*, *Odontolejeunea* and *Spruceanthus*. The cells of the lobe as a rule are isodiametric and consequently they are not arranged in diverging rows.

With respect to other characters listed in Table IV, I would like to make some remarks on the oil bodies (Pl. XXIII) and on the seta.

Oil bodies are presently known in all genera of Ptychanthoideae, except in *Phaeolejeunea* and *Symbiezidium*. In *Brachiolejeunea* subg. *Brachiolej.*, which has homogeneous oil bodies, they are reported here for the first time (fide *Br. laxifolia*, Cleef 398b, Colombia)

One should be careful with observations on oil bodies in dried material (if present!), because homogeneous oil bodies tend to become segmented upon degeneration, whereas segmented oil bodies become almost homogeneous before falling apart. This observation was confirmed by JONES, who kindly informed me that in *Archilejeunea* "It is the simple oil bodies that are degenerate; fresh plants have compound oil bodies" (letter of 14.X.1974). In *Archilejeunea* JONES found segmented oil bodies in *A. linguaeifolia*, *A. abbreviata*, and *A. autoica*

from Africa. I found segmented oil bodies in *A. cf. parviloba* from Suriname (Mc. Gillavry s.n., obs. fide A. Luiting). Previously this genus was stated to have homogeneous oil bodies (SCHUSTER & HATTORI 1954), which statement was based on observations of the oil bodies in *A. kiushiana* from Japan. Since homogeneous oil bodies are present in the closely related Indo-Pacific genus *Spruceanthus* it is possible that *A. kiushiana* should in fact be referred to the latter genus.

The presence of an articulate or non-articulate seta is presently the only sporophytic character which has diagnostic value for circumscribing genera of Ptychanthoideae. I may report here that it serves to distinguish between *Acrolejeunea* and *Schiffneriolejeunea*, which were previously distinguished only by gametophytic characters (GRADSTEIN 1974a). In the meantime I found that *Schiffneriolejeunea* has an articulate seta, whereas in *Acrolejeunea* the seta is always non-articulate.

3. Synopsis

PTYCHANTHOIDEAE Mizut. (Table IV, VI, VII; Pl. XXIII, XXIV)

I Tribus PTYCHANTHEAE emend.

Stem leaves when dry + convoluted and suberect (except in *Caudalejeunea*), when moist widely spreading. Lobe cells elongated, + arranged in diverging rows. Trigones cordate (or semicordate). Sporeling *Lopholejeunea*-type.

1. Ptychanthus-complex

Dorsal cortical cells usually not larger than medullary cells (larger in *Schiffneriolejeunea*). Oil bodies segmented. Disciform gemmae absent. Male bracts hypostatic, rarely epistatic (in some species of *Thysananthus*). Seta articulate or non-articulate.

- (1) *Ptychanthus* Nees
- (2) *Thysananthus* Lindenb.
- (3) *Mastigolejeunea* (Spruce) Schiffn.
- (4) *Schiffneriolejeunea* Verd.

2. Brachiolejeunea-complex

Dorsal cortical cells larger than medullary cells. Oil bodies homogeneous.

Disciform gemmae absent. Male bracts epistatic. Seta non-articulate.

(5) *Brachiolejeunea* (Spruce) Schiffn.

a. subg. *Brachiolejeunea*

b. subg. *Plicolejeunea* Schust. (= *Frullanoides* Raddi).

(6) *Trocholejeunea* Schiffn.

(7) *Acrolejeunea* (Spruce) Schiffn.

3. Caudalejeunea-complex

Dorsal cortical cells larger than medullary cells. Oil bodies homogeneous.

Disciform gemmae present. Male bracts hypostatic. Seta non-articulate.

(Leaf cells small or large, when large cell-walls with 2-4 intermediate thickenings and leaves widely spreading when dry)

(8) *Caudalejeunea* (Steph.) Schiffn.

II Tribus ARCHILEJEUNEAE Gradst. trib. nov.

Folia caulina in sicco late patula, plana vel deflexa, haud suberecto-convolutiva. Cellulae loborum isodiametrae, trigonis haud cordatis.

Type-genus: *Archilejeunea* (Spruce) Schiffn.

Stem leaves when dry widely spreading, flat or involuted. Lobe cells isodiametrical. Trigones simple-triangular with straight or equally bulging sides, or radiate, rarely weakly cordate (*Dicranolejeunea*). Sporeling *Lopholejeunea*-type or *Stictolejeunea*-type.

4. Archilejeunea-complex

Plants without blackish secondary pigmentation. Dorsal cortical cells not larger than medullary cells (except in *Phaeolejeunea*). Trigones simple or radiate with short and wide rays. Oil bodies segmented or homogeneous. Ocelli absent. Male bracts hypostatic. Perianth with 2-5 ventral plicae.

(9) *Tuxibeanthus* Hatt.

(10) *Archilejeunea* (Spruce) Schiffn.

(11) *Spruceanthus* Verd.

(12) *Phaeolejeunea* Mizut.

5. Lopholejeunea-complex

Plants usually with blackish secondary pigmentation. Dorsal cortical cells larger than medullary cells. Trigones simple or radiate with long and narrow rays. Oil bodies homogeneous. Ocelli absent. Male bracts hypostatic. Perianth with 0-2 ventral plicae.

(13) *Marchesia* S.F. Gray

(14) *Lopholejeunea* (Spruce) Schiffn.

(15) *Symbiesidium* Trev.

6. Dicranolejeunea-complex

Plants without blackish secondary pigmentation. Dorsal cortical cells larger

than medullary cells. Trigones simple, sometimes weakly cordate. Oil bodies homogeneous. Ocelli absent. Male bracts epistatic. Perianth with 0-1 (-2?) ventral plicae. (Ventral merophyte 2-4 cells wide).

(16) *Dicranolejeunea* (Spruce) Schiffn.

(17) *Odontolejeunea* (Spruce) Schiffn.

7. *Stictolejeunea*-complex (sporophyte unknown !)

Plants with or without blackish secondary pigmentation. Dorsal cortical cells not larger than medullary cells. Trigones simple, or indistinct when cell walls almost evenly thickened. Oil bodies finely segmented. Ocell usually present. Male bracts hypostatic. Perianth without ventral plicae.

(18) *Stictolejeunea* (Spruce) Schiffn.

(19) *Neurolejeunea* (Spruce) Schiffn.

4. Concluding remarks

Though based on several new taxonomic principles, the generic arrangement given here is not essentially different from other recent arrangements. This might indicate that my generic classification reflects natural relationships. In Table V the present arrangement is compared with the arrangements by MIZUTANI (1961) and SCHUSTER (1963). The recent treatment of the *Holostipas* by BISCHLER (1965) could not be taken into account, because she lists the genera alphabetically.

In MIZUTANI's arrangement (l.c.: 146-147) - which includes only 11 (Japanese) genera in Ptychanthoideae - the genera are placed singly (*Archilejeunea*, *Spruceanthus*) or in pairs. In SCHUSTER's arrangement the genera presently assigned to Ptychanthoideae are grouped in 12 genus complexes. SCHUSTER's genus complexes are smaller than mine, and usually they consist of only one or two genera.

Differences between the three arrangements are obvious from Table V. Noteworthy is the difference in the position of the genus *Tuxibeanthus*. I agree with MIZUTANI & HATTORI (1967) that this genus is related to *Ptychanthus*, and that SCHUSTER's placing this genus as a subgenus in *Mastigolejeunea* is an error. However, because of its flat, spreading leaves (dry and wet) and its isodiametric cells with triangular-radiate trigones, the genus should go into *Archilejeuneae*, in which it shows relationship to *Archilejeunea* and *Spruceanthus*. Therefore I have placed *Tuxibeanthus* in the *Archilejeunea*-complex, where it links the

MIZUTANI (1961)	SCHUSTER (1963)	GRADSTEIN (1975)
<i>Ptychanthus</i> <i>Tusibeanthus</i>	<i>Ptychanthus</i> <i>Mastigolej.</i> (+ <i>Tusibeanthus</i>)	1. <i>Ptychanthus</i> <i>Thysananthus</i> <i>Mastigolej.</i> <i>Schiffneriolej.</i> (+ <i>Phragmillej.</i>)
<i>Thysananthus</i> <i>Mastigolej.</i>	<i>Thysananthus</i> <i>Schiffneriolej.</i> <i>Phragmillej.</i>	
<i>Brachiolej.</i> (+ <i>Trocholej.</i>) <i>Ptychocoleus</i>	<i>Brachiolej.</i> (+ <i>Trocholej.</i>) <i>Ptychocoleus</i>	2. <i>Brachiolej.</i> <i>Trocholej.</i> <i>Acrolej.</i> (= <i>Ptychocoleus</i> p.p.)
	<i>Caudalej.</i> <i>Bryopteris</i>	3. <i>Caudalej.</i>
<i>Spruceanthus</i>	<i>Spruceanthus</i>	4. <i>Tusibeanthus</i> <i>Archilej.</i> <i>Spruceanthus</i> <i>Phaeolej.</i> (?)
<i>Archilej.</i>	<i>Archilej.</i>	5. <i>Marchesinia</i> <i>Lopholej.</i> <i>Symbiezidium</i>
	<i>Marchesinia</i>	
	<i>Symbiezidium</i>	
<i>Lopholej.</i> <i>Dicranolej.</i>	<i>Lopholej.</i>	6. <i>Dicranolej.</i> <i>Odontolej.</i>
	<i>Dicranolej.</i> <i>Odontolej.</i> <i>Cyclolej.</i>	7. <i>Stictolej.</i> <i>Neurolej.</i> <i>Cardiolej.</i>

Table V: Comparison of recent arrangements of the genera of Ptychanthoideae. *Bryopteris*, *Cardiolej.* and *Cyclolej.* (SCHUSTER 1963) do not belong in this subfamily.

the *Archilejeunea*-complex to the *Ptychanthus*-complex.

In the linear arrangement of the genera in Table IV the relationship between *Ptychanthus* and *Tusibeanthus* could not be expressed, but a phenetic diagram as drawn earlier for *Acrolejeunea* shows it clearly (Pl. XXIV). In this chart the size of the discs correlates with the estimated number of species in each genus (Table VI). The geographic distribution of the genera, as far as presently known (Table VII), is indicated as well. Continuous lines indicate relationships between genera belonging to a single genus complex, whereas re-

relationships between genus complexes are shown by broken lines.

As yet the relationships between the genus complexes in Archilejeuneae are more difficult to trace than in Ptychantheae. Some genera (*Phaeolejeunea*, *Stictolejeunea*, *Neurolejeunea*) are still difficult to place. Subsequent taxonomic studies of the genera of Ptychanthoideae -none of which has been monographed before (!)- may throw more light on those matters we are still in the dark about.

	SCHIFFNER	STEPHANI	GRADSTEIN ^{*)}
	1893	1911-13	1975
<i>Acrolejeunea</i>	38 spp.	85 spp. ¹⁾	15 spp.
<i>Archilejeunea</i>	30	70	10-20
<i>Brachiolejeunea</i>	23	65	
subg. <i>Brachiolej.</i>			1-4
subg. <i>Plicolej.</i>			5-10
<i>Caudalejeunea</i>	8	16	10-15
<i>Dicranolejeunea</i>	12	28	10-15
<i>Lopholejeunea</i>	27	74	15-25
<i>Marchesinia</i>	16 ²⁾	26	5-10
<i>Mastigolejeunea</i>	31	55	c. 10
<i>Neurolejeunea</i>	3	5	3
<i>Odontolejeunea</i>	18	22	3-5
<i>Phaeolejeunea</i>	-	- ³⁾	2-3
<i>Ptychanthus</i>	20	27	2-3
<i>Schiffneriolejeunea</i>	- ⁴⁾	- ⁵⁾	15-20
<i>Spruceanthus</i>	-	- ⁶⁾	3
<i>Stictolejeunea</i>	2	2	4
<i>Symbiezidium</i>	10	19	c. 5
<i>Thysananthus</i>	20	34	10-20
<i>Trocholejeunea</i>	-	- ⁷⁾	2-3
<i>Tusibeanthus</i>	-	- ⁸⁾	1
	c. 250	c. 525	130-190

Table VI: Comparative list of the number of species assigned to the genera of Ptychanthoideae. 1) : sub *Ptychocoleus*; 2) : sub *Homalolej.*; 3) : sub *Archilej.*, *Brachiolej.*, *Hygrolej.*, and *Lopholej.*; 4) : sub *Acrolej.*; 5) : sub *Ptychocoleus*; 6) : sub *Archilej.*, *Ptychanthus*, and *Thysananthus*; 7) : sub *Brachiolej.*, *Lopholej.*, *Omphalanthus*; and *Ptychocoleus*; 8) : sub *Ptychanthus*.

^{*)} My figures, which are rough estimates of the number of species presently to be accepted in each genus, correspond with the sizes of the discs in Plate XXIV.

	Eur.	Amer.	Afr.	S.E. As.	Austr.	Pacif.
<i>Acrolejeunea</i>	-	x	x	<u>x</u> ¹⁾	x ¹⁾	x ¹⁾
<i>Archilejeunea</i>	-	<u>x</u>	<u>x</u>	<u>x</u> ¹⁾	<u>x</u> ¹⁾	<u>x</u> ¹⁾
<i>Brachiolejeunea</i>						
subg. <i>Brachiolej.</i>	-	x	-	-	-	-
subg. <i>Plicolej.</i>	-	<u>x</u>	x	<u>x</u> ²⁾	-	-
<i>Caudalejeunea</i>	-	x	<u>x</u>	x	x	x
<i>Dicranolejeunea</i>	-	<u>x</u>	x	x	-	-
<i>Lopholejeunea</i>	-	x	<u>x</u>	<u>x</u>	x	x
<i>Marchesia</i>	x	<u>x</u>	x	-	-	-
<i>Mastigolejeunea</i>	-	x	x	<u>x</u>	x	x
<i>Neurolejeunea</i>	-	x	-	-	-	-
<i>Odontolejeunea</i>	-	<u>x</u>	x	-	-	-
<i>Phaeolejeunea</i>	-	-	-	<u>x</u> ³⁾	-	<u>x</u>
<i>Ptychanthus</i>	-	-	x	x	x	x
<i>Schiffneriolejeunea</i>	-	x	<u>x</u>	<u>x</u>	-	x
<i>Spruceanthus</i>	-	-	-	<u>x</u> ⁴⁾	x	<u>x</u>
<i>Stictolejeunea</i>	-	<u>x</u>	<u>x</u> ⁴⁾	<u>x</u> ⁵⁾	-	-
<i>Symbiezidium</i>	-	<u>x</u>	<u>x</u> ⁶⁾	- ⁷⁾	-	-
<i>Thysananthus</i>	-	x	x	<u>x</u>	x	x
<i>Trocholejeunea</i>	-	-	-	<u>x</u> ⁸⁾	-	x
<i>Tuzibeanthus</i>	-	-	-	<u>x</u>	-	-

Table VII: Geographical distribution of the genera of Ptychanthoideae;

x = centre of diversity. 1): many species reported, but position in *Archilej.* doubtful (*Spruceanthus* ?!); 2): India only; 3): New Guinea only; 4): tropical West Africa only; 5): Borneo only; 6): E. African islands only; 7): material recorded from these areas belongs to *Leucolej.*, *Phaeolej.*, or *Pycnolej.*; 8): temperate E. Asia only.

REFERENCES

- ANDO, H. (1972): Distribution and speciation in the Genus *Hypnum*. - J. Hattori Bot. Lab. 35: 68-98.
- ARNELL, S. (1953): Hepaticae collected in South Africa 1951. New and little known Species. III. - Bot. Notiser 1953(2): 271-289.
- BENEDIX, E.H. (1953): Indomalayische *Cololejeuneen*. - Feddes Repert. Beih. 134: 1-88.
- BERRIE, G.K. (1958): The nuclear chromosomes in hepatics. I. - Trans. Brit. Bryol. Soc. 3: 422-426.
- BISCHLER, H. (1961): Recherches sur l'anatomie de la tige chez les Lejeuneaceae Paradoxae. - Rev. Bryol. Lichénol. 30: 232-252.
- - (1965): Recherches sur l'anatomie de la tige chez les Lejeuneaceae. II. Les sous-familles Lejeuneoideae, tribu Ptychantheae, Nipponolejeuneoideae et Myriocoleoideae. - Rev. Bryol. Lichénol. 33: 399-458.
- - (1967): Recherches sur l'anatomie de la tige chez les Lejeuneaceae. III. Les sous-familles Lejeuneoideae, tribu Lejeuneaceae, et Tuyamaelloideae. - Rev. Bryol. Lichénol. 34: 601-675.
- - (1969): Notes sur l'anatomie des amphigastres et sur le développement du paramphigastre et des rhizoïdes chez *Drepano-*, *Rhaphido-* et *Lepto-lejeunea*. - Rev. Bryol. Lichénol. 36: 45-55.
- - (1969): Le genre *Leptolejeunea* (Spruce) Steph. en Amérique. - Nova Hedwigia 17: 265-350.
- BISCHLER, H., MILLER, H.A. & BONNER, C.E.B. (1961): Studies in Lejeuneaceae. IV. A historical account of *Lejeunea cucullata* (Reinwardt, Blume & Nees) Nees and its varieties. - Nova Hedwigia 3: 445-462.
- BONNER, C.E.B. (1962): Index Hepaticarum. I, 2: 15-24 (*Acrolejeunea*). - Weinheim.
- BONNER, C.E.B., BISCHLER, H. & MILLER, H.A. (1961): Studies in Lejeuneaceae. II. The transition subgenus-genus of Spruce's segregates of *Lejeunea*. - Nova Hedwigia 3: 351-359.
- BUCH, H. (1928): Die Scapanien Nordeuropas und Sibiriens. II. Systematischer Teil. - Soc. Sci. Fennica Comm. Biol. 3(1): 1-177.
- CARL, H. (1931): Die Arttypen und die systematische Gliederung der Gattung *Plagiochila* Dum. - Ann. Bryol. Suppl.: 1-170.
- CRANDALL, B.J. (1969): Morphology and development of branches in the leafy Hepaticae. - Nova Hedwigia Beih. 30: i-vii, 1-261.
- CRONQUIST, A. (1969): On the relationship between taxonomy and evolution. - Taxon 18: 177-187.

- DEGENKOLBE, W. (1937): Brutorgane bei beblätterten Lebermoosen. *Ann. Bryol.* 10: 43-96.
- DOUIN, Ch. (1925): La théorie des initiales chez les hépatiques à feuilles. - *Bull. Soc. Bot. France* 72: 565-591.
- EVANS, A.W. (1902): The Lejeuneae of the United States and Canada. - *Mem. Torrey Bot. Cl.* 8: 113-183.
- - (1904): Hepaticae of Puerto Rico. IV. *Odontolejeunea*, *Cyclojeunea* and *Prionolejeunea*. - *Bull. Torrey Bot. Cl.* 31: 163-226.
 - - (1907): *Leucojeunea*, a new genus of hepaticae. - *Torreya* 7(12): 225-229.
 - - (1907): Hepaticae of Puerto Rico. VIII. *Symbiezidium*, *Marchesia*, *Mastigolejeunea*, *Caudalejeunea*, and *Bryopteris*. - *Bull. Torrey Bot. Cl.* 34: 533-568.
 - - (1908): Hepaticae of Puerto Rico. IX. *Brachiolejeunea*, *Ptychocoleus*, *Archilejeunea*, *Leucojeunea*, and *Anoplolejeunea*. - *Bull. Torrey Bot. Cl.* 35: 155-179.
 - - (1912): Notes on North American Hepaticae. 3. - *Bryologist* 15: 54-63.
 - - (1918): Noteworthy Lejeuneae from Florida. - *Amer. J. Bot.* 5: 131-150.
 - - (1922): Notes on North American Hepaticae. 9. - *Bryologist* 25: 25-33.
 - - (1935): The anatomy of the stem in the Lejeuneae. - *Bull. Torrey Bot. Cl.* 62: 187-214, 259-280.
- FULFORD, M. (1951): Distribution patterns of the genera of leafy Hepaticae of South America. - *Evolution* 5: 243-264.
- - (1956): The young stages of the leafy Hepaticae: a résumé. - *Phytomorphology* 6: 199-235.
 - - (1961): The shoot sporophyte relationship in *Brachiolejeunea laxifolia*. - *Bull. Bot. Soc. Univ. Saugar* 13: 6-12.
 - - (1964): Contemporary thought in Plant Morphology: Hepaticae and Anthocerotae. - *Phytomorphology* 14: 103-119.
- GISEKE, P.D. (1792): *Praelectiones in ordines naturales plantarum*. - Hamburg.
- GOTTSCHKE, C.M., LINDENBERG, J.B.G. & NEES VON ESENBECK, C.G. (1844-1847): *Synopsis Hepaticarum*. Fasc. 2 & 3: 145-464 (1845), Fasc. 5: 625-834 (1847). - Hamburg.
- GILMARTIN, A.J. (1974): Variation within populations and classification. - *Taxon* 23: 523-536.
- GOLA, G. (1908): *Species novae in excelsis Ruwenzori in expeditione Ducis Aprutii lectae*. III. Hepaticae. - *Ann. Bot. Pirota* 6: 274.

- GOTTSCHE, C.M. (1882): Reliquiae Rutenbergianae. Lebermoose. - Abh. Naturwiss. Ver. Bremen 7: 338-365.
- GRADSTEIN, S.R. (1974a): Studies on Lejeuneaceae subfam. Ptychanthoideae. I. Nomenclature and taxonomy of *Ptychocoleus*, *Acrolejeunea* and *Schiffneriolejeunea*. J. Hattori Bot. Lab. 38: 327-336
- - (1974b): Studies on Lejeuneaceae subfam. Ptychanthoideae. II. Two remarkable species of *Caudalejeunea*: *C. grolleana* spec. nov. and *C. cristiloba* (Steph.) comb. nov. - Acta Bot. Neerl. 23: 333-343.
- - (1974c): A new look at the taxonomy of holostipous Lejeuneaceae (Ptychanthoideae Mizut.). - J. Bryol. 8: 181.
- GROLLE, R. (1964) Notulae hepaticologicae X-XIII. - Rev. Bryol. Lichénol. 33: 224-229.
- - (1966): *Dicranolejeunea* auf den Atlantischen Inseln. - Trans. Brit. Bryol. Soc. 5: 95-99.
- - (1966): Die Lebermoose Nepals. - Ergebn. Forsch.-Untern. Nepal Himalaya 1,4: 262-298.
- - (1973): Lejeuneaceae Casares-Gil nom. cons. prop. - Taxon 22: 504.
- HATTORI, S. (1943): Hepaticarum species novae et minus cognitae nipponenses. (I). - Bot. Mag. Tokyo 57: 357-363.
- - (1947): Five new genera of Hepaticae. - Biosphaera 1: 3-7.
- - (1951): Contributio ad floram hepaticarum yakusimensis. V. - J. Hattori Bot. Lab. 5: 43-68.
- - (1966): Anthocerotae and Hepaticae, in H. Hara, Flora of Eastern Himalaya p. 501-536. - Tokyo.
- - (1972): *Frullania tamarisci*-complex and the species concept. - J. Hattori Bot. Lab. 35: 202-251.
- HATTORI, S & MIZUTANI, M. (1969): Studies in the flora of Thailand. 59. Hepaticae. - Dansk Bot. Ark. 27: 93-98.
- HERZOG, Th. (1931): Beiträge zur Flora von Borneo. II. Hepaticae. - Mitt. Inst. Bot. Hamburg 7: 182-216.
- - (1948): Two new African species of Lejeuneaceae. - Trans. Brit. Bryol. Soc. 1: 104-107.
- - (1951): Kritik des Lejeuneaceensystems. - Feddes Repert. 54: 172-184.
- - (1951): Hepaticae Standleyanae Costaricensis et Hondurenses. II. Rev. Bryol. Lichénol. 20: 126-175.
- HOLMGREN, P.K. & KEUKEN W. (1974): Index Herbariorum. I. The Herbaria of the world. Regn. Veg. 92. - Utrecht.
- INOUE, H. (1958): Studies on spore germination of Hepaticae. 3. *Brachiolejeunea sandwicensis* (G.) Evans and *Frullania hamatiloba* Steph. J. Jap.

- Bot. 33: 6-10.
- INOUE, H. (1967): Studies on oil bodies of some Malayan liverworts. - J. Hattori Bot. Lab. 30: 54-70.
- JONES, E.W. (1953): African Hepatics. IV. The genus *Caudalejeunea*. - Trans. Brit. Bryol. Soc. 2: 164-171.
- - (1954): African Hepatics. IX. Some species of *Ptychocoleus*. - Trans. Brit. Bryol. Soc. 2: 396-407.
- - (1957): African Hepatics. XII. Some new or little known Lejeuneaceae. - Trans. Brit. Bryol. Soc. 3: 191-207.
- - (1958): A provisional key to the genera of tropical African hepatics. - J. W. African Sci. Assoc. 4(1): 50-73.
- - (1970): African Hepatics. XXII. *Dicranolejeunea* and *Marchesinia*. - Trans. Brit. Bryol. Soc. 6: 72-81.
- KODAMA, T. & KITAGAWA, N. (1974): A new species of *Ptychocoleus* from Sabah (North Borneo). - J. Hattori Bot. Lab. 38: 443-446.
- LAWRENCE, G.H.M. (1951): Taxonomy of Vascular Plants. - New York.
- LEHMANN, J.G.G. (1834): Novarum et Minus Cognitarum Stirpium Pugillus 6: 1-66. - Hamburg.
- LINDENBERG, J.B.G. & GOTTSCHKE, C.M. (1851): Plantae Kegelianae. - Linnaea 24: 625-639.
- MAYR, E. (1969): Principles of Systematic Zoology. - New York.
- MEIJER, W. (1953): The study of hepatics in the Malaysian Tropics. - Bryologist 56: 95-98.
- MILLER, H.A., WHITTIER, H.O. & BONNER, C.E.B. (1963): Bryoflora of the atolls of Micronesia. - Nova Hedwigia Beih. 11: 1-89.
- MITTEN, W. (1861): Hepaticae Indiae Orientalis. - J. Proc. Linn. Soc. London 5: 89-128.
- - (1879): Hepaticae, in I.B. Balfour, The Botany of Rodriguez. - Philos. Trans. 168: 396-401.
- - (1887): The mosses and hepatics collected in Central Africa by the late Right Rev. James Hannington. - J. Linn. Soc. 22: 298-328.
- MIZUTANI, M. (1961): A revision of Japanese Lejeuneaceae. - J. Hattori Bot. Lab. 24: 115-302.
- - (1964): A small collection of hepatics from Caroline Islands. - J. Jap. Bot. 39: 159-160.
- - (1968): Studies of little known Asiatic species of Hepaticae in the Stephani Herbarium. 4. *Phaeolejeunea*, a new genus of Lejeuneaceae. - J. Hattori Bot. Lab. 31: 130-134.
- - (1969): Lejeuneaceae subfamily Ptychanthoideae from Sabah (North Borneo). - J. Hattori Bot. Lab. 32: 129-139.

- MIZUTANI, M. & HATTORI, S. (1967): The distribution of *Tusibeanthus* (Hepaticae). - J. Jap. Bot. 42: 124-128.
- MONTAGNE, C. (1843): Quatrième Centurie de plantes cellulaires exotiques nouvelles. Décades I-VI. - Ann. Sci. Nat. Paris 2: 238-266.
- MOORE, R.J. (1972): Index to plant chromosome numbers for 1970. - Regn. Veg. 84. - Utrecht.
- MÜLLER, K. (1939): Untersuchungen über die Öllkörper der Lebermoose. - Ber. Deutsch. Bot. Gesell. 57: 325-370.
- - (1951): Neue für die Lebermoostaxonomie wichtige Merkmale. - Mitt. Bad. Landes Ver. Nat. Freiburg. N.F. 5(4/5): 4 pp.
- NEES von ESENBECK, C.G. (1830): Enumeratio Plantarum Cryptogamicarum Javæ et Insularem Adjacentium. I. Hepaticas complectens. - Breslau.
- NEHIRA, K. (1966): Sporelings in Jungermanniales. - J. Sci. Hiroshima Univ. ser. b, 2 (II): 1-49.
- - (1974): Phylogenetic significance of the sporeling pattern in Jungermanniales. - J. Hattori Bot. Lab. 38: 151-160.
- PEARSON, W.H. (1922): Hepaticae, in Compton, R.H., A Systematic account of the plants collected in New Caledonia and the Isle of Pines in 1914. - J. Linnean Soc. Bot. 46: 13-44.
- PULLE, A. (1938): Remarks on the system of the Spermatophytes. - Meded. Bot. Mus. Herb. Utrecht. 43: 17 pp.
- RAVEN, P.H. & AXELROD, D.I. (1974): Angiosperm biogeography and past continental movements. - Ann. Miss. Bot. Gard. 61: 539-673.
- SANDE LACOSTE, C.M. (1856): Synopsis Hepaticarum Javanicarum. - Verh. Koninkl. Akad. 5: 112 pp.
- SCHIFFNER, V. (1890): Lebermoose mit Zugrundelegung der von Dr. A.C.M. Gottsche ausgeführten Vorarbeiten. - Forschungsreise S.M.S. "Gazelle" 4, 4: 1-48.
- - (1893): Hepaticae, in Engler & Prantl, Nat. Pflanzenfam. 1(3): 3-141. (publication date: sept. 1893, fide Stafleu 1972).
- - (1894): Revision der Gattungen *Bryopteris*, *Thysananthus*, *Ptychanthus* und *Phragmicoma* im Herbarium des Berliner Museums. - Hedwigia 33: 170-189.
- - (1897): Revision der Gattungen *Omphalanthus* und *Lejeunea* im Herbarium des Berliner Museums. - Bot. Jahrb. 23: 578-600.
- - (1898): Conspectus Hepaticarum Archipelagi Indici. - Batavia.
- - (1929): Über epiphyll Lebermoose aus Japan nebst einigen Beobachtungen über Rhizoiden, Elateren und Brutkörper. - Ann. Bryol. 2: 87-106.

- SCHIFFNER, V. (1932): Bryophyta Nova. II. *Trocholejeunea* Schiffn. n.gen. - Ann. Bryol. 5: 160-162.
- - (1941): Eine neue Gattung der Lejeuneaceae. - Hedwigia 80: 87-89.
- SCHUSTER, R.M. (1954): Notes on Nearctic Hepaticae. VIII. Lejeuneaceae Holostipae of North America. - J. Elisha Mitchell Sci. Soc. 70: 42-56.
- - (1955): North American Lejeuneaceae. I. Introduction; keys to subfamilies and genera. - J. Elisha Mitchell Sci. Soc. 71: 106-126.
- - (1961): The genera *Thysananthus*, *Ptychocoleus*, *Tuzibeanthus*, *Phragmi-lejeunea*, and *Brachiolejeunea* (Lejeuneaceae Holostipae). - Bryologist 64: 156-167.
- - (1963): An annotated synopsis of the genera and subgenera of Lejeuneaceae. - Nova Hedwigia Beih. 9: 1-203.
- - (1966): The Hepaticae and Anthocerotae of North America. I. - New York.
- - (1969): Problems of antipodal distribution in lower land plants. - Taxon 18: 46-91.
- - (1970): Studies on Hepaticae. XLIX-LIII. New Lejeuneaceae from Dominica and Jamaica. - Bull. Torrey Bot. Cl. 97: 336-352.
- - (1972): Evolving taxonomic concepts in the Hepaticae. - J. Hattori Bot. Lab. 35: 169-201.
- SCHUSTER, R.M. & HATTORI, S. (1954): The oil bodies of the Hepaticae. II. The Lejeuneaceae. - J. Hattori Bot. Lab. 11: 11-86.
- SCHWEINFURTH, U. (1957): Die horizontale und vertikale Verbreitung der Vegetation im Himalaya. - Bonner Geogr. Abh. 20: 372 pp.
- SPRUCE, R. (1884): Hepaticae Amazonicae et Andinae. - Trans. Proc. Bot. Soc. Edinburgh 15: i-xi, 1-590.
- STAFLEU, F.A. (1971): Linnaeus and the Linnaeans, the spreading of their ideas in systematic botany. - Regn. Veg. 79. - Utrecht.
- - (1972): The Volumes on Cryptogams of "Engler und Prantl". - Taxon 21: 501-511.
- STAFLEU, F.A. et al. (1972): International Code of Botanical Nomenclature. - Regn. Veg. 82. - Utrecht.
- STEENIS, C.G.G.J. van (1957): Specific and intraspecific delimitation. - Flora Malesiana Ser. 1, 5(3): CLXVII-CCXXXIV.
- STEPHANI, F. (1886): Hepaticae, in J. Henriquez, Flora de S. Thomé. - Bol. Soc. Broteriana 6: 170-184.
- - (1888): Hepaticae Africae. - Hedwigia 27: 59-63., 106-113.
- - (1889): Hepaticae Australiae 2. - Hedwigia 28: 155-175.
- - (1890): Die Gattung *Lejeunea* im Herbarium Lindenberg. - Hedwigia 29: 1-23, 68-99, 133-142.

- STEPHANI, F. (1895): *Hepaticarum species novae*. VII. Lejeuneae. - *Hedwigia* 34: 56-65.
- STEPHANI, F. & LINDMAN, C.A.M. (1897): Die Lebermoose der ersten Regnellschen Expedition. - *Bihang K. Svenska Vetensk.-Akad. Handl.* 23, 3(2): 1-36.
- STEPHANI, F. (1908): *Hepaticae*, in K. Reehinger, Botanische und zoologische Ergebnisse einer wissenschaftliche Forschungsreise nach der Samoa-Inseln, dem Neuguinea-Archipel und den Salomons-Inseln. - *Denkschr. Math. Naturwiss. Akad. Wiss. Wien* 85: 197-201.
- - (1911, 1912, 1913): vide Stephani (1898-1924).
- - (1898-1924): *Species Hepaticarum*. I-VI. - Geneva. (*Ptychocoleus* in Vol. V: 19-60, dated 21 May 1912).
- STOTLER, R.E. (1969): The genus *Frullania* subgenus *Frullania* in Latin America. - *Nova Hedwigia* 18: 397-555.
- STOTLER, R.E. & CRANDALL, B.J. (1969): The sporophyte anatomy of *Dicranolejeunea axillaris*. - *Bryologist* 72: 287-397.
- STOTLER, R.E. & CRANDALL-STOTLER, B.J. (1974): A monograph of the genus *Bryopteris* (Swartz) Nees von Esenbeck. - *Bryophyt. Biblioth.* 3: 1-159. - Lehre.
- Syn.Hep.: vide Gottsche, Lindenberg & Nees (1844-1847).
- TATUNO, S. & NAGATOMO, N. (1969): Karyological studies of some Japanese species of Lejeuneaceae (Hepaticae). - *J. Hattori Bot. Lab.* 32: 44-49.
- TAYLOR, T. (1846): *New Hepaticae*. - *London J. Bot.* 5: 365-417.
- TOUW, A. (1971): A taxonomic revision of the Hypnodendraceae (Musci). - *Blumea* 19: 211-354.
- TREVISAN, V. (1877): Schema di una nuova classificazione delle Epatiche. - *Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser.* 3,4: 383-451.
- TROLL, C. (1974): Die dreidimensionale Landschaftsbau der Erde. - *Repr. Akad. Wiss. Lit. Mainz* 1949-1974: 16 pp.
- VAN DEN BERGHEN, C. (1945): *Genera des Lejeuneaceae*. - *Lejeunea*, Mem. 6: 1-59.
- - (1948): Note sur le genre *Ptychocoleus* Trev. en Afrique Tropicale. - *Bull. Jard. Bot. Bruxelles* 19: 37-49.
- - (1948): Un nouveau genre d'Hépatiques: *Evansiolejeunea* nov. gen. *Rev. Bryol. Lichénol.* 17: 86-90.
- - (1965): Hépatiques recoltés par le Dr. J.J. Symoens dans la Région Péri-Tanganyikaise. - *Bull. Soc. Roy. Bot. Belg.* 98: 129-174.
- - (1972): Hépatiques et Anthocerotées, in J.J. Symoens, *Exploration hydrobiologique du bassin du Lac Bangweolo et du Luapula* 8, 1: 1-202.

- VAN DER BURGH, J. (1973): Hölzer der Niederrheinischen Braunkohlenformation. 2. - Rev. Palaeobot. Palyn. 15: 73-275.
- VERDOORN, F. (1933a): Die von V. Schiffner (1893-1894) und von Fr. Verdoorn (1930) auf den Indomalaischen Inseln gesammelten Lejeuneaceae Holostipae (De Frullaniaceis XI). - Rec. Trav. Bot. Neerl. 30: 212-233.
- - (1933b): Revision der von Java und Sumatra angeführten Lejeuneaceae Holostipae (De Frullaniaceis XII). - Ann. Bryol. 6: 74-91.
- - (1933c): Ueber zwei neue Gattungen der Lebermoose (De Frullaniaceis XIII). Ann. Bryol. 6: 88-91.
- - (1934a): Revision der von Ozeanien, Australien und Neuseeland angeführten Lejeuneaceae Holostipae (De Frullaniaceis XIV). - Blumea 1: 216-240.
- - (1934b): Lejeuneaceae Holostipae. - Nova Guinea 18(1): 8 pp.
- - (1934c): Studien über Asiatische Jubuleae (De Frullaniaceis XV-XVII). - Ann. Bryol. Suppl. 4: I-XII, 1-231.
- WINKLER, S. (1968): Die epiphyllen Moose der Nebelwälder von El Salvador C.A. - Rev. Bryol. Lichénol. 35: 303-369.
- - (1970): Zur Anatomie der Rhizoidplatten neotropischer Lejeuneaceen. - Rev. Bryol. Lichénol. 37: 47-55.
- ZWICKEL, W. (1932): Verbreitung der Ocellen bei Lebermoosen. - Ann. Bryol. 5: 145-158.

INDEX OF NAMES

Accepted names are in plain type; synonyms are in *italics*; new names and combinations are underlined.

- Acanthocoleus: 139
 fulvus: 139
 Acrolejeunea: 52
 subg. Acrolejeunea: 59
 subg. Isolejeunea: 83
 sect. Acrolejeunea: 63
 sect. Isolejeunea: 103
 sect. Pusillae: 59
 sect. Regulares: 83
 allisonii: 103-105
 angustispica: 71
 arcuata: 121-124
 atroviridis: 125
 aulacophora: 72
 aulacophora: 91-95
 borgenii: 125
 borneensis: 125
 caledonica: 91, 100-101
 comptonii: 130
 confertissima: 76
 convexa: 126
 cordistipula: 126
 crisniloba: 126
 cucullata: 109
 densifolia: 126
 domingensis: 126
 emergens: 66, 71-79
 var. confertissima: 76-77, 79
 var. emergens: 76
 ssp. madagascariensis: 72, 76
 ferruginea: 126
 fertilis: 85-91
 fuscescens: 126
 hartmannii: 99
 hasskarliana: 126
 heterophylla: 68-71
 integribracteata: 86
 javanica: 126
 juliformis: 126
 linguaeifolia: 127
 luzonensis: 127
 malaccensis: 127
 marquesana: 128
 micholitsii: 99, 100
 mollis: 106-108
 novaequineae: 128
 occulta: 128
 orchidae: 128
 pappeana: 128
 parviloba: 128
 parvula: 115-117
 peradeniensis: 129
 polycarpa: 129
 pulopenangensis: 129
 pusilla: 59-62
 pusilla: 72
 pyncoclada: 108-115
 var. rostrata: 109
 ssp. pyncoclada: 113
 ssp. latistipula: 113, 115
 rechingeri: 129
 recurvata: 79-82
 renauldii: 91
 rocoatii: 129
 rostrata
 var. minor: 109
 var. major: 129
 +) securifolia: 95-96, 99
 ssp. caledonica: 100-102
 ssp. hartmannii: 89, 99-100, 102
 ssp. pallida: 101-102
 ssp. securifolia: 36, 96-99, 102
 setacea: 129
 sikkimensis: 46, 83-85
 subinnovans: 109
 terminalis: 109
 tjibodensis: 117-120
 torulosa: 63-68
 var. obtusa: 67
 var. torulosa: 67
 torulosa: 72
 trigona: 129
 tumida: 130
 ustulata: 86
 wichurae: 86
 wildii: 96
 Anoplolejeunea: 138
 conferta: 138
 Archilejeunea: 140-151
 abbreviata: 144
 autoica: 144
 fuscescens: 126
 juliformis: 127
 kiushiana: 145
 linguaeifolia: 144
 parviloba: 145
 plantuscula: 131
 polyphylla: 63
 pusilla: 59
 rufa: 127
 +) subaloba: 142
 Blepharolejeunea: 137, 135
 Brachiolejeunea: 50, 140-151
 subg. Brachiolejeunea: 140-151
 subg. Plicolejeunea: 51, 140-151
 subg. Trocholejeunea: 135

- corticalis*: 66
laxifolia: 144
micholitzii: 86
tortifolia: 86
Bryopteridaceae
Bryopteridoideae: 139
Bryopteris: 48, 138-139
Cardiolejeunea: 135, 142
Caudalejeunea: 140-151
 cristiloba: 126, 143
 dusenii: 143
 reniloba: 127
 yangambiensis: 143
Cheilolejeunea: 138
Cyclolejeunea: 135, 142
Dicranolejeunea: 139-151
Echinolejeunea: 135, 142
Evansiolejeunea: 138
 roccatii: 129
+ *Frullaniaceae*: 138-139
+ *Heterolejeunea*: 139, 142
 javanica: 139
Holostipae: 134-135
Jubula: 138
Jungermannia
 arcuata: 121
 fertilis: 85
 bèta tenerior: 121
 filiformis: 127
 juliformis: 127
 securifolia: 96
 torulosa: 63
Lejeunea
 subg. *Acrolejeunea*: 52
 abnormis: 130
 amplectens: 125
 arcuata: 121
 aulacophora: 91
 confertissima: 76
 cucullata: 109
 emergens: 71
 fertilis: 85
 fulva: 130
 hartmannii: 99
 inflexa: 131
 juliformis: 127
 marsupitfolia: 128
 mollis: 106
 pallida: 101
 planiuscula: 131
 polyphylla: 63
 pycnoclada: 108
 renauldii: 91, 94
 rostrata var. *minor*: 109
 rufa: 127
 securifolia: 96
 terminalis: 109
 torulosa: 63
 var. *polyphylla*: 63
 var. *torulosa*: 66
 ustulata: 86
 wildii: 96
Lejeuneaceae: 134, 138-139
Lejeuneoideae: 134-142
Leucolejeunea: 138
Lopholejeunea: 139-151
Marchesia: 140-151
 aulacophora: 91
 fertilis: 85
 securifolia: 96
 torulosa: 63
 ustulata: 86
Mastigolejeunea: 140-151
 subg. *Tuzibeanthus*: 147
 sect. *Brachiolejeuneoides*: 125
 sect. *Nigrae*: 125
+) *malaccensis*: 86
 recondita: 125
 trigona: 129
Neurolejeunea: 140-151
Odontolejeunea: 140-151
Omphalanthus: 138
 subg. *Evansiolejeunea*: 135
 subg. *Peltolejeunea*: 135
 roccatii: 129
Peltolejeunea: 138
Phaeolejeunea: 140-151
Phragmicoma
 abnormis: 130
 arcuata: 121
 aulacophora: 91
 caledonica: 100
 cucullata: 109
 emergens: 71
 fertilis: 85
 fulva: 130
 hartmannii: 99
 inflexa: 131
 juliformis: 127
 var. *bèta*: 127
 pallida: 101
 securifolia: 96
 torulosa: 63
 ustulata: 86
+ *Phragmilejeunea*: 14
+) *Ptychanthoideae*: 134-151
Ptychanthus: 140-151
 mollis: 106
 pycnocladus: 108
 striatus: 143
Ptychocoleus: 12-14, 52
 sect. *Arcuatae*: 13
 sect. *Brachiolejeuneoides*: 13
 sect. *Cristilobae*: 13
 sect. *Dentatae*: 13
 sect. *Mediae*: 13
 sect. *Minores*: 13, 103
 sect. *Regulares*: 13, 83

Plate I. Leaves and cells in *Acrolejeunea*.

Fig. 1. Leaf, with indication of characters and method of measurement: a = apical tooth, d = dorsal leaf margin, f = lobule free margin, k = keel, l = leaf length, $p_1, 2, 3$ = hyaline papillae, s = sinus, $t_1, 2, 3$ = lobule teeth, v = ventral leaf margin, w = leaf width. Fig. 2. Dorsal (d) cortex cells arranged in an oblique zig-zag row (*A. torulosa*), x 65. Fig. 4. Dorsal (d) cortex cells arranged in a straight longitudinal row (*A. aulacophora*), x 55. Figs. 3, 5. Diagrams of figs. 2 and 4, showing merophyte boundaries (broken lines) and leaf and underleaf insertion-lines (d = dorsal, v = ventral). Figs. 6-7. Lobe and lobule in transverse section (schematic), showing gradual (fig. 6) and abrupt (fig. 7) transition from the sac (s) into the flattened portion. Fig. 8. Caducous leaf, showing cell arrangement (*A. emergens*), x 225. Fig. 9-10. Median lobe cells in different arrangements (*A. tjibodensis*): with acute ends (fig. 9), with truncate ends (fig. 10), x 500.

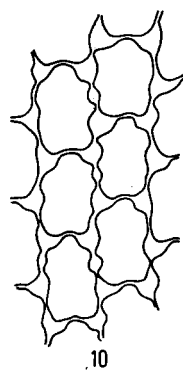
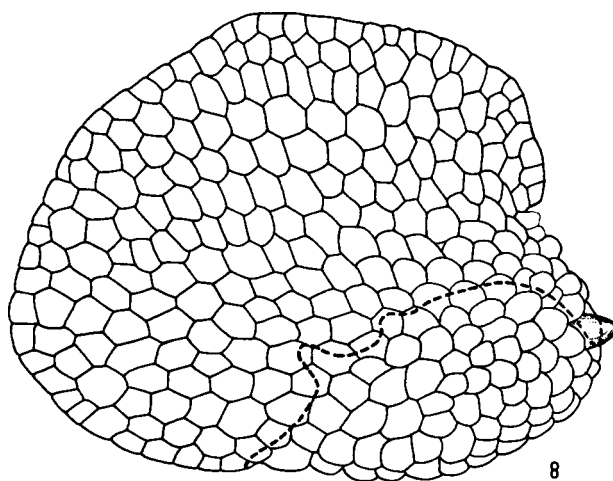
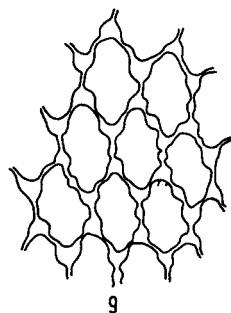
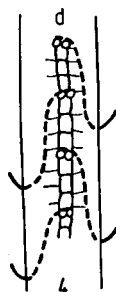
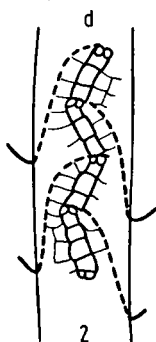
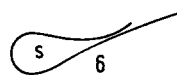
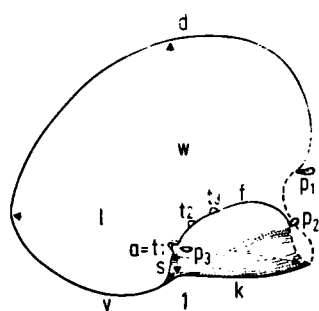
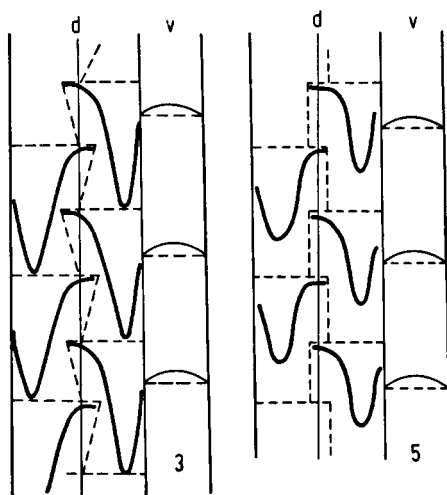


Plate II. Transverse sections of the stem in *Acrolejeunea*

Fig. 1. *A. recurvata*, x 300 (from the type). Fig. 2. *A. torulosa*, showing the dorsal leaf insertion (dl), the *Lejeunea*-type branch initial cell (br), and the leaf brace-cells (lb), x 300 (from Manaus, Smith 11718). Fig. 3. *A. emergens*, showing the two dorsal leaf-insertion cells (dli), the *Lejeunea*-type branch initial cell (br), the leaf brace-cells (lb), and cells of the ventral lobule base (lo), somewhat diagrammatic, x 300 (from the type). Fig. 4. *A. fertilis*, x 300 (from Singapore, Sipman 6883). Fig. 5. *A. aulacophora*, x 225 (from Réunion, de L'Isle s.n.). Fig. 6. *A. securifolia* ssp. *hartmannii*, showing the four superior central cells (s) at the underleaf base, x 225 (from the type of *Ptychoooleus nicholitzii*). Fig. 7. *A. arcuata*, x 350 (from N.Borneo, Mizutani 2625). Fig. 8. *A. pycnoclada*, x 350 (from the type of *Ptychoooleus subinnovans*). Fig. 9. *A. parvula*, x 350 (from the type).

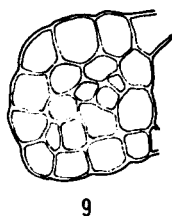
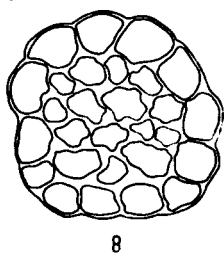
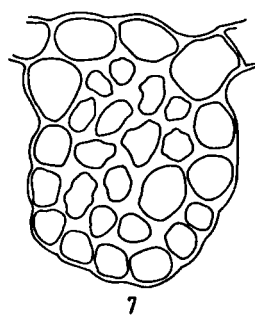
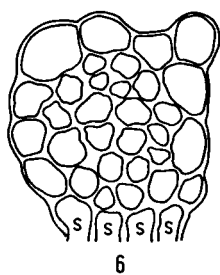
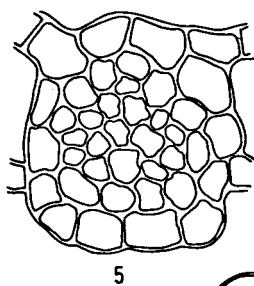
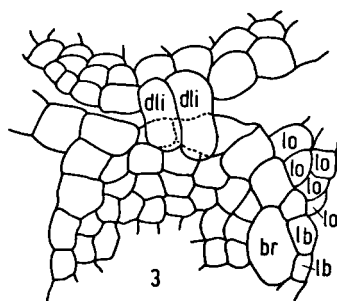
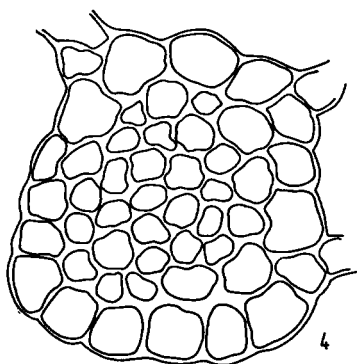
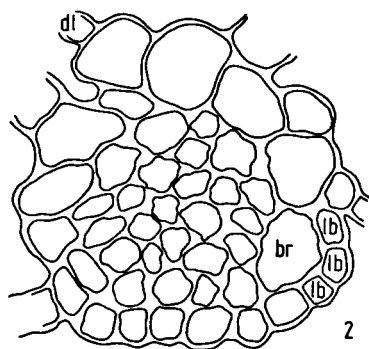
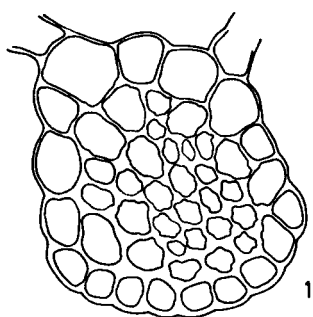


Plate III. Underleaves, primary rhizoid disc and branching in *Acrolejeunea*.

Fig. 1. Underleaf, x 60. Fig. 2. Underleaf base, showing primary rhizoid disc, x 200. Fig. 3. Underleaf base in longitudinal section, x 200. Fig. 4. Ibid. in transverse section, x 200. Fig. 5. Base of *Frullania*-type branch (ventral view), showing first leafy appendage, x 70. Fig. 6. Ibid. in longitudinal section, showing primary rhizoid disc structure, x 200. Fig. 7. Unfertilized gynoeceium, producing fertile innovation, somewhat diagrammatic. Fig. 8. Fertilized gynoeceium, producing pseudo-innovation, x 50.

Figs. 1-2 from the type of *A. torulosa* var. *obtusa*. Figs. 3-4 from the type of *Pt. renauldii*. Fig. 5. from *A. aulacophora*, Reunion, de l'Isle s.n. Fig. 6. from *A. tjibodensis*, Java, van Leeuwen s.n. Fig. 7. from *A. fertilis*, Berlinhafen, Fleischer 738b. Fig. 8. from *A. emergens*, Katanga, Mullenders 427.

c = cortex cell; i = inferior central cell; mc = modified cortex cell; r = rhizoid initial cell; s = superior central cell; u = underleaf cell.

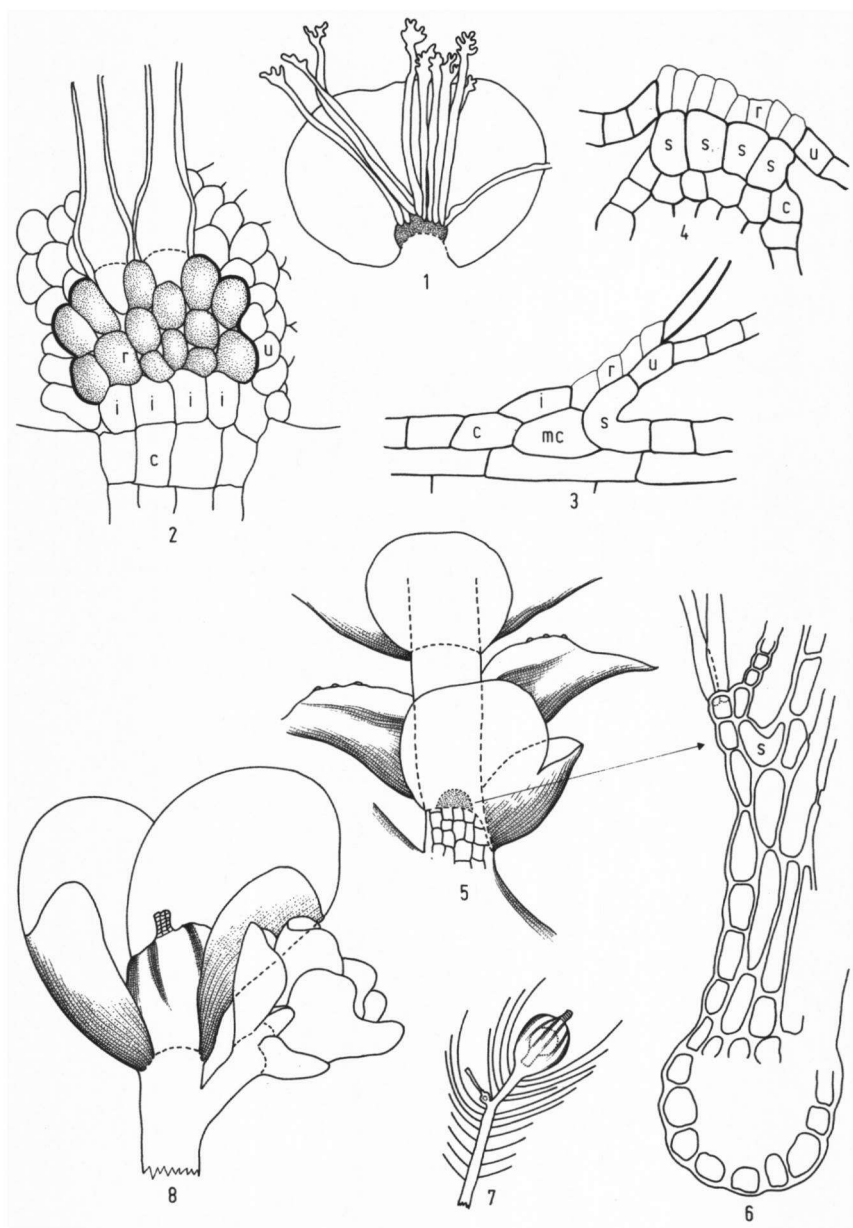
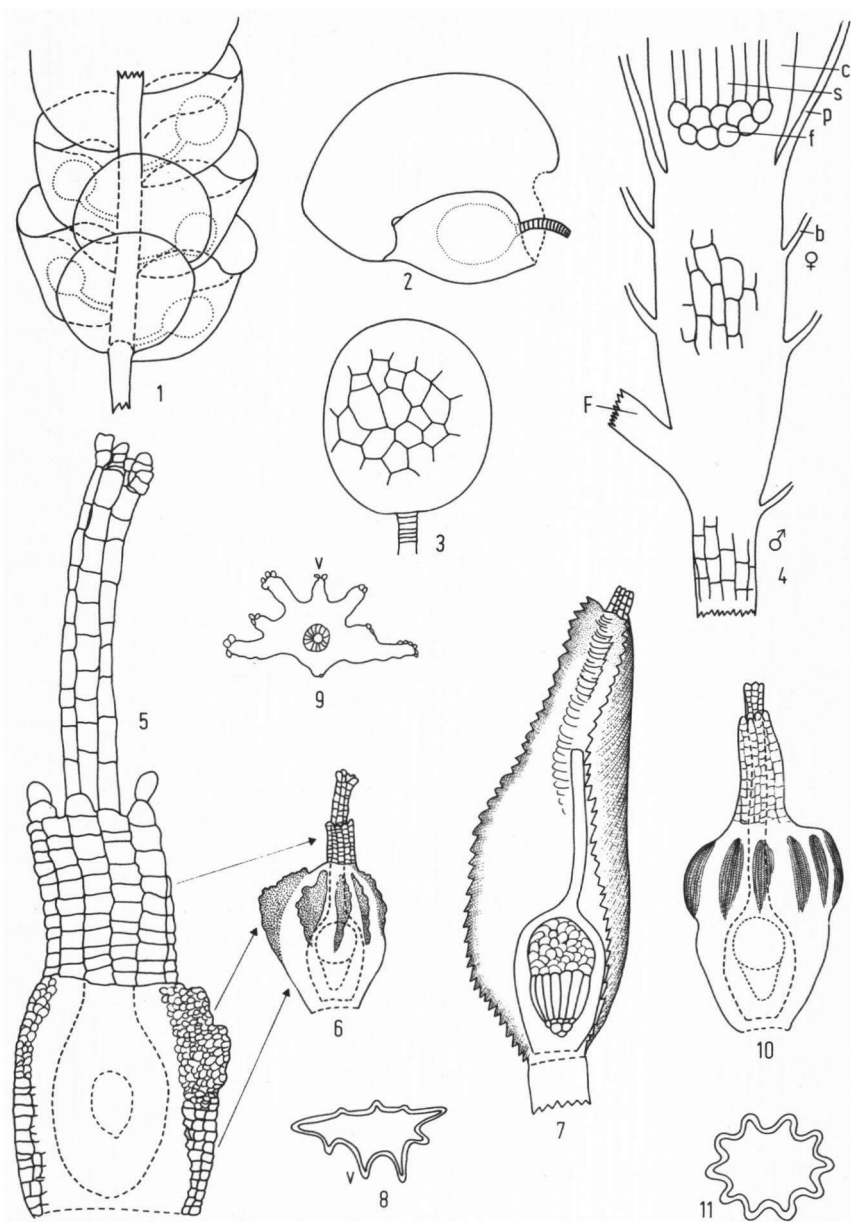


Plate IV. Gametoecia in *Acrolejeunea*.

Fig. 1. Portion of male branch, showing monandrous, epistatic bracts, x 50. Fig. 2. Male bract, x 60. Fig. 3. Antheridium, x 200. Fig. 4. Swollen gynoecial axis in *A. mollis*, somewhat diagrammatic (b = female bract, c = calyptra, f = sporophyte foot, F = *Frullania*-type branch, p = perianth, s = seta). Fig. 5. Juvenile anisoplicate perianth with protruding archegonial neck, x 250. Fig. 6. Ibid., somewhat later stage of development (ventral view), x 60. Fig. 7. Almost mature anisoplicate perianth in longitudinal section, showing immature sporophyte inside calyptra, x 60. Fig. 8. Cross section of anisoplicate perianth (v = ventral). Fig. 9. Juvenile anisoplicate perianth in top view, showing "rough" plicae (v = ventral), x 60. Fig. 10. Juvenile isoplicate perianth, x 70. Fig. 11. Cross section of isoplicate perianth.

Figs. 1, 3 from the type of *Pt. micholitzii*. Fig. 2. from *A. heterophylla*, Honduras, Wilson s.n. Figs. 5-9 from *A. torulosa*, Brazil, Smith 11718. Figs. 10-11 from *A. pycnoclada*, Samoa, Schultze-Motel 3750.



Pl.V. Sporophyte and sporeling development in *Acrolejeunea*.

Fig. 1. Mature sporophyt, just before dehiscence (a = archegonical neck, c = calyptra, f = foot), x 70. Fig. 2. Schematic representation of seta cross section and capsule valves (inner sides), showing the points of attachment of the elaters as well as monofenestrate and plurifenestrate cell-wall thickening patterns (in *A. mollis*). Fig. 3. Outer side of capsule valve, showing cell arrangement, x 65. Figs. 4-5. Cells of the outer layer of the capsule valve, surface view, x 400. Fig. 6. Cells of the inner layer of the capsule valve, surface view, with plurifenestrate layer of thickening, x 400. Fig. 7. Spore, x 400. Fig. 8. Sporeling development, *Lopholejeunea*-type (a = apical cell, p = protonema cell), x 400. Fig. 9. Ibid., later stage (pl = primary leaf, jl = juvenile leaf), x 225. Fig. 10. Juvenile gametophyte, showing pendular sequence of segmentation, x 60.

Figs. 1,3-4 from *A. aulacophora*, Samoa, Schultze-Motel 3926b. Fig. 5. from *A. pyenoclada*, Reunion, Onraedt 73 R 4. Fig. 6. from *A. arcuata*, Java, Treub s.n. Fig. 7. from *A. mollis*, Wairoa, Hodgson s.n. Figs. 8-10 from *A. torulosa*, Brazil, Vital 2846.

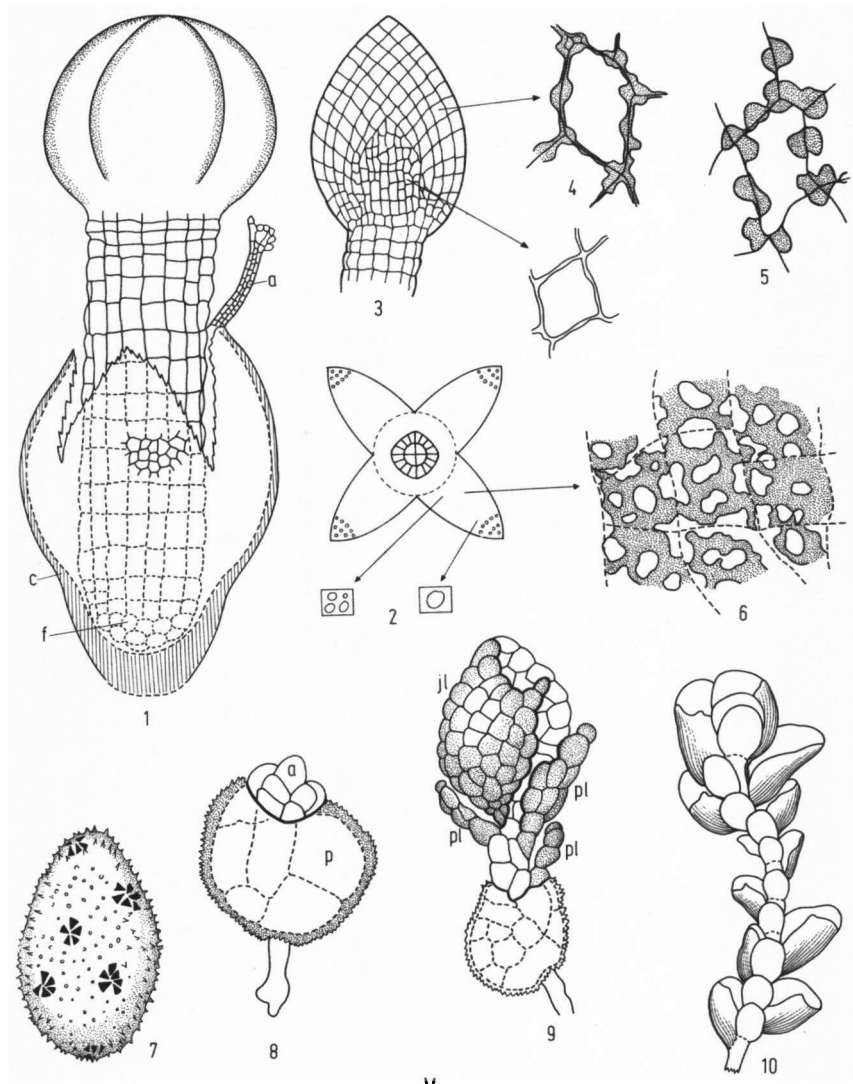


Fig. VI. Vegetative reproduction in *Acrolejeunea* subg. *Acrolejeunea*.

Fig. 1. Branch with terminal flagella, x 20. Fig. 2a. Unbranched solitary flagella. Fig. 2b. Unbranched, clustered flagellae. Fig. 2c. Pinnately branched flagella. Fig. 3. Longitudinal section of the transition leafy shoot - flagella, showing shortening of internodes and modification of underleaves and cortex cells (b = leafy branch, D = dorsal, f = flagella, s = superior central cell, u = underleaf), x 65. Fig. 4. Transverse section of flagella (D = dorsal), x 270. Figs. 5-7. Caducous leaves (g = gemmaling), x 65. Fig. 8. Germination of gemmaling (g), showing primary leaves and underleaf, x 270. Fig. 9. Gemmaling (dorsal view), later stage, x 65. Fig. 10. Ibid. (ventral view), showing primary and juvenile leaves and underleaves in pendular sequence of segmentation, x 225.

Figs. 1,7-9 from *A. torulosa*, Suriname, Lanjouw 124. Figs. 3-4 from *A. torulosa*, Brazil, Smith 11728. Fig. 5. from *A. recurvata*. Fig. 6. from *A. heterophylla*. Fig. 10. from *A. torulosa*, Brazil, Vital 2086.

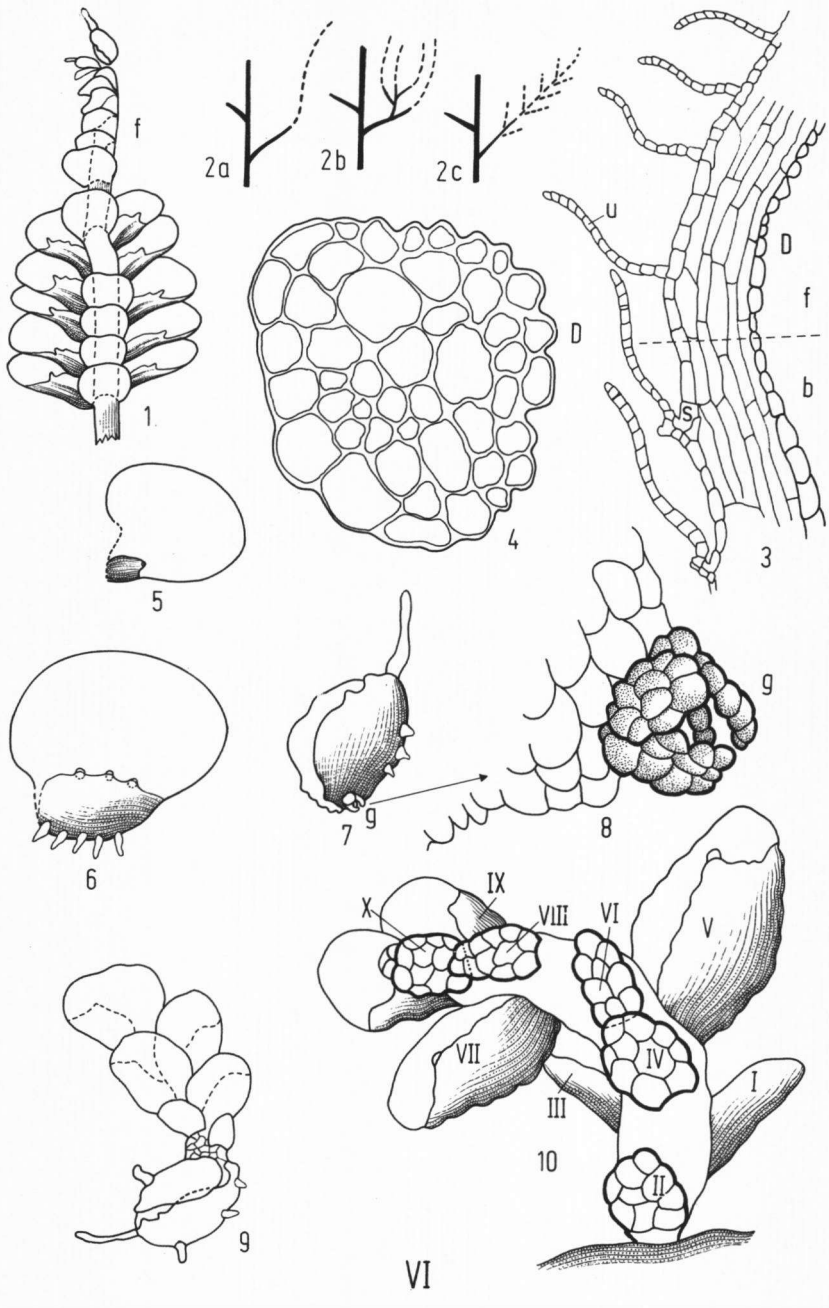


Plate VII. Figs. 1-7. *Acrolejeunea pusilla* (Steph.) Grolle & Gradst.

Figs. 8-14. *Acrolejeunea heterophylla* (Evans) Grolle & Gradst.

Fig. 1. Portion of stem with gynoeceium, sporophyte, and two flagellae (producing caducous leaves), x 30. Fig. 2. Portion of male branch, x 30. Fig. 3. Leaves and underleaf, x 70. Fig. 4. Apex of lobule (a = apical tooth), x 250. Figs. 5-7. Caducous leaves, x 70. Figs. 8-9 Leaves, x 50. Figs. 10-11. Lobule free margin (a = apical tooth), x 225. Fig. 12. Caducous leaf, x 60. Figs. 13-14. Inner female bract and bracteole, x 20.

Figs. 1, 3-4, 7 from Mayebará 618. Fig. 2 from Kodama 9359. Figs. 5-6 from Hattori 4197. Figs. 8, 11-12 from the type of *A. heterophylla*. Figs. 9, 10, 13-14 from Nicaragua, Hamilton 225.

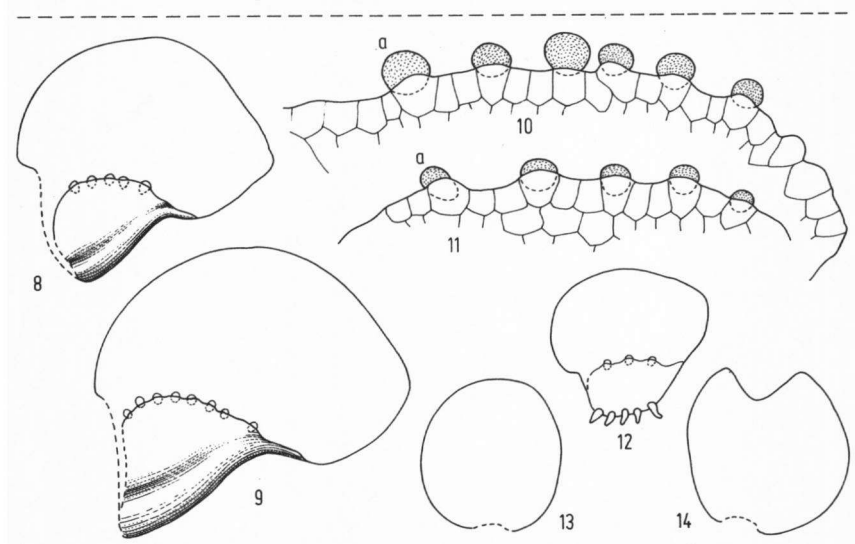
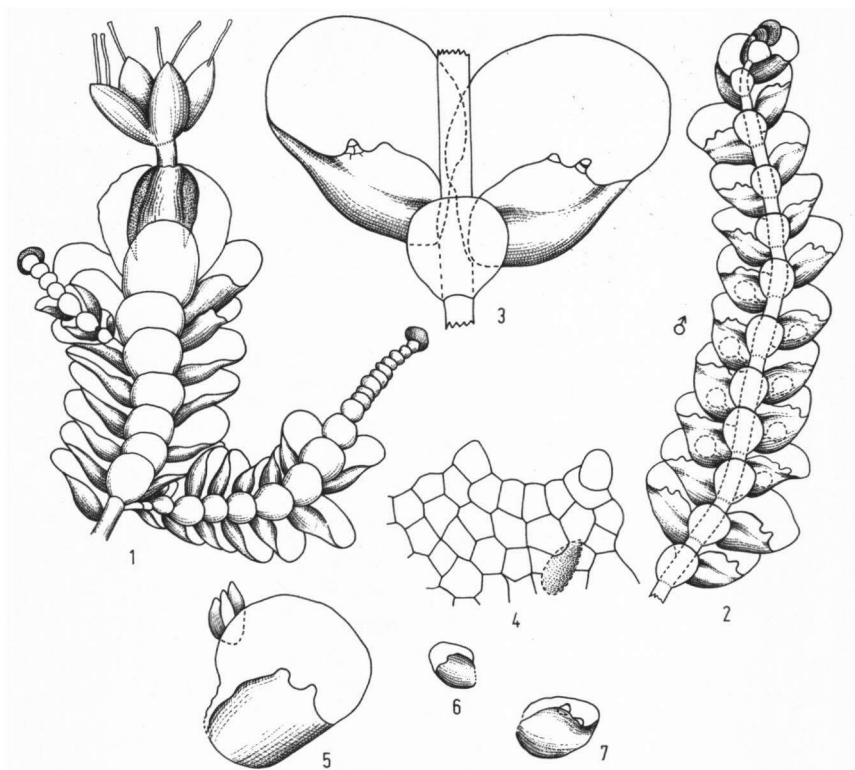


Plate VIII. *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. Figs. 1, 3-8, 11-13. var. *torulosa*. Figs. 2, 9-10, 14. var. *obtusa* Gradst.

Fig. 1. Habitus, with female branch and two flagellae (producing caducous leaves). Figs. 2-3. Leaves, x 60. Fig. 4. Lobule free margin (a = apical tooth), x 250. Fig. 5. Tib., x 225. Fig. 6. Leaf and underleaf, x 60, Fig. 7. Underleaf, x 60. Fig. 8. Median lobe cells, showing oil bodies, x 600, Figs. 9-10. Caducous leaves, x 60. Fig. 11. Male bract, x 60. Fig. 12. Inner female bracteole, x 15. Figs. 13-14. Inner female bracts, x 15.

Fig. 1 from Brazil, Vital 2109. Figs. 2, 9-10, 14 from the type of var. *obtusa*. Figs. 3, 12-13 from the type of *A. torulosa*. Figs. 4, 6 from Suriname, Lanjouw 124. Fig. 7 from Venezuela, Lützelburg 22552. Figs. 8, 11 from Brazil, Smith 11718.

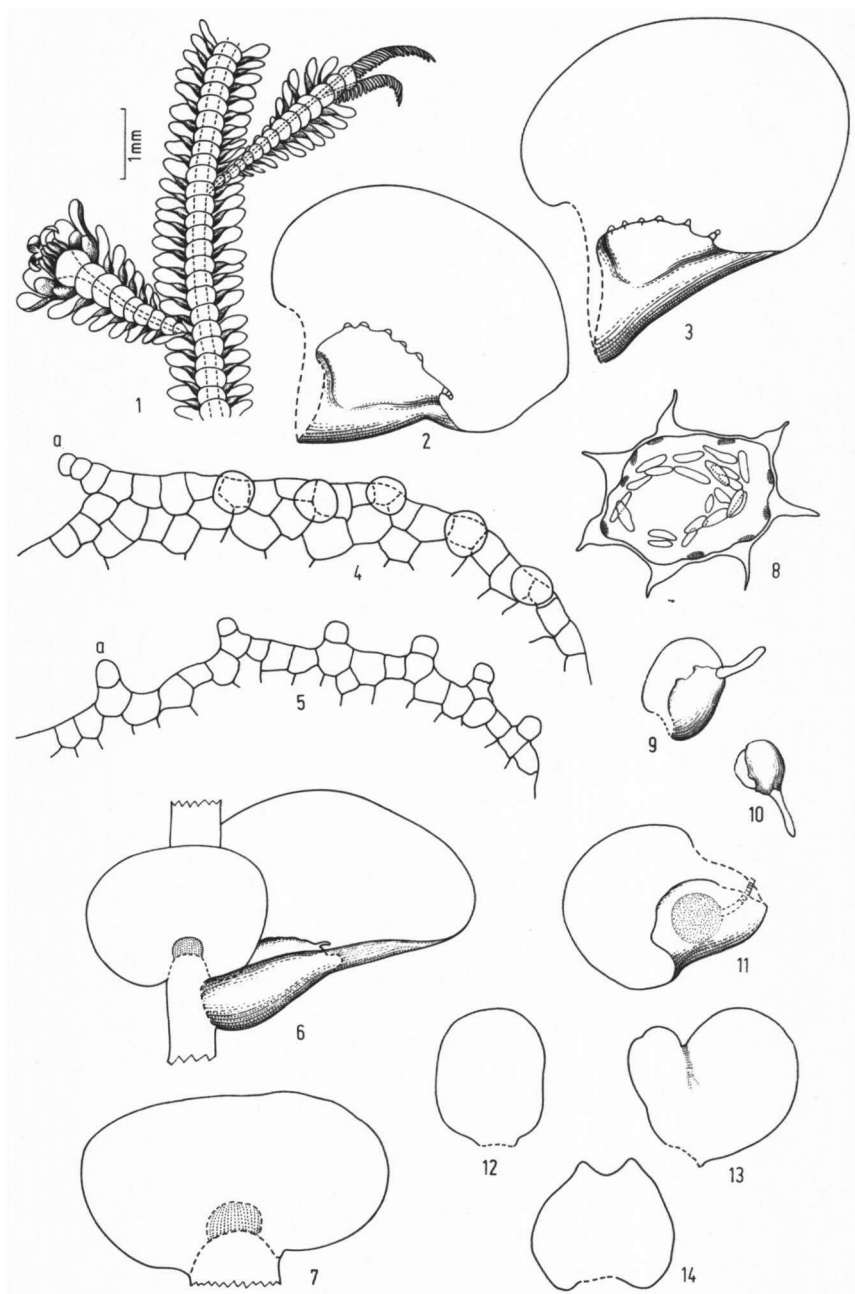


Plate IX. *Acrolejeunea emergens* (Mitt.) Steph. Figs. 1-5, 8-10, 13 var. *emergens*. Figs. 6-7, 11-12 var. *confertissima* (Steph.) Gradst.

Fig. 1. Portion of female branch, x 18. Fig. 2. Inner female bract and bracteole, x 18. Fig. 3. Perianth, x 25. Figs. 4-5, 8. Perianth, in transverse section, x 55. Fig. 6. Perianth, x 55. Fig. 8. Male bract, x 35. Fig. 9. Branch terminating in flagella (producing caducous leaves), x 18. Fig. 10. Caducous leaf, x 35. Fig. 11. Median lobe cells, x 400. Fig. 12. Marginal lobe cells, x 400. Fig. 13. Underleaf, showing auriculate base, x 75.

Figs. 1-3, 8-9 from the type of *A. emergens*. Fig. 4 from Angola, Welwitsch 249. Fig. 5 from Katanga, Mullenders 431. Figs. 6-7, 11-12 from the type of var. *confertissima*. Fig. 10 from French Guiana, Broadway 843. Fig. 13 from the type of *Ptychocoleus renauldii* var. *victoriae*.

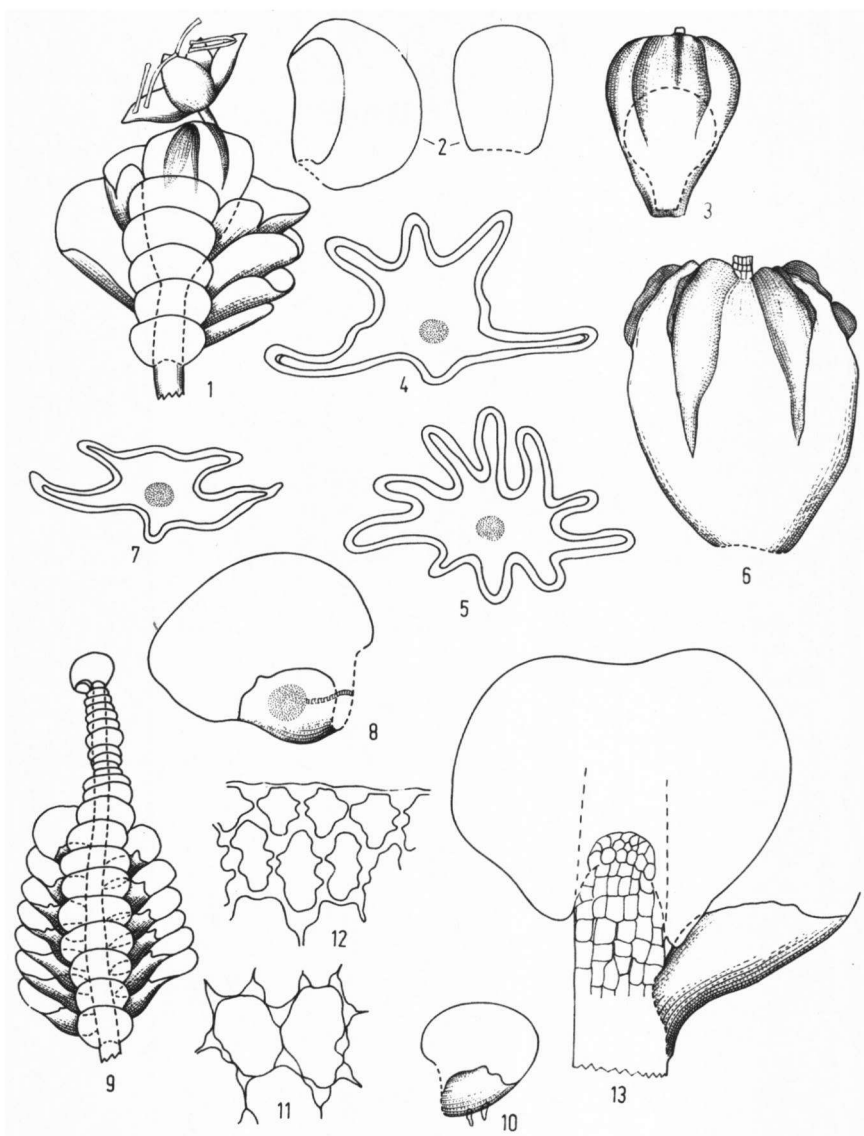


Plate X. *Acrolejeunea emergens* (Mitt.) Steph. - lobule variation.

Fig. 1. Lobule, x 60. Figs. 2, 4, 6, 9, 10. Leaves, x 50. Figs. 3, 5. Free margin of lobule (a = apical tooth), x 200. Figs. 7-8, 11-12. Ibid., x 250.

Fig. 1 from Katanga, Mullenders 431. Figs. 2-3 from French Guiana, Broadway 843. Figs. 4-5 from the type of *Acrolejeunea emergens*. Figs. 6-8 from Madagascar, Borgen s.n. Fig. 9 from the type of var. *confertissima*. Figs. 10-11 from Angola, Welwitsch 249. Fig. 12 from the type of *Ptychocoleus renauldii* var. *victoriae*.

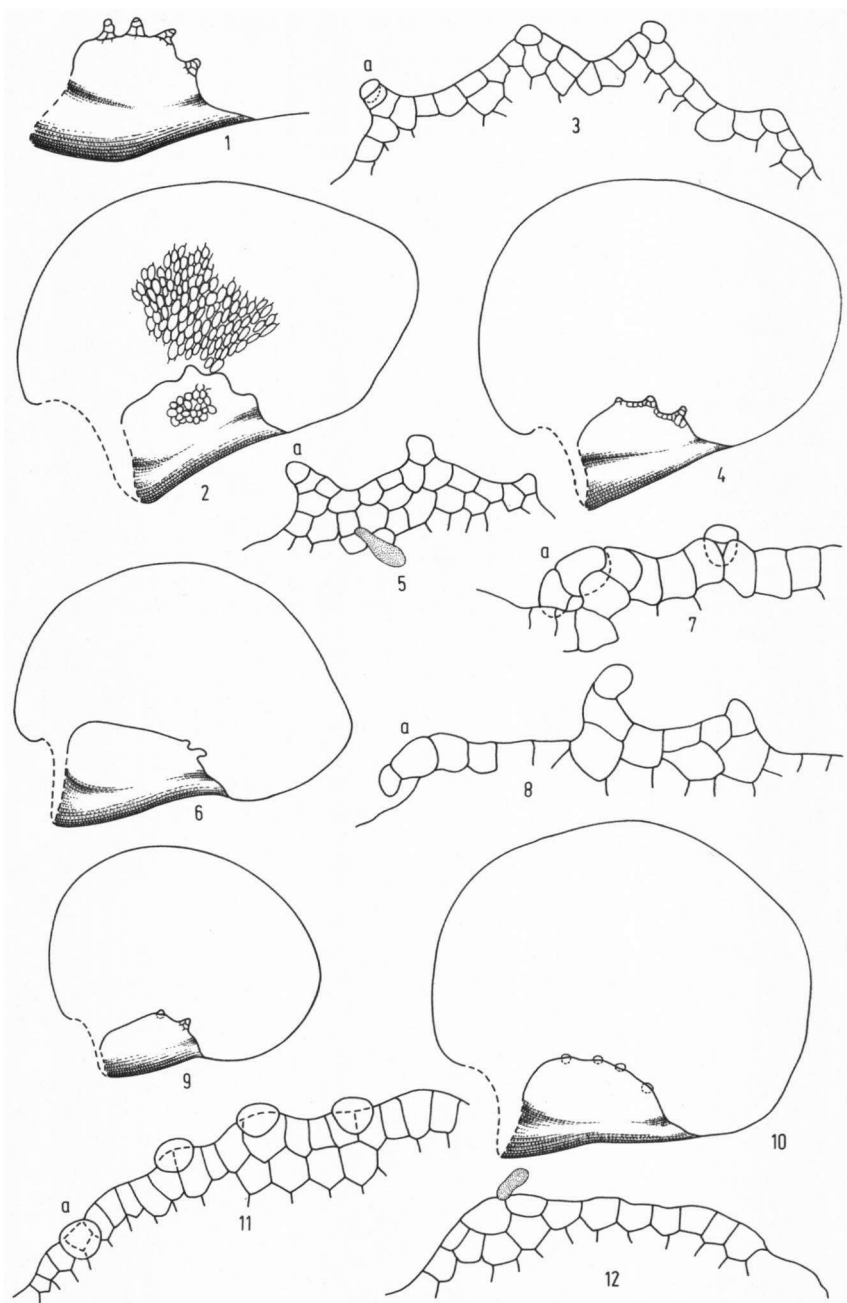


Plate XI. *Acrolejeunea recurvata* Gradst.

Fig. 1. Portion of female branch, x 30. Figs. 2-3. Leaves, x 50. Fig. 4, Lobule, x 50. Fig. 5. Caducous leaf, x 50. Fig. 6. Lobule free margin, seen from the inner side (a = apical tooth), x 200. Fig. 7. Leaf cells, along dorsal margin near lobe base, x 300. Fig. 8. Ibid., near lobe apex, x 300. Fig. 9-11. Underleaves, x 50.

Fig. 1-2, 5-9 from the type. Fig. 3, 10 from Thailand, Touw 10372. Fig. 4, 11 from Laos, Tuyama s.n.

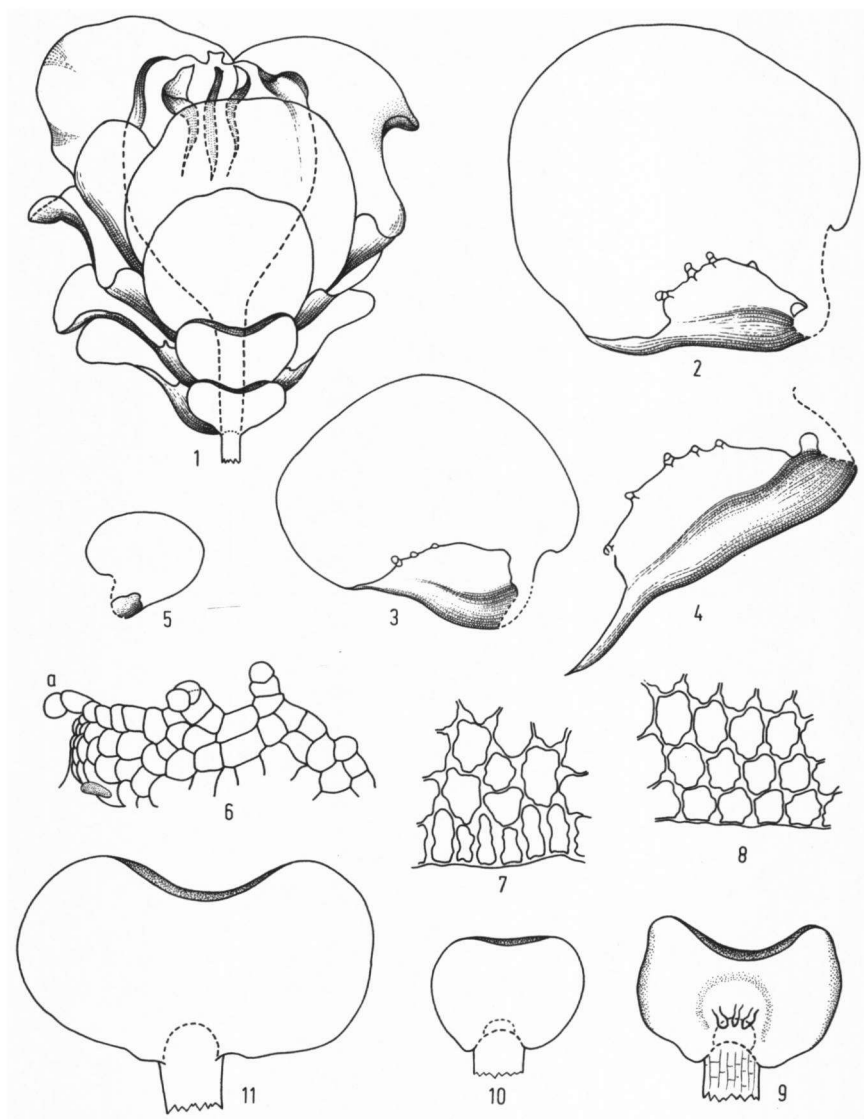


Plate XII. Figs. 1-4. *Acrolejeunea sikkimensis* (Mizut.) Gradst.

Figs. 5-8. *Acrolejeunea mollis* (Hook. & Tayl.) Schiffn. Figs. 9-10. *Acrolejeunea allisonii* Gradst.

Fig. 1. Portion of stem, x 30. Fig. 2. Portion of female branch, x 30. Fig. 3. Leaf, x 30. Fig. 4. Free margin of lobule, x 70. Figs. 5, 9. Portion of fertile branch (paroicous), x 20. Fig. 6 Leaf, x 70. Fig. 7. Median lobe cells, x 450. Figs. 8, 10. Inner female bract, x 70.

Figs. 1-4 from the type. Figs. 5-8 from N.Zealand, Hodgson s.n., 1945. Figs. 9-10 from the type.

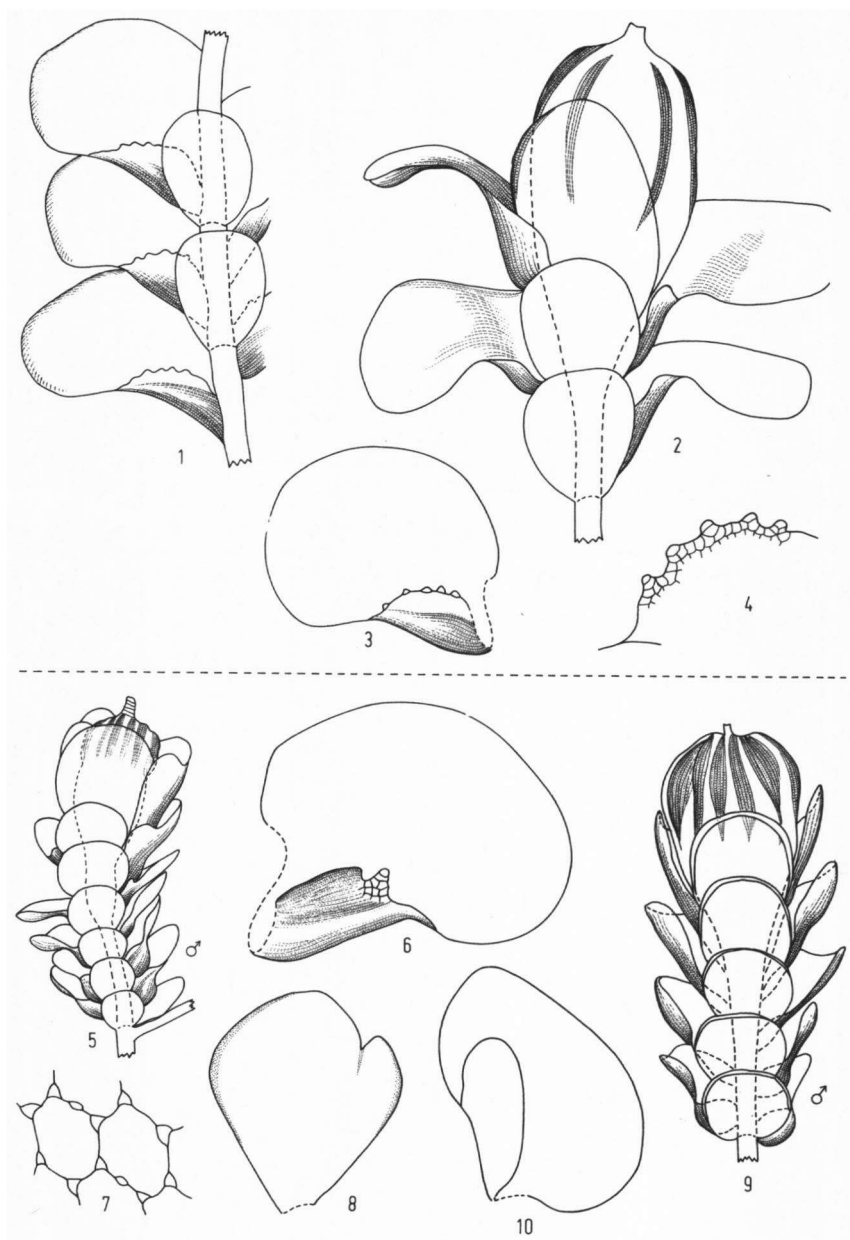


Plate XIII. *Acrolejeunea fertilis* (Reinw., Blume & Nees) Schiffn.

Fig. 1. Portion of female branch, x 30. Figs 2-4. Perianth and inner bract, showing variation, x 30. Fig. 5. Inner female bract, x 30. Inner female bracteole, x 30. Figs. 7-9. Leaves, x 50. Figs. 10-11. Median lobe cells, showing oil bodies, x 400. Fig. 12. Lobule free margin, seen from the inner side (a = apical tooth), x 200. Fig. 13. Underleaves, x 50. Fig. 14. Male bract, x 70.

Figs. 1, 5-7, 10, 12-13 from the type. Fig. 2 from the type of *A. wichurae*. Fig. 3 from Vietnam, Eberhardt s.n. Figs. 4, 12 from the type of *Ptychocoleus intergribracteatus*. Fig. 8 from Borneo, Ledru s.n. Fig. 9 from Andaman Is., Prain s.n. Fig. 11 from Singapore, Sipman 6883.

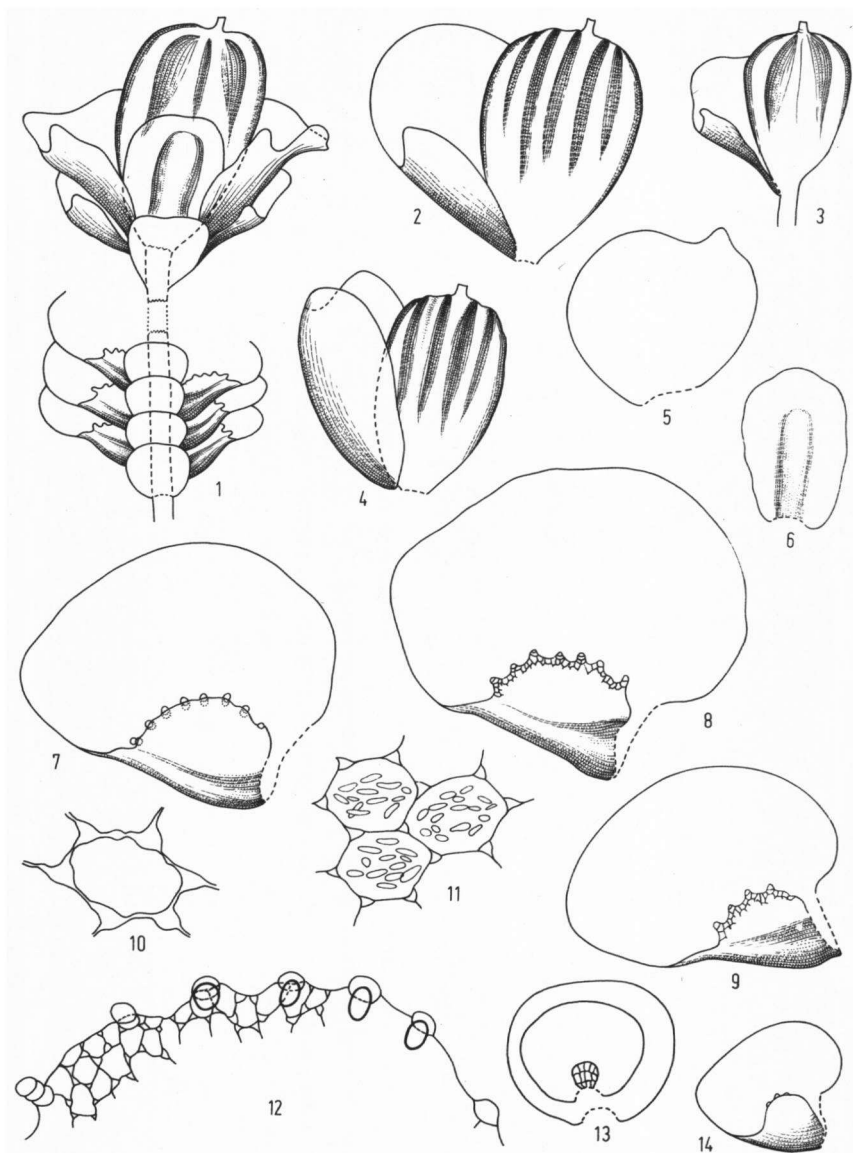


Plate XIV. Figs. 1-8. *Acrolejeunea aulacophora* (Mont.) Steph. Figs. 9-13. *Acrolejeunea securifolia* (Nees) Watts: fig. 9. ssp. *pallida* (Aongstr.) Gradst; figs. 10-12. ssp. *hartmannii* (Steph.) Gradst.; fig. 13. ssp. *securifolia*.

Fig. 1. Portion of female branch, x 20. Fig. 2. Leaf and underleaf, x 70. Fig. 3. Leaf, x 70. Fig. 4. Lobule free margin, seen from the inner side (a = apical tooth), x 200. Fig. 5. Leaf cell near dorsal leaf margin, showing oil bodies, x 450. Median lobe cell, x 450. Fig. 7. Inner female bracts and bracteole, x 20. Fig. 8. Perianth, in transverse section, x 65. Figs. 9-10. Portion of female branches, x 30. Fig. 11. Inner female bract, x 20. Fig. 12. Inner female bracteole, x 20. Fig. 13. Inner female bracts and bracteole, x 20.

Figs. 1, 3-4, 6-8 from the type of *Pt. renauldii*. Fig. 2 from the type. Fig. 5 from Samoa, Schultze-Motel 3118. Fig. 9 from Rarotonga, unkn. coll. Figs. 10-12 from the type of *A. miholitsii* (Philippines). Figs. 13 from Australia, Watts 64.

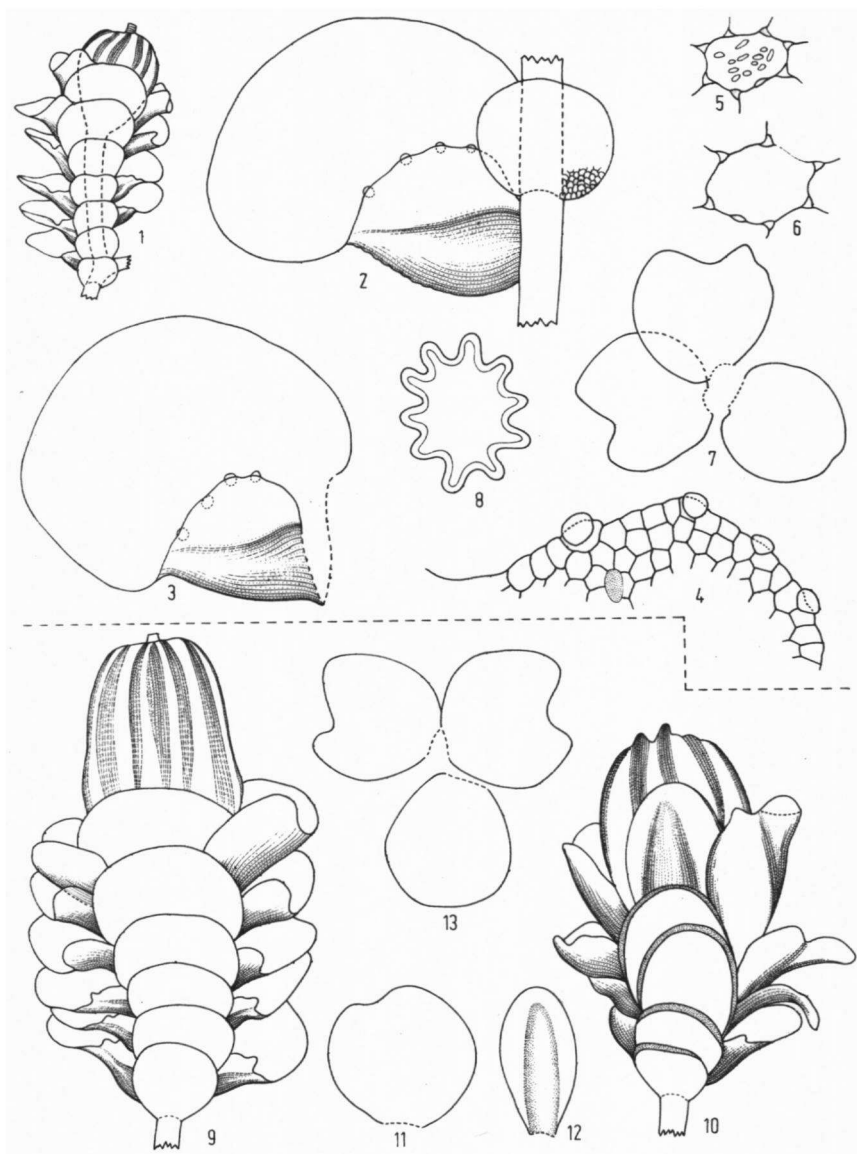


Plate XV. *Acrolejeunea securifolia* (Nees) Watts. Figs. 1, 2, 7, 10, 13. ssp. *securifolia*. Figs. 3, 9, 12. ssp. *hartmannii* (Steph.) Gradst. Figs. 5, 6, 8. ssp. *caledonica* (Steph.) Gradst. Figs. 4, 11. ssp. *pallida* (Aongstr.) Gradst.

Figs. 1-4. Leaves, x 50. Figs. 5-6. Leaves, x 30. Fig. 7. Underleaf, x 50. Fig. 8. Ibid., x 30. Fig. 9. Portion of stem, x 50. Fig. 10. Median lobe cells, x 400. Figs. 11-12. Apex of lobule, x 275. Fig. 13. Ibid., seen from the inner side, showing hyaline papilla, x 200.

Figs. 1, 13 from Australia, Watts 64. Figs. 2, 7, 10 from the type (Norfolk I.). Figs. 3, 9, 12 from the type of *A. micholitzii* (Philippines). Figs. 4, 11 from Rarotonga, unkn. coll. Fig. 5 from the type (N. Caledonia). Figs. 6, 8 from Hürlimann 2061.

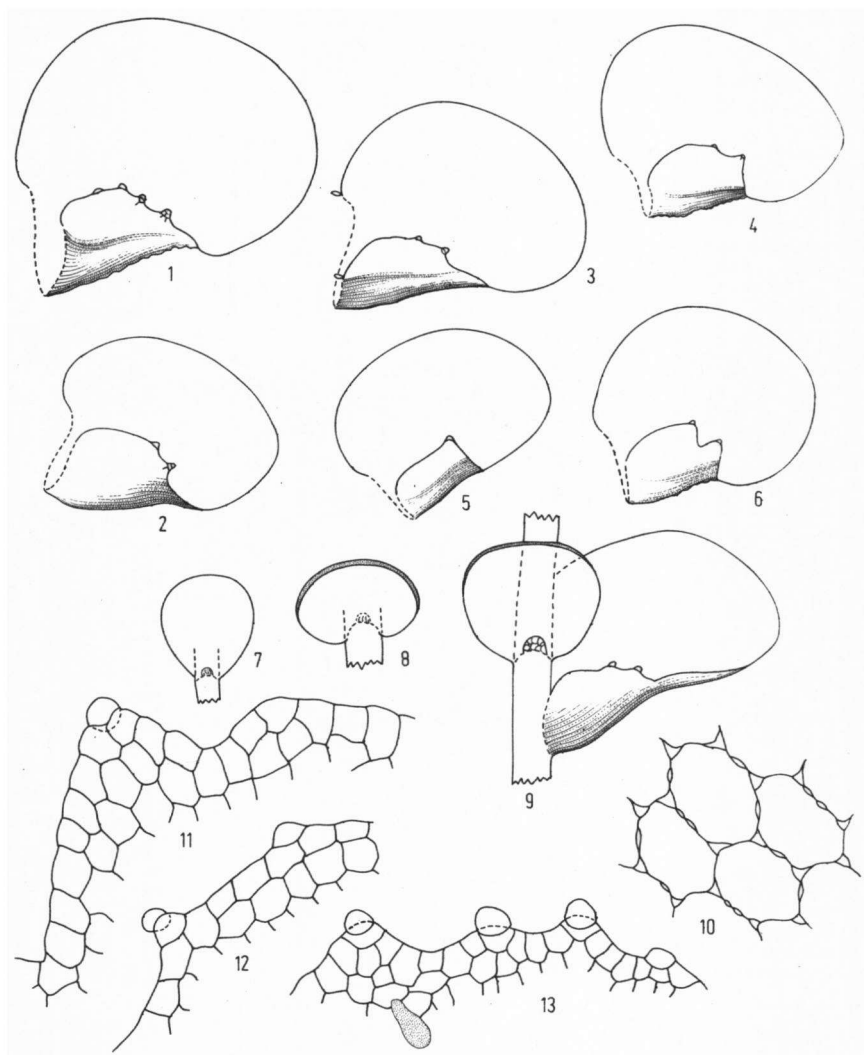


Plate XVI. *Acrolejeunea pycnoclada* (Tayl.) Schiffn. Figs. 1-10. ssp. *pycnoclada*. Figs. 11-12. ssp. *latistipula* Gradst.

Fig. 1. Portion of stem with gynoecium, x 30. Figs. 2-4. Leaves, x 70. Fig. 5. Apex of lobule (a = apical tooth), x 300. Figs. 6-7. Median lobe cells, showing oil bodies, x 450. Fig. 8. Inner female bract, x 30. Fig. 9. Apex of inner female bract, x 70. Fig. 10. Juvenile gynoecium, with longly emergent involucre, x 30. Fig. 11. Leaf (a = apical tooth), x 30. Fig. 12. Underleaf, x 30.

Figs. 1, 2, 8 from the type. Fig. 3 from the type of *A. pycnoclada* var. *rostrata*. Figs. 4-5, 9 from Reunion, Onraedt 73 R 4. Fig. 6 from Onraedt 71 M 5017. Fig. 7 from Samoa, Schultze-Motel 3922. Fig. 10 from Samoa, Schultze-Motel 3750. Figs. 11-12 from the type.

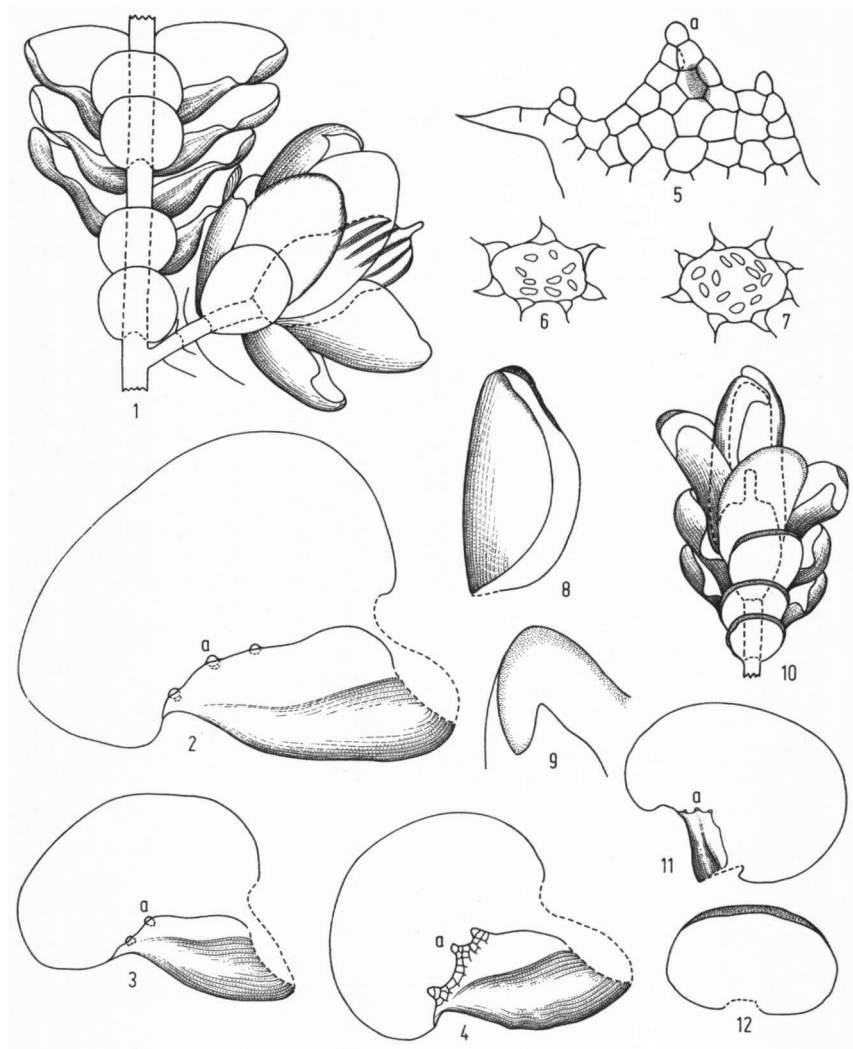


Plate XVII. *Acrolejeunea parvula* (Mizut.) Gradst.

Fig. 1. Portion of stem, ventral view, x 75. Fig. 2. Ibid., in detail showing 2-cells wide ventral merophyte and 4 superior central cells (s) at underleaf-insertion, x 200. Figs. 3-4, Leaves, x 75. Fig. 5. Portion of female branch, x 30. Fig. 6. Inner female bract and bracteole, x 30. Fig. 7. Gynoecium, x 75.

Figs. 1-6 from the type. Fig. 7 from Andaman Is., Balu Ghat, Man s.n.

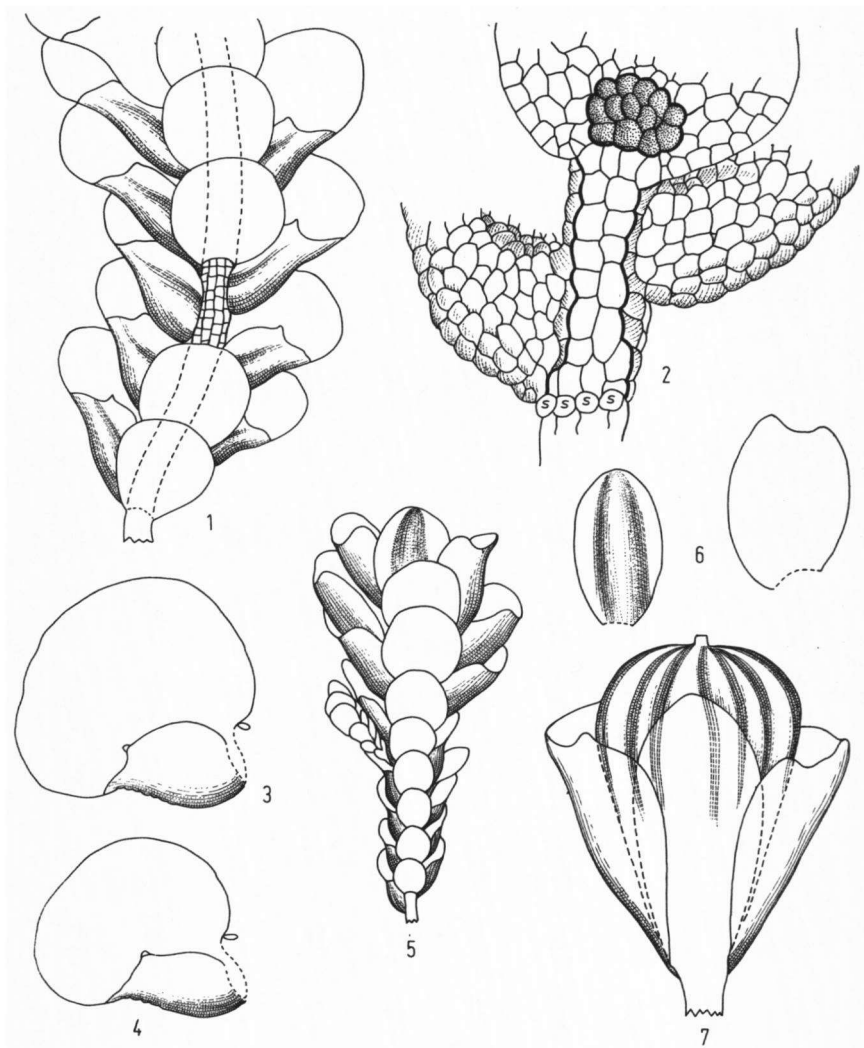


Plate XVIII. *Acrolejeunea tjibodensis* (Verd.) Grolle & Gradst.

Fig. 1. Portion of female branch, x 30. Figs. 2-5. Leaves, x 30. Fig. 6. Median leaf cell, x 400. Fig. 7. Apex of lobule (a = apical tooth), x 250. Figs. 8-9. Underleaves, x 30. Figs. 10-11. Inner female bracts, x 30. Figs. 12-13. Inner female bracteoles, x 30.

Figs. 1-3, 6-7, 8, 10-13 from the type (Tjibodas at 1420 m.). Figs. 4, 12 from Java, Schiffner s.n. (Artja at 1100 m.). Figs. 5, 11 from Java, van Leeuwen s.n. (Goenoeng Kawi at 2650 m.). Fig. 9 from N. Guinea, van Zanten 559 (Ok Sibil at 1260 m.).

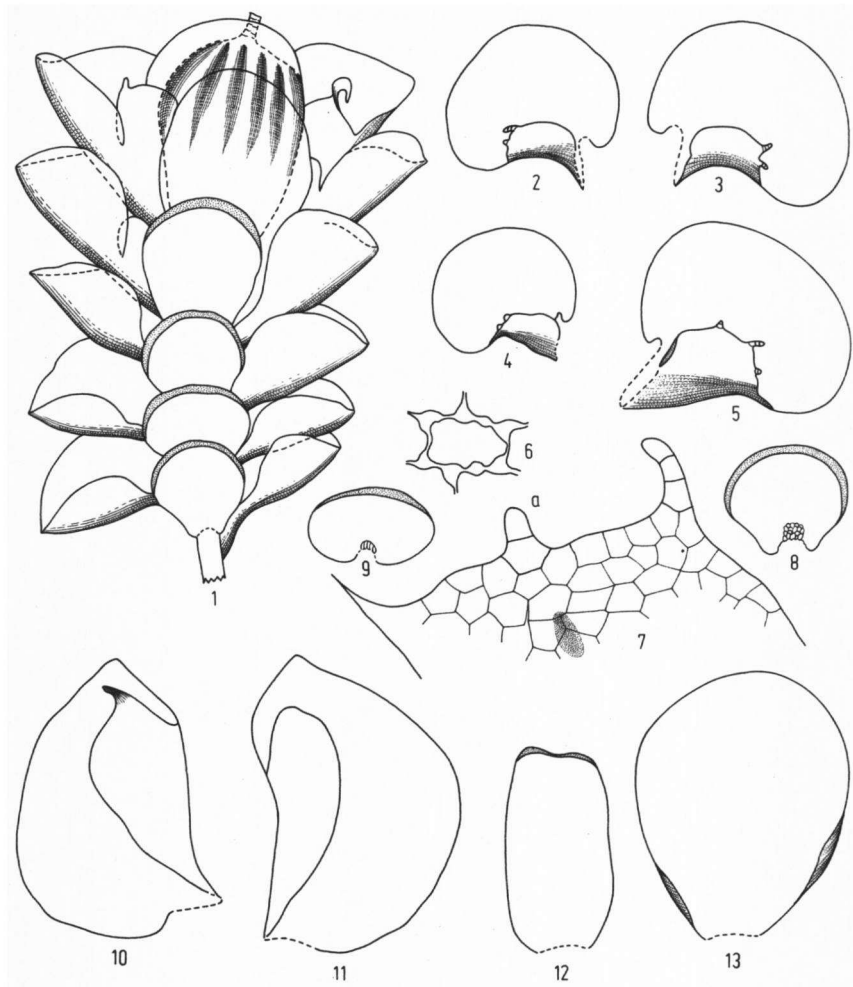
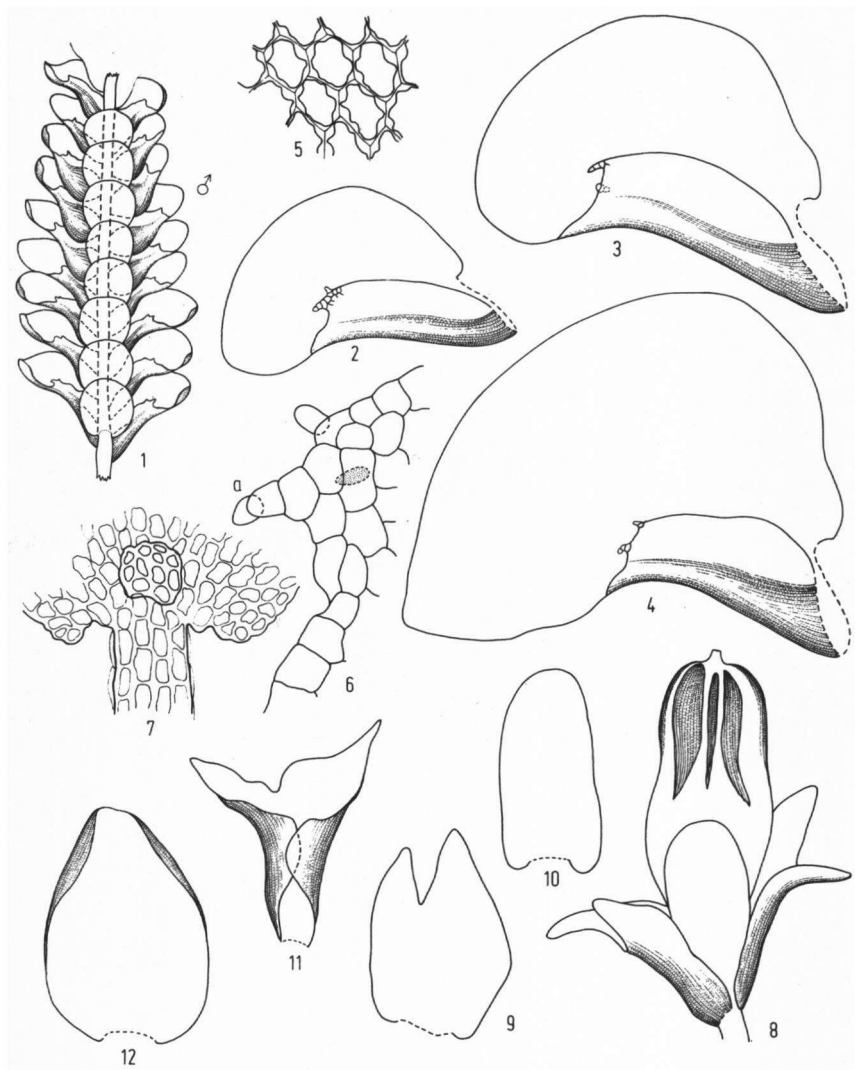


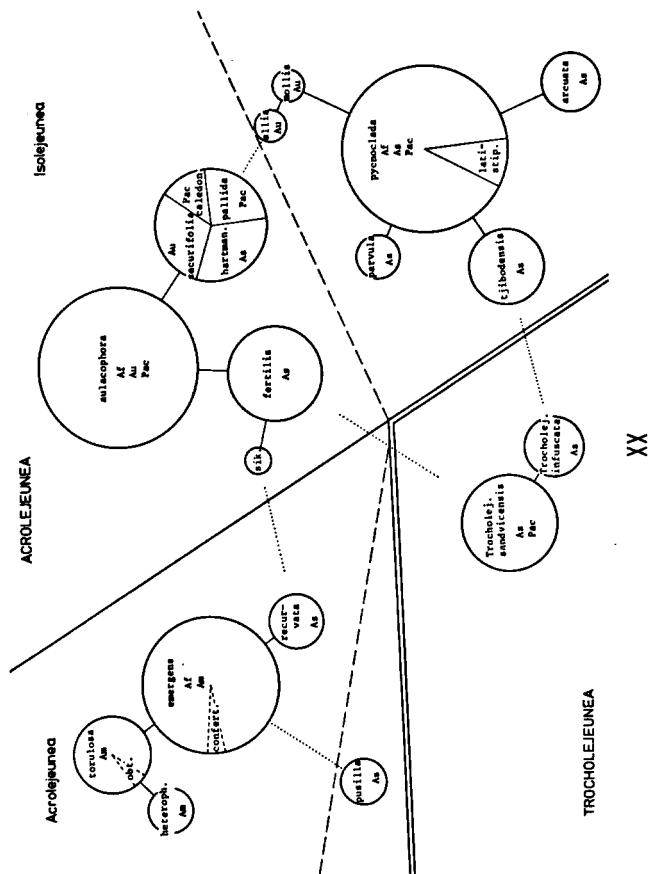
Plate XIX. *Acrolejeunea arcuata* (Nees) Grolle & Gradst.

Fig. 1. Portion of male stem, x 30. Figs. 2, 3, 4. Leaves, x 70.
Fig. 5. Median lobe cells, x 400. Fig. 6. Apex of lobule (a = apical tooth),
x 400. Fig. 7. Base of the underleaf, x 200. Fig. 8. Gynoecium, x 30. Fig. 9.
Inner female bract, x 30. Fig. 10. Inner female bracteole, x 30. Figs. 11, 12
Inner female bract and bracteole, juvenile, x 30.
Figs. 1, 2, 5, 6, 7 from the type. Fig. 3. from the type of *Pt. hians*. Fig.
4. from N. Guinea, Pulle s.n. Figs. 8, 9, 10 from Java, Treub s.n. Figs. 11,
12 from N. Guinea, Carr 15118.



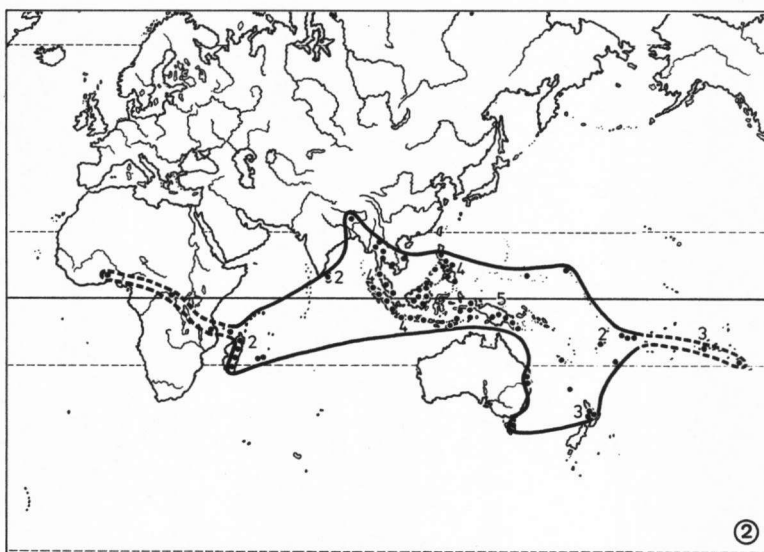
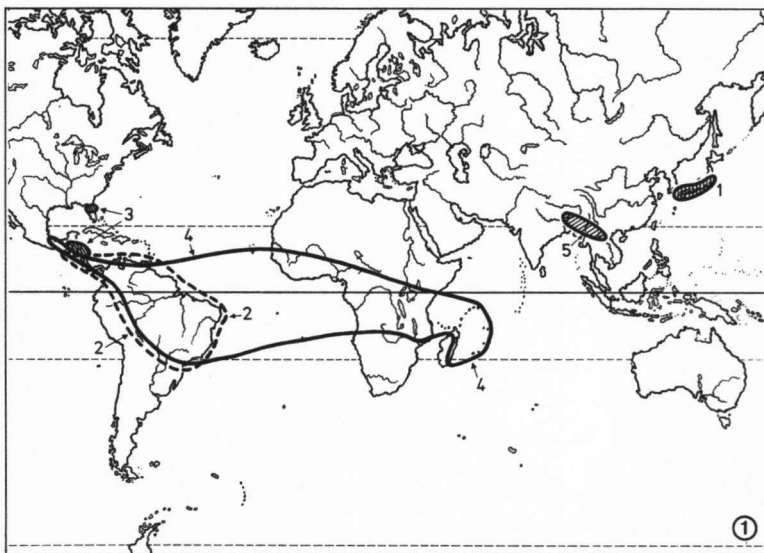
Pl.XX. *Acrolejeunea* - phenetic relationships.

For explanation see p. 42 and 50.



Pl.XXI. *Acrolejeunea* - total distribution.

- ① *A. subg. Acrolejeunea*: 1. *A. pusilla*; 2. *A. torulosa*; 3. *A. heterophylla*;
4. *A. emergens*; 5. *A. recurvata*.
- ② *A. subg. Isolejeunea*: the figures indicate the total number of species
present in the area.



Pl.XXII. *Acrolejeunea* - species distribution types.

- ③ Sect. *Regulares*: 7. *A. fertilis*; 9. *A. securifolia*: 9a. ssp. *securifolia*, 9b. ssp. *hartmannii*, 9c. ssp. *caledonica*, 9d. ssp. *pallida*.
- ④ Sect. *Regulares*: 8. *A. aulacophora*.
- ⑤ Sect. *Isolejeunea*: 11. *A. mollis*; 12. *A. pycnoclada*; 13. *A. parvula*.

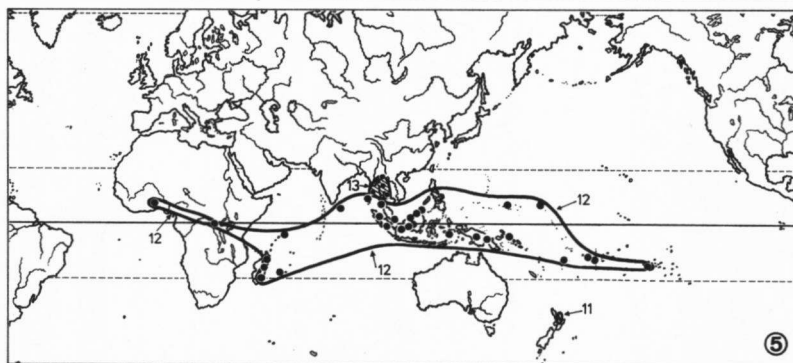
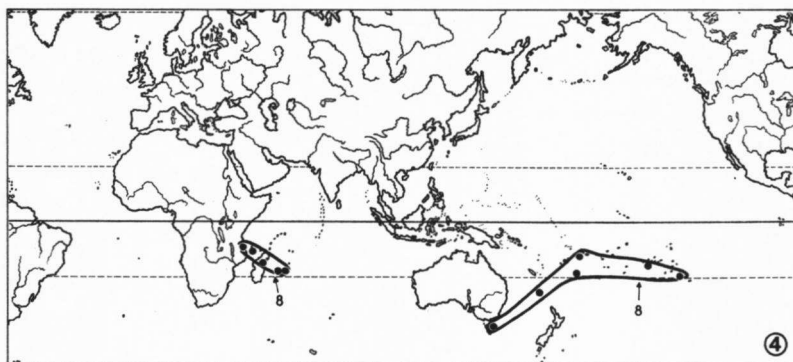
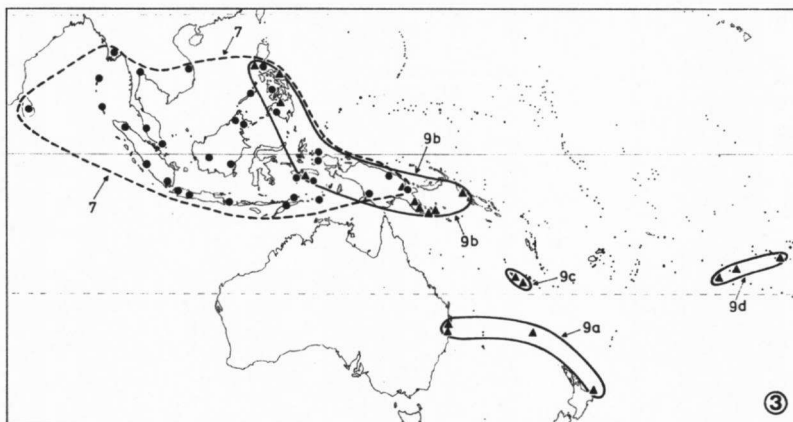
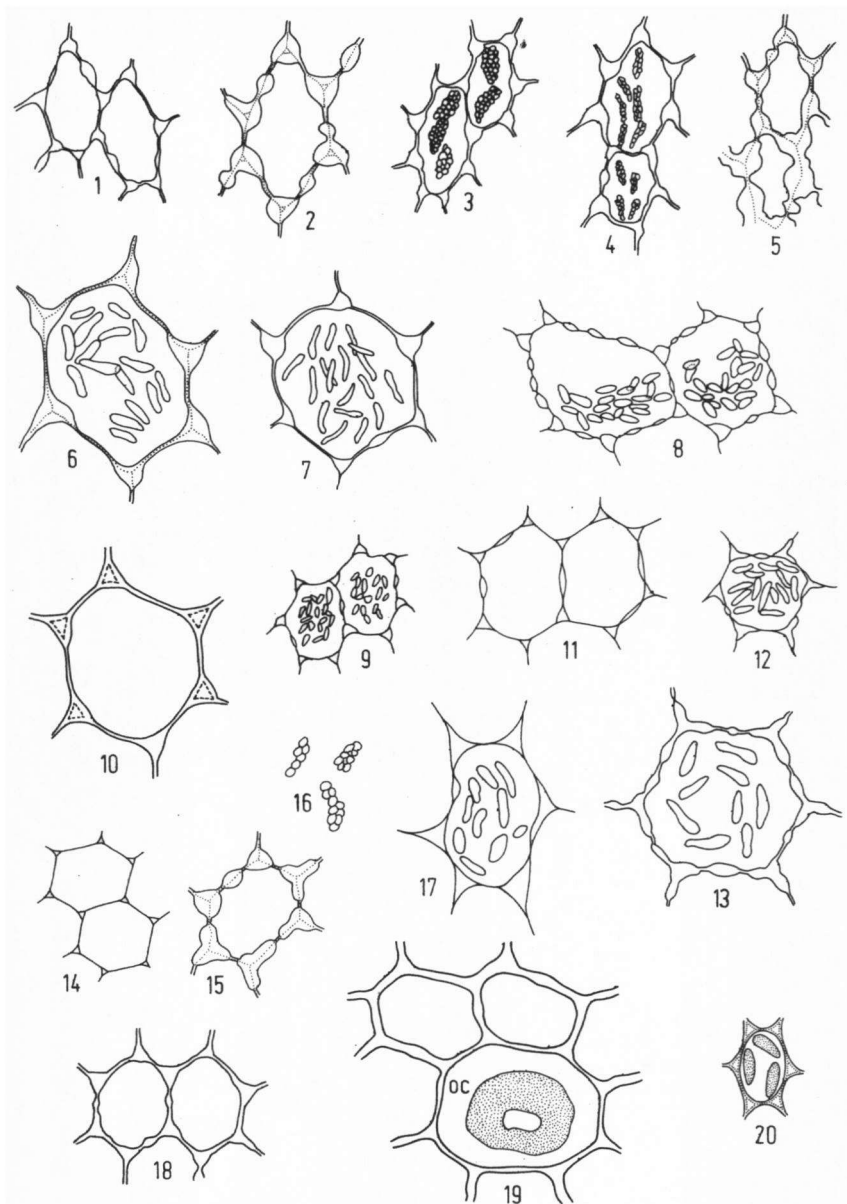


Plate XXIII. Trigones and oil bodies in Ptychanthoideae.

Figs. 1-2. *Ptychanthus*. Fig. 3. *Mastigolejeunea*. Figs. 4-5. *Schiffneriolejeunea*. Fig. 6. *Acrolejeunea*. Fig. 7. *Brachiolejeunea*. Fig. 8. *Caudalejeunea*. Figs. 9-10. *Dicranolejeunea*. Figs. 11-12. *Lopholejeunea*. Fig. 13. *Marchesia*. Figs. 14-16. *Archilejeunea*. Fig. 17. *Spruceanthus*. Fig. 18. *Tuxibeanthus*. Fig. 19. *Stictolejeunea*, showing ocellus (oc). Fig. 20. *Neurolejeunea*.

Fig. 1 from *Pt. striatus*, Ethiopia, De Wilde 7680B (x 500). Fig. 2 from *Pt. striatus*, Java, Hep. Crit. Sel. Verdoorn 265 (x 750). Fig. 3 from *M. auriculata*, Brazil, Vital 2353 (x 500). Fig. 4 from *S. pulopenangensis*, Samoa, Schultze-Motel 4249 (x 500). Fig. 5 from *S. omphalanthoides*, Celebes, type (x 500). Fig. 6 from *A. torulosa*, Brazil, Smith Pl1728 (x 750). Fig. 7 from *Br. laxifolia*, Colombia, Cleef 398b (x 750). Fig. 8 from *C. hanningtonii*, Sierra Leone, Berrie s.n. (x 500). Fig. 9 from *D. phyllorhiza*, Brazil, Vital 2158 (x 500). Fig. 10 from *D. spec.*, Tanzania, Pocs 6734b (x 1500). Fig. 11 from *L. sagraeana*, Florida, Verdoorn s.n. (x 1000). Fig. 12 from *L. subfusca*, Sierra Leone, Berrie s.n. (x 500). Fig. 13 from *M. brachiata*, Brazil, Vital 2509 (x 750). Fig. 14 from *A. linguaeifolia*, Africa, type (x 500). Fig. 15 from *A. porelloides*, Brazil, Spruce s.n. (x 500). Fig. 16 from *A. cf. parviflora*, Suriname, Mc Gillavry s.n., drawn by A. Luitingh. Fig. 17 from *S. polymorphus*, Hawaii, Hoe/ s.n. (x 750). Fig. 18 from *T. chinensis*, Japan, Kodama s.n., Bryophyta Sel. Exsicc. Inoue 125 (x 500). Fig. 19 from *S. squamata*, Peru, Hegewald 6377 (x 750). Fig. 20 after SCHUSTER & HATTORI 1954: 77 (x 450).



Pl.XXIV. Ptychanthoideae - phenetic relationships.

For explanation see p. 148. Af = Africa; Am = America; As = Asia; Au = Australasia; Eu = Europa; Pac = Pacific; PAN = pantropical.

PTYCHANTHOIDEAE

Ptychantheae

Archilejeuneae

