Contributions to a Monograph of the

Lejeuneaceae

Subfamily

Ptychanthoideae

edited by

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To the memory of
FRANS VERDOORN
1906 - 1984

whose "Studien über Asiatische Jubuleae" (1934)
paved the way for monographic research in Lejeuneaceae

Preface

This volume presents a collection of studies on Lejeuneaceae, that large and taxonomically troublesome liverwort family whose members dwell in great profusion in forests of the Tropics. Main emphasis is on the taxonomy and distribution of members of the subfamily Ptychanthoideae, in the older literature known as "Holostipae". Some data pertinent to the family as a whole are included as well.

At an earlier occasion (*Systematics Association Special Volume* 14: 83-107. 1979) I outlined the two approaches to Lejeuneaceae systematics that I consider called for today: 1) studies on new or neglected characters, exploring their nature and taxonomic relevance, and 2) revisions of individual genera, aiming at establishing better generic and specific concepts and at elucidation of the biogeographic and evolutionary histories of the individual taxa. Accordingly, papers in this volume are arranged into two different sections.

Monographic work today is a team effort. For this volume contributions were written by several colleagues and students, to all of whom I express my gratitude. Professor Yoshinori Asakawa and Miss Reiko Matsuda (Tokushima) checked, with unfailing enthusiasm, numerous samples of Lejeuneaceae for the presence of terpenoids and aromatic compounds; Dr. Barbara Thiers (New York) presented an innovative analysis of the complicated branching systems in Ptychanthoideae; Professor Constant Vanden Berghen (Bruxelles) contributed to the taxonomy of *Schiffneriolejeunea* with his expert knowledge of the African flora; and my students Michiel van Slageren, Rob Kruijt, Trudy Buskes and Jos van Beek helped revising the taxonomy of several neotropical genera.

Special thanks are due to Michiel van Slageren and Rob Kruijt who prepared the Index. Michiel van Slageren consented to the reproduction of some of his excellent SEM photographs of Lejeuneaceae sporophytes. I also acknowledge travel support from the Netherlands Organization for the Advancement of Pure Research (ZWO) and the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

Half a century has elapsed since the appearance of Professor Frans Verdoorn's thesis on Asiatic Ptychanthoideae ("*Studien über Asiatische Jubuleae*"). For Lejeuneaceae this publication was a breakthrough, as it marked the beginning of modern taxonomic work on the group. Even though being involved in different aspects of biology during his later years, Professor Verdoorn kept an interest in bryology and supported me, his former student, in many ways to pursue my bryological work. Late May 1984 Professor Verdoorn died. To his memory this volume is dedicated.

S. Rob Gradstein

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Section one

Keys and Characters

1 A Guide to the Holostipous Lejeuneaceae

by

S.R. Gradstein

ABSTRACT: This paper provides a generic key, emphasizing vegetative characters, as well as references to the main literature on the genera and species of Lejeuneaceae with entire underleaves ("holostipous Lejeuneaceae"). The group is polyphyletic according to recent classifications, comprising taxa of five different subfamilies. The following taxonomic novelties are proposed: *Schiffneriolejeunea amazonica* sp. nov., *Spruceanthus sulcatus* (Nees) comb. nov. and *Spruceanthus theobromus* (Spruce) comb. nov.

Introduction

Lejeuneaceae include species with or without underleaves. Those with underleaves (the majority) have traditionally been classified (e.g. Spruce 1884) into "Lejeuneaceae Holostipae" (underleaves undivided) and "Lejeuneaceae Schizostipae" (underleaves bifid). This system has now become obsolete and has been replaced by a more natural classification into subfamilies, based on several gametophytic as well as sporophytic characters (Schuster 1984, Grolle 1983). The current subfamily system of Lejeuneaceae is shown in Table I, which also lists the genera containing holostipous species. From this table it becomes apparent that holostipous Lejeuneaceae are a clearly unnatural, polyphyletic group, comprising taxa of 5 different subfamilies. Two subfamilies and 34 genera are purely holostipous, including most notably the Ptychanthoideae (23 genera). Notwithstanding their unnaturalness, "Holostipae" and "Schizostipae" are still recognised in practical Lejeuneaceae taxonomy as the most distinct groups. The present paper focuses on the holostipous members of the family and presents an up-to-date generic key emphasizing vegetative characters, to facilitate identification of sterile material. In addition, references to the main literature on individual genera and species are provided.

Table I. The genera of holostipous Lejeuneaceae arranged according to the currently recognised subfamilies. Total number of genera in each subfamiliy in brackets (after Grolle 1983, slightly modified).

BRYOPTERIDOIDEAE (1 genus)
Bryopteris

COLOLEJEUNEOIDEAE (7 genera)
Calatholejeunea
Diplasiolejeunea p.p. min. (1 sp)

LEJEUNEOIDEAE (40 genera)
Amblyolejeunea
Amphilejeunea
Anoplolejeunea
Aureolejeunea
Ceratolejeunea p.p. min.
Cheilolejeunea p.p. min.
Cyclolejeunea p.p.
Cyrtolejeunea
Evansiolejeunea
Lejeunea (s.l.) p.p. min.
Lepidolejeunea p.p.
Leucolejeunea
Omphalanthus
Physantholejeunea

METZGERIOPSOIDEAE (1 genus)
—

MYRIOCOLEOIDEAE (2 genera)
—

NIPPONOLEJEUNEOIDEAE (1 genus)
—

PTYCHANTHOIDEAE (23 genera)
Acrolejeunea
Archilejeunea
Blepharolejeunea
Brachiolejeunea
Caudalejeunea
Cephalolejeunea
Dicranolejeunea
Lindigianthus
Lopholejeunea
Marchesinia
Mastigolejeunea
Neurolejeunea
Odontolejeunea
Phaeolejeunea
Ptychanthus
Schiffneriolejeunea
Spruceanthus
Stictolejeunea
Symbiezidium
Thysananthus
Trocholejeunea
Tuzibeanthus
Verdoornianthus

TUYAMAELLOIDEAE (5 genera)
Tuyamaella p.p. min. (1 sp)

Key

1\. Leaf cells longer than wide, with cordate trigones: 2 sides convex, 1 side concave. Leaves when dry strongly wrapped around the stem............. 2

1\. Leaf cells isodiametric (elongate in *Neurolejeunea*), the trigones various but not cordate. Leaves when dry spreading, curved downwards or folded, but usually not wrapped around the stem....................................... 16

2. Branches predominantly of the *Frullania*-type........................ 3

2. Branches predominantly of the *Lejeunea*-type (a few vigorous *Frullania*-type branches may be present).. 9

3. Plants pendulous, ± regularly (bi)pinnate. Ventral cortex cells not larger than the medulla cells (stem cross section), walls of the stem cells strongly thickened, the stems rigid. Leaves dentate, occasionally entire. Perianth with about 10 keels, on branches with one subfloral innovation. Palaeotropical.......... .... 31. *Ptychanthus striatus*

3. Plants creeping, ascending or pendulous, dichotomous or irregularly branched. Ventral cortex cells distinctly larger than the medulla cells, walls of the stem cells thin or thickened... 4

4. Leaf lobule with (1-)2 teeth. Leaves dentate or entire................. 5

4. Leaf lobule with 3 or more teeth. Leaves entire (sometimes dentate in *Brachiolejeunea* (subg. *Plicolej.*) *laciniatiflora* from Peru)............ 7

5. Lobule apex truncate, with 2 dissimilar teeth, the second tooth more conspicuous than the first one: first tooth situated in the sinus, incurved and blunt, second tooth at lobule angle, sharp, pointing outwards. Latin America, montane... 7. *Blepharolejeunea*

5. Lobule apex rounded or oblique, the teeth identical or the first tooth more conspicuous.. 6

6. Leaves strongly convoluted. Underleaves large, auriculate at base. Ventral merophyte 6 or more cells wide. Perianth inflated, ca. 10-keeled. Southeast Asia................................. 37. *Trocholejeunea infuscata*

6. Leaves convoluted or spreading. Underleaves small or large, decurrent, not auriculate. Ventral merophyte 2-4 cells wide. Perianth flattened, 3-5-keeled. Pantropical................................... 17. *Dicranolejeunea*

7. Plants greenish, soon turning blackish. Perianth with 5-11 keels. Tropical America, Africa, Himalaya.......... 8. *Brachiolejeunea* subg. *Plicolejeunea*

7. Plants greenish to brownish, not turning blackish. Perianth with 3-10 keels. 8

8. Stems on dorsal surface bearing a 1-3 cells high longitudinal lamella. Perianth 3-keeled. Female bracts always with enlarged lobules (innovations *Radula*-type) and a winged keel. Latin America, montane...................... .... 8. *Brachiolejeunea* subg. *Brachiolejeunea*

8. Stem without longitudinal lamella on its dorsal surface. Perianth with ca. 10 keels. Female bracts dimorphic, with or without lobule (innovation *Frullania*-type), the keel without wing. Southeast Asia (lacking in Malesia) and northern Pacific.................. 37. *Trocholejeunea sandvicensis*

9. Ventral cortex cells in cross section not distinctly higher than the medulla cells, the cortical walls often brownish pigmented, thickwalled; stems rigid*..... 10

9. Ventral cortex cells in cross section distinctly higher than the medulla cells, the cortical walls colourless, thinwalled or thickened; stems fragile or ± rigid.. 14

**Spruceanthus semirepandus*, which might key out here, has isodiametric leaf cells with triangular to radiate (not cordate) trigones.

10. Leaves dentate.. 11
10. Leaves entire.. 12

11. Plants pendulous, ± regularly (bi)pinnate or dichotomous. Leaves without vitta. Leaf cells with numerous intermediate thickenings, 1-3 on each wall. Oil bodies more than 10 per cell, homogeneous. Perianth without subfloral innovation. Tropical America, (?) Madagascar...................... 9. *Bryopteris*
11. Plants creeping to pendulous, irregularly to regularly pinnate. Leaves with or without vitta. Leaf cells with few intermediate thickenings, 0-1 per cell wall. Oil bodies less than 8 per cell, segmented. Perianth with 1-2 subfloral innovations. Pantropical.................................. 36. *Thysananthus*

12. Plants regularly and densely (bi)pinnate, feather-like, lacking blackish pigmentation. Oil bodies homogeneous. See 11................ 9. *Bryopteris*
12. Plants irregularly branched or dichotomous, with or without blackish pigmentation. Oil bodies segmented.................................. 13

13. Plants turning brownish on age, never becoming blackish. Perianth with 0-6 keels, lacking *Radula*-type subfloral innovations. Pantropical.. 32. *Schiffneriolejeunea*
13. Plants turning blackish. Perianth with 3-10 keels and with 1-2 *Radula*-type subfloral innovations. Pantropical.................... 25. *Mastigolejeunea* (and entire-leaved species of *Thysananthus: T. convolutus, T. anguiformis*).

14. Ventral merophyte 2-3(4) cells wide. Perianth flattened, with ± dentate to laciniate lateral keels and 1-2 *Radula*-type innovations. Pantropical.. 17. *Dicranolejeunea*
14. Ventral merophyte 4 or more cells wide. Perianth flattened or inflated, keels smooth or dentate, without *Radula*-type subfloral innovations (when present: go to 4).. 15

15. Leaves dentate or entire, convolute or spreading. Intermediate thickenings numerous, 1-3 per cell wall. Asexual reproduction lacking or by discoid gemmae from leaf surfaces. Perianth with 3-5(-7) keels, the female bracts with reduced lobules. Male bracts hypostatic. On leaves or twigs. Pantropical.. 11. *Caudalejeunea*
15. Leaves always entire, regularly convolute. Intermediate thickenings fewer, 0-1 per cell wall. Asexual reproduction lacking or by means of caducous leaves from flagelliform shoots (subg. *Acrolejeunea*). Perianth with 5-10 keels, the lobule of the female bracts well-developed, enlarged. Male bracts epistatic. On bark, rock or soil. Pantropical.......................... 1. *Acrolejeunea*

16. Plants blackish.. 17
16. Plants not blackish.. 21

17. Leaf cells small, ± elongated, ca. 10-20 μm long, intermediate thickenings lacking. Leaves often with a vitta or with ocelli in a row. Perianth with 2 innovations, the keels expanded into auricles or horns. Lobule with 1 long, curved tooth. Tropical America....................... 26. *Neurolejeunea*

17. Leaf cells larger, isodiametric, 20-40 µm in diam., with intermediate thickenings. Vitta or ocelli lacking. Perianth with or without innovations, the keels not expanded. Lobule teeth various, sometimes reduced................. 18

18. Lobule (when developed) at least in the proximal part strongly inflated-saccate, bulging with the free margin incurved, without or with 1 short tooth. Ventral cortex cells distinctly larger than medulla cells (cross section). Perianth keels ciliate-laciniate, rarely smooth........................ 19

18. Lobule (when developed) inflated but not strongly so, not bulging outwards, the free margin plane, with 1-4 teeth. Ventral cortex cells not larger than medulla cells. Perianth keels smooth or somewhat denticulate.......... 20

19. Stem with leaves (1,5)2-5 mm wide. Underleaf insertion line strongly arched, ca. 200 µm deep (in *S. madagascariensis* shallowly curved only). Lobule entirely saccate, small, hidden behind the sometimes very large underleaves. Perianth on an abbreviated branch, with 1 short *Radula*-type innovation. Male bracteoles limited to the base of the spike. Tropical America, East African Islands. .... 35. *Symbiezidium*

19. Stem with leaves up to 2 mm wide. Underleaf insertion line straight or curved, to 100 µm deep. Lobule saccate below, the apex ± flattened, small or large. Perianth on an elongated shoot, without *Radula*-type innovation (when innovations present: *Dicranolejeunea*). Male bracteoles present throughout the spike. Pantropical.................................. 23. *Lopholejeunea*

20. All or at least some lobules reduced, with 0-2 teeth. Ventral merophyte 4(6) cells wide. Leaf cell walls colourless. Perianth with 4-5 keels. Pantropical.... .... 5. *Archilejeunea* subg. *Dibrachiella*

20. Lobules usually not reduced, with (1)2-4 teeth. Ventral merophyte 4-12 cells wide. Leaf cell walls often darkish pigmented. Perianth flat, with 2 lateral keels only. Tropical America, Africa, Europe............ 24. *Marchesinia*

21. Leaf lobules as large as the lobes or larger, jointly forming a tubular structure, the lobules strongly involuted. Leaf segmentation pendulum-type: 1 underleaf per lateral leaf. Eastern Malesia.............. 10. *Calatholejeunea paradoxa*

21. Leaves different, lobules smaller than lobes. 1 underleaf per lateral leaf pair*.. 22

22. Leaves with numerous, scattered ocelli............................. 23

22. Ocelli lacking or 1-2 at leaf base only.............................. 25

23. Ventral merophyte 4 or more cells wide. *Frullania*-type branches present or lacking. Gynoecium on an abbreviated lateral branch. Pantropical........... .... 34. *Stictolejeunea*

23. Ventral merophyte 2 cells wide. *Frullania*-type branches lacking. Gynoecium on an elongated shoot.. 24

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*Except in 17a. *Diplasiolejeunea integerrima* Tix. from Madagascar, which has one undivided underleaf for each leaf, and juvenile plantlets of various holostipous genera, which may also possess this type of leaf segmentation.

24. Plants tiny, ca. 1-1,5 mm wide. Leaf apex entire, with a whitish group of fragile, dead, thinwalled cells (often in *Stictolejeunea* as well). Tropical America.......................... 30. *Physantholejeunea portoricensis*
24. Plants larger, ca. 1,5-3 mm wide. Leaf apex dentate or entire, lacking a whitish group of dead cells. Pantropical........... 20. *Lepidolejeunea* spp

25. Ventral merophyte 4 or more cells wide.............................. 26
25. Ventral merophyte 2(3) cells wide.. 40

26. Vegetative branches predominantly *Frullania*-type.................... 27
26. Vegetative branches predominantly *Lejeunea*-type..................... 29

27. Leaves entire, regularly spreading when dry, the cells isodiametric......... 28
27. Leaves dentate or entire, at least in part folded or convoluted, the cells isodiametric or elongated.. 3

28. Stems pendulous. 3-10 cm long, regularly pinnate. Perianth with 10 keels, on branches with 1 innovation. Japan, China...... 39. *Tuzibeanthus chinensis*
28. Stems creeping, shorter, irregularly branched. Perianth 5 keeled, with 2 innovations. Lobule free margin at apex inflexed, with one large, erect tooth (lobule with 2 small teeth: *Dicranolejeunea*). Pacific and Eastern Malesia .... 29. *Phaeolejeunea*

29. Ventral cortex cells not higher than medulla cells...................... 30
29. Ventral cortex cells distinctly higher than medulla cells................. 38

30. Leaf cells usually with large, bulging trigones, intermediate thickenings absent (present in *Leucolejeunea*). Hyaline papilla situated in a small sinus (or on the inner lobule surface) distal of the apical tooth. Male bracteoles limited to the base of the spike. Oil bodies 1-5 per cell, 10-20 μm long, segmented.. 31
30. Trigones small or large, intermediate thickenings present. Hyaline papilla proximal of the apical tooth. Male bracteoles present throughout the spike. Oil bodies more than 5 per cell, up to 12 μm long, homogeneous or segmented 34

31. Stems ± pendulous, long and slender, little branched. Ventral merophyte 4-12 cells wide. Leaf apex rounded to acuminate. Tropical America, montane...... .... 28. *Omphalanthus*
31. Stems creeping to ascending, branching infrequent or frequent. Ventral merophyte (2)4 cells wide. Leaf apex always rounded.................... 32

32. Plants deep brownish pigmented. Tropical America, montane............ .... 6. *Aureolejeunea*
32. Plants pale-coloured, yellowish-green to grayish...................... 33

33. Leaf cells with intermediate thickenings. Leaves usually closely imbricated, shoots compact. Female bracts not larger than leaves. 2 innovations. Pantropical... 21. *Leucolejeunea*
33. Leaf cells lacking intermediate thickenings. Leaves laxly imbricated, shoots less compact. Female bracts much larger than leaves; innovations lacking. East Africa, montane.......................... 18. *Evansiolejeunea roccatii*

34. Ventral merophyte 4-6(8) cells wide. Leaf margins entire. Lobule with 0-2 teeth. Perianth keels 2-5.................................... 35
34. Ventral merophyte 6-12 cells wide. Leaves dentate or entire. Lobule with 2-4 teeth. Perianth keels 2-10.................................... 37

35. All or at least some lobules reduced. Perianth 4-5-keeled. See 20............. .... 5. *Archilejeunea* subg. *Dibrachiella*
35. Lobules well developed, not showing a tendency for reduction (*Marchesinia* sometimes excepted). Perianth 2-5-keeled.............................. 36

36. Plants greenish to brownish to blackish. Lobule apex rounded or oblique, not continuing into the ventral margin of the lobe, with 1-2 (or more) teeth. Perianth ventral surface flat, without keels. Innovations *Radula-Lejeunea*-type. See 20... 24. *Marchesinia*
36. Plants brownish. Lobule apex truncate (in *Verdoornianthus marsupiifolius* from Amazonia oblique and continuing into the ventral lobe margin), with 1-2 teeth. Perianth ventral surface swollen, with 1-2 keels. Innovations *Radula-Jubula*-type or lacking.................................. 36a

36a. Plants glossy brownish. Leaves when moist widely spreading, plane or convex, not squarrose. Underleaf base in cross section bistratose. Innovations 1-2. Tropical South America, common...... 5. *Archilejeunea* subg. *Archilejeunea*
36a. Plants dull brownish, leaves when moist suberect, not spreading widely, ± squarrose. Underleaf base in cross section tristratose. Innovations lacking. Amazon basin, rare................................ 40. *Verdoornianthus*

37. Perianth flat, subrectangular-obovate, 2-keeled. See 20.... 24. *Marchesinia*
37. Perianth inflated, cylindrical, 6-10 keeled. Tropical Asia, Australasia, Pacific, Tropical America............................ 33. *Spruceanthus*

38. Plants tiny, fragile, leafy stems up to 1,5 cm long, ca. 1 mm wide, pale-coloured. Leaf lobule with 1 rudimentary tooth. Perianth inflated-swollen, near apex with 8-10 crenulate keels, otherwise smooth; 1 subfloral innovation. Borneo................................ 13. *Cephalolejeunea parviloba*
38. Plants different... 39

39. Leaf apex acuminate-denticulate, strongly reflexed. Lobule inflated along the keel, flattened along the free margin, with 2 teeth. Perianth with 2 innovations. Male bracts epistatic (same characters except for leaves entire, with apex ± plane: *Dicranolejeunea*). Tropical America, montane............ .... 22. *Lindigianthus cipaconeus*
39. Leaf apex rounded or acute, entire or toothed, plane or reflexed. Lobule at at least in the lower part strongly inflated-saccate with the free margin incurved, teeth 0-1. Perianth with 0-1 innovations. Male bracts hypostatic.. 19

40. Leaf margins with teeth, at least near apex............................ 41
40. Leaves entire.. 43

41. On bark, rock or soil (rarely on leaves), creeping or pendulous, rhizoid discs small or lacking. A few *Frullania*-type branches usually present. Asexual reproduction lacking. Pantropical................. 17. *Dicranolejeunea*

41. Creeping over leaves or twigs, usually producing large rhizoid discs. *Frullania*-type branches lacking. Asexual reproduction present (by caducous branches or gemmae) or absent.................................... 42

42. Underleaf base auriculate, the line of insertion long and deeply arched. Lobule with (1)2-4 teeth. Ocelli lacking. Asexual reproduction, when present, by means of caducous branches. Tropical America, Africa........ 27. *Odontolejeunea*
42. Underleaf base not auriculate, the line of insertion short, slightly curved only. Leaf base with 2 ocelli. Lobule with 1 tooth only. Asexual reproduction, when present, via discoid gemmae from leaf margins. Tropical America............ .... 15. *Cyclolejeunea* spp

43. Lobules uniformily swollen and strongly involute, the free margin inrolled 2-3 times. Tropical America, montane......... 4. *Anoplolejeunea conferta*
43. Lobules not or only weakly involute (except sometimes in *Ceratolejeunea*, see 44)... 44

44. Primary middle lamella of the cell walls distinct, darkish pigmented; plants brown. Perianth keels extended into horns. Pantropical 12. *Ceratolejeunea* spp
44. Primary middle lamella indistinct, colourless; plants green, usually rather pale-coloured... 45

45. Leaf lobes with a 2-4 cells wide whitish border of large, hyaline cells, at least near apex. Leaves inserted to the stem by only 2-3 cells. Indochina.......... .... 38. *Tuyamaella hattorii*
45. Leaf lobes lacking a whitish border. Leaf insertion line longer.......... 46

46. Hyaline papilla of the lobule situated in a small sinus distal to the apical tooth. Trigones usually well developed (except in some species of *Cyrtolejeunea*).. 47
46. Hyaline papilla proximal to the apical tooth. Trigones small*............. 48

47. Underleaves small, up to 2× stem width, orbicular, distant. Tropical America... 16. *Cyrtolejeunea*
47. Underleaves larger, more than 3× stem width, mostly wider than long, imbricated. Pantropical......................... 14. *Cheilolejeunea* spp

48. Lobule with 2 distinct teeth. See 6..................... 17. *Dicranolejeunea*
48. Lobule with 1 tooth.. 49

49. Lobule large, 1/3-1/2× lobe length. Leaves deeply concave............ 50
49. Lobule smaller, less than 1/3× lobe length. Leaves ± plane............ 51

50. Perianth 5-keeled. Andes above 1500 m.................................. .... 19. *Lejeunea catinulifera* and *L. patellifera*
50. Perianth without keels, terete. Guadeloupe..... 2. *Amblyolejeunea fulfordiae*

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*Here might also key out. 3. *Amphilejeunea viridissima* Schust., from high altitudes (above 3000 m) in Venezuela which has an entally displaced hyaline papilla, large imbricated underleaves and 5 armed perianth keels. The short description (Schuster 1978) lacks data on cells and trigones.

51. Underleaf apex ± recurved, entire. Tropical America, below 1500 m....... .... 19. *Lejeunea reflexistipula*

51. Underleaf apex plane, entire or minutely bifid (incision 1-2 cells deep)*..... .... 19. *Lejeunea* spp.

Annotations

1. **Acrolejeunea** (Spruce) Schiffn. 1893

Gradstein (1975) recognised 15 species in this pantropical genus.

2. **Amblyolejeunea** Jovet-Ast 1948

Monotypic, contains *A. fulfordiae* Jovet-Ast from Guadeloupe.

3. **Amphilejeunea** Schust. 1978

Monotypic, contains *A. viridissima* Schust. from Venezuela, Merida.

4. **Anoplolejeunea** (Spruce) Schiffn. 1893

Monotypic, contains the common neotropical *A. conferta* (Meissn.) Schiffn., described in detail by Evans (1908).

5. **Archilejeunea** (Spruce) Schiffn. 1893

Four species in tropical America, in 2 subgenera (Gradstein & Buskes, this volume), a few in Africa (Vanden Berghen 1952), several in Asia and the Pacific (Mizutani 1961, Udar & Awasthi 1981, 1982) and 1-2 in Australasia (Schuster 1963a, Gradstein & Buskes, this volume).

6. **Aureolejeunea** Schust. 1978

Four species in the páramos of northern South America (Schuster 1978). *Aureolejeunea decurrens* (Steph.) Schust. from Indomalesia belongs in *Leucolejeunea* (as *L. decurrens* (Steph.) Mizut.), because it lacks the glossy pigmentation characteristic for *Aureolejeunea*.

7. **Blepharolejeunea** S. Arn. 1962

Van Slageren & Kruijt (this volume) recognize five species in tropical America.

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*An interesting species, which might key out here, is the tiny, Asiatic *Lejeunea exilis* Grolle (= *Byssolejeunea* Herz.), which has bifid underleaves on ordinary stems and smaller, narrowly elongated, undivided underleaves on weak shoots and innovations. Another species which keys out here is *Lejeunea luteola* (Steph.) Mizut. from Borneo.

8. **Brachiolejeunea** (Spruce) Schiffn. 1893

About 10 species in two distinct groups: subg. *Brachiolejeunea* (neotropical) and subg. *Plicolejeunea* (tropical America, 1 sp. in Africa, 1 sp. in Nepal). A monograph by M. van Slageren is in preparation.

9. **Bryopteris** (Nees) Lindenb. 1845

Stotler & Crandall-Stotler (1974) recognised 7 species: 6 in tropical America, where the genus is very common, and 1 or 2 in Madagascar, based on a few unconfirmed 19th century records.

10. **Calatholejeunea** Goebel 1928

Monotypic, contains *Calatholejeunea paradoxa* (Schiffn.) Goebel from eastern Malesia (Ambon, West Irian).

11. **Caudalejeunea** (Steph.) Schiffn. 1893

One species in tropical America (Schuster 1980), 11 species in Africa (Vanden Berghen 1984) and about 5 species in Asia (Verdoorn 1934, Gradstein 1974, Udar et al. 1982). Schuster (1980) recognised three subgenera.

12. **Ceratolejeunea** (Spruce) Schiffn.

A large, mainly schizostipous genus with numerous species in tropical America. The subgenus *Ceratophora* Schust. (2 spp.) is purely holostipous (Schuster 1980).

13. **Cephalolejeunea** Mizut. 1979

Monotypic, contains *Cephalolejeunea parviloba* Mizut. from Sabah, Borneo (Mizutani 1979a).

14. **Cheilolejeunea** (Spruce) Schiffn. 1893

A large, mainly schizostipous pantropical genus. Holostipous are (see Schuster 1980): in tropical Asia *C. excisula* (Steph.) Mizut. (*Cheilolej.* subg. *Tegulifolium*), in Africa *C. montagnei* (Gott.) Schust. (*Cheilolej.* subg. *Renilej.*) and in tropical America *C. fragmentissima* (Spruce) Steph. or some closely allied species (*Cheilolej.* subg. *Euosmolej.*).

15. **Cyclolejeunea** Evans 1904

Holostipous or schizostipous, probably purely neotropical. Stephani (1912-17) recognised 11 holostipous species (group "*Integristipula*"), including the common *C. convexistipa* (L. & L.) Evans. The genus is in need of revision.

16. **Cyrtolejeunea** Evans 1903

Neotropical, includes 4-5 species (Schuster 1970, 1978, Gradstein & Buskes this volume). Schuster (1970) provided a key to 3 species.

17. **Dicranolejeunea** (Spruce) Schiffn. 1893

Kruijt (this volume) recognizes 9 species in this pantropical genus.

17a. **Diplasiolejeunea** (Spruce) Schiffn. 1893

One holostipous species has been described in this large genus of Cololejeuneoideae: *D. integerrima* Tix. from Madagascar (Tixier 1979). Apparently the species was based on sterile shoots. Judging from the illustration I believe this plant might as well represent a juvenile shoot of some species of Ptychanthoideae (or holostipous Lejeuneoideae), characterised by pendulum-type leaf segmentation.

18. **Evansiolejeunea** Vanden Berghen 1949

Monotypic, contains *E. roccatii* (Gola) Vanden Berghen from East African mountains (Vanden Berghen 1960).

19. **Lejeunea** Libert 1820

When *Taxilejeunea, Hygrolejeunea, Crossotolejeunea, Macrolejeunea* etc. are considered synonyms of *Lejeunea* (e.g. Grolle 1983), the latter genus contains several holostipous species, particularly from among neotropical *Hygrolejeunea* (see Spruce 1884).

20. **Lepidolejeunea** Schust. 1963

Schuster (1980a) attributes ten species to this pantropical genus, including the holostipous *L. graeffii* (Jack & Steph.) Schust. and *L. integristipula* (Jack & Steph.) Schust. from tropical Asia and the Pacific. Further holostipous taxa are *L. spongia* (Spruce) B. Thiers 1982 and *L. herzogii* (Buchloh) Grolle & Gradst. (Gradstein, this volume), both from tropical America.

21. **Leucolejeunea** Evans 1907

About 5 species in tropical America, 3 in Africa and 5-6 in tropical Asia (Schuster 1980).

22. **Lindigianthus** Kruijt & Gradstein this volume

Monotypic, contains *L. cipaconeus* (Gott.) Kruijt & Gradst. (= *Dicranolejeunea cipaconeus* (Gott.) Steph.) from Costa Rica and the high Andes of northern South America.

23. **Lopholejeunea** (Spruce) Schiffn. 1893

Four species in tropical America (Schuster 1980), 10 in Africa (Vanden Berghen 1973) and about 10 in Asia (Verdoorn 1934, Mizutani 1979). The genus is in need of revision.

24. **Marchesinia** S. Gray 1821

A few species in tropical America and Africa, and 1 in western Europe. A monograph by Dr. E.P. Geissler is in preparation.

25. **Mastigolejeunea** (Spruce) Steph. 1889

One or two species in tropical America (Schuster 1980), 4-5 in Africa (Vanden Berghen 1949, Jones 1957) and several in Asia and Australasia. The genus is probably congeneric with *Thysananthus* and in bad need of revision.

26. **Neurolejeunea** (Spruce) Schiffn. 1893

Neotropical, includes 3 species (Schuster 1980).

27. **Odontolejeunea** (Spruce) Schiffn. 1893

Several species in tropical America (Evans 1904, Herzog 1957), including the very common epiphyllous *O. lunulata* (Web.) Schiffn., and one in Africa (Vanden Berghen 1962). The genus is in need of revision.

28. **Omphalanthus** Lindenb. & Nees 1845

Neotropical. A key to 5 species was provided by Gradstein et al. (1981). Two further species are recognised: *O. wallisii* (Steph.) Gradst. (related to *O. ovalis* but leaves and underleaves broadly rounded) and *O. huanucensis* (Steph.) Gradst., which has revolute leaves and underleaves.

29. **Phaeolejeunea** Mizut. 1968

Pacific and eastern Malesia, contains 3 species (Mizutani 1968).

30. **Physantholejeunea** Schust. 1978

Monotypic, contains *P. portoricensis* (Hampe & Gott.) Schust. (= *Ceratolejeunea portoricensis* (Hampe & Gott.) Evans) from tropical America.

31. **Ptychanthus** Nees 1838

Monotypic, contains the variable, widespread palaeotropical *P. striatus* (L. & L.) Nees. *Ptychanthus sulcatus* (Nees) Nees and *P. theobromae* (Spruce) Schiffn. have *Lejeunea*-type branching and are transferred to *Spruceanthus* (see below). *P. chinensis* Steph. belongs in *Tuzibeanthus.*

32. **Schiffneriolejeunea** Verd. 1934

Six species in Asia (Gradstein & Terken 1981, Udar & Awashti 1982a), 8 in Africa (Gradstein & Vanden Berghen, this volume) and 2 in tropical America: *S. polycarpa* (Nees) Gradst. and *S. amazonica* sp. nov.

Schiffneriolejeunea amazonica sp. nov.

S. occulta affinis sed differt lobulis longioris bidentatis et bracteis foeminarum acuminatis.

Diagnosis: plants 1-2 cm long, 1-1,5 mm wide, creeping, brown to blackish. Stems up to 0,1 mm in diam., the ventral merophyte 4 cells wide. Leaves when dry suberect appressed to the stem (not convoluted), when moist spreading (not widely), ovate-oblong, plane, up to 0,9 × 0,55 mm, the apex rounded; median leaf cells ca. 30-40 × 20 μm, trigones conspicuous, cordate, intermediate thickenings rare, 0-1 per wall; lobule very conspicuous, 1/2-3/5 × lobe length, narrow rectangular, up to 0,55 × 0,2 mm, the apex truncate, with (1)2 teeth, the first tooth 2-3 cells long, the second tooth similar or shorter, sometimes merely a bluntish angle. Underleaves plane, imbricated, (sub)quadrate, 0,35-0,4 mm wide, 4× stem width, the apex truncate, the bases rather broad, slightly decurrent, the insertion line curved. Monoicous. Male spikes terminating branches, the bracts in 5-8 series, hypostatic, unequally bilobed, smaller than leaves. Gynoecium lacking innovations, bracts in 2-3 series, becoming larger than leaves, the inner bract elongated, up to 1,3 mm long, obliquely spreading, sharply keeled over 2/3 of its length, lobe and lobule of equal length but the lobule narrower, both acute-acuminate at apex; inner bracteole very large, about as long as the bracts, oblong, narrowed towards apex, very short bifid, the incision narrow, the lobes overlapping. Perianth immersed, pyriform, the apex ± retuse, up to 0,8 mm long, somewhat inflated with 4 long, sharp keels which are winged (1-2 cells wide) and irregularly notched above; rostrum conspicuous, 7-10 cells long.

BOLIVIA: Beni, 22 km NW of Guayaramerin along the road to Cachuela Esperanza Forest, on branch of small tree in pampa, W.D. Reese 12815, 26.I.1978 (U holotype; isotypes in INPA, LAF and NY). PERU: Loreto, Laguna Quistococha near Iquitos, on tree Hegewald 6357, VII.1973 (hb Hegewald, U). BRAZIL: Rondonia, vicinity of first rapids on Rio Pacaas Novos, on small *Bixa* sp., Reese 13562, III.1978 (INPA, LAF, NY, U); Amazonas, Manaus-Caracarai Road km 45, on sapling tree in caatinga, Prance et al. 11372, IV.1971 (INPA, NY, U).

Schiffneriolejeunea amazonica is closely related to *S. occulta* (Steph.) Gradst. from West Africa. The two species stand rather isolated in *Schiffneriolejeunea* (by the form of the female bracts and perianth) and form a distinct Afro-American vicariant species pair. *S. amazonica* mainly differs from *S. occulta* by its narrower and longer leaves, lobules and bracts (especially the lobules: 2-3× as long as wide and at least half the lobe length in *S. amazonica;* ca. 1,5× longer than wide and 2/5× lobe length in *S. occulta*), the presence of 2 instead of 1 lobule teeth (the 2nd one sometimes only weakly indicated, though) and the narrower, acute-acuminate apices of the bracts (± obtuse in *S. occulta*).

33. Spruceanthus Verd. 1934

Verdoorn (1934) recognised two species: *S. semirepandus* (Nees) Verd. (the type) and *S. polymorphus* (Sande Lac.) Verd., both from Asia. A third species, *S. marianus* (Gott.) Mizut. 1966, has segmented oil bodies and is therefore better placed in *Archilejeunea* (Udar & Awasthi 1982, Gradstein & Buskes this volume). Gradstein (in Hiepko & Schultze-Motel 1981) added *S. pluriplicatus* (Steph.)

Gradst. from New Guinea, subsequently placed in *Spruceanthus* sect. *Pluriplicati* (Schust.) Gradst. & Grolle (Grolle 1982) because of its 10-plicate perianth.

Two further species, formerly placed in *Ptychanthus* but possessing *Lejeunea*-type (in stead of *Frullania*-type) branches and non-convoluted leaves, and lacking cordate trigones, should be placed in *Spruceanthus:*

Spruceanthus sulcatus (Nees) comb. nov.

Jungermannia sulcata Nees, Hep. Jav.: 36 (1830); *Ptychanthus sulcatus* (Nees) Nees, Hep. Eur. 3: 213 (1838); for full synonymy see Schiffner, Consp. Hep. Arch. Ind.: 318 (1898). Type: Java, Blume s.n. (L iso).

Spruceanthus sulcatus belongs in the sect. *Pluriplicati* (= *Ptychanthus* subg. *Metaptychanthus* Inoue 1976 syn. nov.) because of its 10-12- plicate perianth. *S. sulcatus* is closely related to *S. pluriplicatus*, from which it differs by 1) its smaller underleaves, which are about 3 × stem width, with straight insertion line (about 6 × stem width and with strongly arched insertion line in *S. pluriplicatus*), 2) its narrower leaf apex, and 3) its sulcate perianth apex. *S. sulcatus* has been recorded from Sumatra, Java and Borneo.

Spruceanthus theobromae (Spruce) comb. nov.

Lejeunea (Ptycho-lejeunea) theobromae Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 99 (1884); *Ptychanthus theobromae* (Spruce) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1, 3: 130 (1893). Syntypes: Ecuador, "Rio Ventana prope Guayaquil, in *Theobromae* cortice", Spruce s.n. (MANCH 17343, 17344).

By its 5-7-anisoplicate perianth *Spruceanthus theobromae* resembles *S. semirepandus,* from which it otherwise differs by its rounded, entire leaves and bracts (only the female bracteole is weakly erose-dentate), the elongated leaf cells with very small, irregularly triangular-radiate trigones, and the autoicous inflorescence. *S. theobromae* is the only neotropical representative of the genus *Spruceanthus,* and has so far been recorded from Ecuador and Costa Rica.

34. **Stictolejeunea** (Spruce) Schiffn. 1893

Gradstein (this volume) recognizes 3 species, in 2 subgenera, in this pantropical genus.

35. **Symbiezidium** Trevis. 1877

Gradstein & van Beek (this volume) accept 3 species: 2 in tropical America (subg. *Symbiezidium*) and 1 in Madagascar and the Seychelles (subg. *Eosymbiezidium*).

36. **Thysananthus** Lindenb. 1844

Four species in tropical America (Fulford 1941), 1 in Africa (Vanden Berghen 1950) and about 5-6 in tropical Asia and Australasia. The genus is in need of revision.

37. **Trocholejeunea** Schiffn. 1932

Contains *T. sandvicensis* (Gott.) Mizut. and *T. infuscatus* (Mitt.) Verd. from S.E. Asia and the Pacific, and the fossil *T. contorta* (Göppert & Berendt) Gradst. & Grolle from Eocenic amber of Europe (Grolle 1982).

38. **Tuyamaella** Hatt. 1947

One holostipous species, the only one for the subfamily Tuyamaelloideae, has been described: *T. hattorii* Tix. (Tixier 1973) from S.E. Asia. The identity of this peculiar species was recently confirmed by Dr. Grolle (in litt.).

39. **Tuzibeanthus** Hatt. 1947

Monotypic, contains *T. chinensis* (Steph.) Mizut. from the Far East. The genus is closely related to *Ptychanthus* and sometimes considered a subgenus of the latter (Inoue 1976).

40. **Verdoornianthus** Gradst. 1978

Amazonia only, contains 2 species (Gradstein 1978).

References

EVANS, A.W. 1904. Hepaticae of Puerto Rico IV. *Odontolejeunea, Cyclolejeunea* and *Prionolejeunea*. Bull. Torrey Bot. Club 31: 183-226.

EVANS, A.W. 1908. Hepaticae of Puerto Rico IX. *Brachiolejeunea, Ptychocoleus, Archilejeunea, Leucolejeunea* and *Anoplolejeunea*. Bull. Torrey Bot. Club 35: 155-179.

FULFORD, M. 1941. Studies on American Hepaticae I. Revision of the genus *Thysananthus*. Bull. Torrey Bot. Club 68: 32-42.

GOEBEL, K. von 1928. Malesische Lebermoose. Ann. Jard. Bot. Buitenzorg 39: 1-116.

GRADSTEIN, S.R. 1974. Two remarkable species of *Caudalejeunea* : *C. grolleana* spec. nov. and *C. cristiloba* (Steph.) comb. nov. Acta Bot. Neerl. 23: 333-343.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea*. Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. 1978. *Verdoornianthus*, a new genus from Amazonas, Brazil. Bryologist 80: 606-611.

GRADSTEIN, S.R. & TERKEN, L. 1981. A revision of *Schiffneriolejeunea* sect. *Saccatae* from Asia. Occas. Pap. Farlow Herb. 16: 71-81.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

GROLLE, R. 1982. *Trocholejeunea* fossil in Europa. J. Hattori Bot. Lab. 51: 175-193.

GROLLE, R. 1983. Nomina Generica Hepaticarum: references, types and synonymies. Acta. Bot. Fenn 121: 1-62.

HERZOG, T. 1957. Über einige Arten der Lebermoosgattungen *Odontolejeunea* und *Cyclolejeunea*. Revue Bryol. Lichénol. 26: 51-59.

HIEPKO, P. & SCHULTZE-MOTEL, W. 1981. Floristische und ethnobotanische Untersuchungen im Eipomek-Tal, Irian Jaya (West-Neuguinea), Indonesien. Berlin.

INOUE, H. 1976. Illustrations of Japanese Hepaticae-2. Tokyo.

JONES, E.W. 1957. African Hepatics XII. Some new or little known Lejeuneaceae. Trans. Brit. Bryol. Soc. 3: 191-207.

JOVET—AST, S. 1948. Hépatiques des Antilles françaises récoltées par P. et V. Allorge en 1936. Revue Bryol. Lichénol. 17: 24-34.

MIZUTANI, M. 1961. A revision of Japanese Lejeuneaceae. J. Hattori Bot. Lab. 24: 115-302.

MIZUTANI, M. 1966. Supplement to "Revision of Japanese Lejeuneaceae" II. J. Hattori Bot. Lab. 29: 290-293.

MIZUTANI, M. 1968. *Phaeolejeunea,* a new genus of Lejeuneaceae. J. Hattori Bot. Lab. 31: 130-134.

MIZUTANI, M. 1979. Notes on the Lejeuneaceae 1. Some Asiatic species of the genus *Lopholejeunea.* J. Hattori Bot. Lab. 45: 375-387.

MIZUTANI, M. 1979a. Notes on the Lejeuneaceae 2. Some peculiar Asiatic species in the Rijksherbarium, Leiden. J. Hattori Bot. Lab. 46: 357-372.

SCHUSTER, R.M. 1963. Studies on antipodal Hepaticae I. Annotated keys to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. J. Hattori Bot. Lab. 26: 185-309.

SCHUSTER, R.M. 1970. New Lejeuneaceae from Dominica and Jamaica. Bull. Torrey Bot. Club 97: 336-352.

SCHUSTER, R.M. 1978. Studies on Venezuelan Hepaticae I, II. Phytologia 39: 239-251.

SCHUSTER, R.M. 1980. The Hepaticae and Anthocerotae of North America Vol. IV. New York

SCHUSTER, R.M. 1980a. New combinations and taxa of Hepaticae I. Phytologia 45: 415-437.

SCHUSTER, R.M. 1984. Evolution, Phylogeny and Classification of the Hepaticae. In: R.M. Schuster (ed.), New Manual of Bryology, p. 892-1070. Nichinan.

SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Jubuleae. Trans. Proc. Bot. Soc. Edinburgh 15: i-ix, 1-308.

STEPHANI, F. 1912-17. Species Hepaticarum Vol. V. Geneva.

STOTLER, R.E. & CRANDALL—STOTLER, B. 1974. A monograph of the genus *Bryopteris* (Swartz) Nees von Esenbeck, Bryophyt. Bibl. 3: 1-159.

STOTLER, R.E. & CRANDALL-STOTLER, B. 1974. A monograph of the genus *Bryopteris* (Swartz) Nees von Esenbeck. Bryophyt. Bibl. 3: 1-159.

THIERS, B.M. 1982. Type studies in the Lejeuneaceae I. *Archilejeunea pabstii, Hygrolejeunea pacifica* and *Hygrolejeunea spongia.* Brittonia 34: 294-298.

TIXIER, P. 1973. Le genre *Tuyamaella* Hatt. (Lejeuneacées). Revue Bryol. Lichénol. 39: 221-244.

TIXIER, P. 1979. Nouvelles espèces malgaches de *Diplasiolejeunea* (Diplasiae) II. Revue Bryol. Lichénol. 45: 209-226.

UDAR, R. & AWASTHI, U.S. 1981. The genus *Archilejeunea* (Spruce) Schiffn. in India. Geophytology 11: 72-79.

UDAR, & AWASTHI, U.S. 1982. The status of *Spruceanthus marianus* (Gott.) Mizut. in India. J. Bryol. 12: 33-36.

UDAR, R. & AWASTHI, U.S. 1982a. The genus *Schiffneriolejeunea* Verd. (Hepaticae) in India. Lindbergia 8: 55-59.

UDAR, R., AWASTHI, U.S. & SHALEEN, F. 1982. A new *Caudalejeunea* from India. Bryologist 85: 329-331.

VANDEN BERGHEN, C. 1949. Contribution à l'étude des espèces africaines du genre *Mastigolejeunea* (Spruce) Schiffn. Bull. Jard. Bot. Etat, Bruxelles 19: 371-382.

VANDEN BERGHEN, C. 1950. Le genre *Thysananthus* Lindenb. en Afrique. Revue Bryol. Lichénol. 18: 35-37.

VANDEN BERGHEN, C. 1951. Contribution á l'étude des espèces africaines du genre *Archilejeunea* (Spruce) Schiffn. Revue Bryol. Lichénol. 20: 112-121.

VANDEN BERGHEN, C. 1960. Hépatiques récoltées par le Dr. J.J. Symoens dans la région Peri-Tanganyikaise. Bull. Soc. Bot. Belgique 92: 111-138.

VANDEN BERGHEN, C. 1962. Lejeuneacées épiphylles d'Afrique I. Revue Bryol. Lichénol. 32: 49-55.

VANDEN BERGHEN, C. 1973. Hépatiques récoltées au Gabon par G. le Testu. Revue Bryol. Lichénol. 39: 365-385.

VANDEN BERGHEN, C. 1984. Le genre *Caudalejeunea* (Steph.) Schiffn. en Afrique. Cryptog. Bryol. Lichénol. 5: 99-109.

VERDOORN, F. 1934. Studien über Asiatische Jubuleae. Ann. Bryol. Suppl. 4: 40-192.

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BEIHEFT 80 ZUR NOVA HEDWIGIA

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Branching in Lejeuneaceae III: Ptychanthoideae

by

Barbara M. Thiers

ABSTRACT: Study of branch systems in Lejeuneaceae subfamily Ptychanthoideae reveals that the most important characters for taxonomic use are: branch type, gynoecial position, innovation presence, innovation leaf sequence, growth habit, ramification pattern, innovation number, and inflorescence pattern. The first four characters are often constant at the generic level; the remainder may be variable within a genus. The distribution pattern of branch character states among the 22 genera studied supports the generic complex as the most natural supergeneric unit in the subfamily.

Introduction

As part of a larger study on branching in the entire Lejeuneaceae (Thiers 1984) I examined branch systems of 84 species in 22 genera of Ptychanthoideae. Resulting from this survey is a reevaluation of taxonomically important branch characters, and a synopsis of the branch system in each genus. The information accumulated helps to broaden the data base for interpreting generic interrelationships within the subfamily.

Second in number of species only to Lejeuneoideae, Ptychanthoideae contains the most robust members of Lejeuneaceae, and members of the subfamily are united by the presence of unlobed underleaves, thick stems and setae, and a hyaline papilla usually positioned on the inner surface of the lobule (Schuster 1980). Many workers have discussed branching in Ptychanthoideae. Characters such as branch type, innovation presence and innovation number have been used traditionally in delimiting genera (Spruce 1884-1885, Schiffner 1895, Evans 1907, 1907a, 1908, and Verdoorn 1934). Characters such as growth habit and gynoecial position were noted for some, e.g., *Bryopteris* and *Stictolejeunea* (Evans 1907, 1907a, 1908). In her survey of branching in leafy hepatics, Crandall (1969) described some aspects of branching in a wide variety of ptychanthoid genera. She noted relative branch lengths, branch type, nature of the collar and leaves at the base of *Lejeunea*-type branches, leaf orientation of *Frullania*-type branches, innovation presence or absence, and length and fertility of innovations. Although providing a fairly

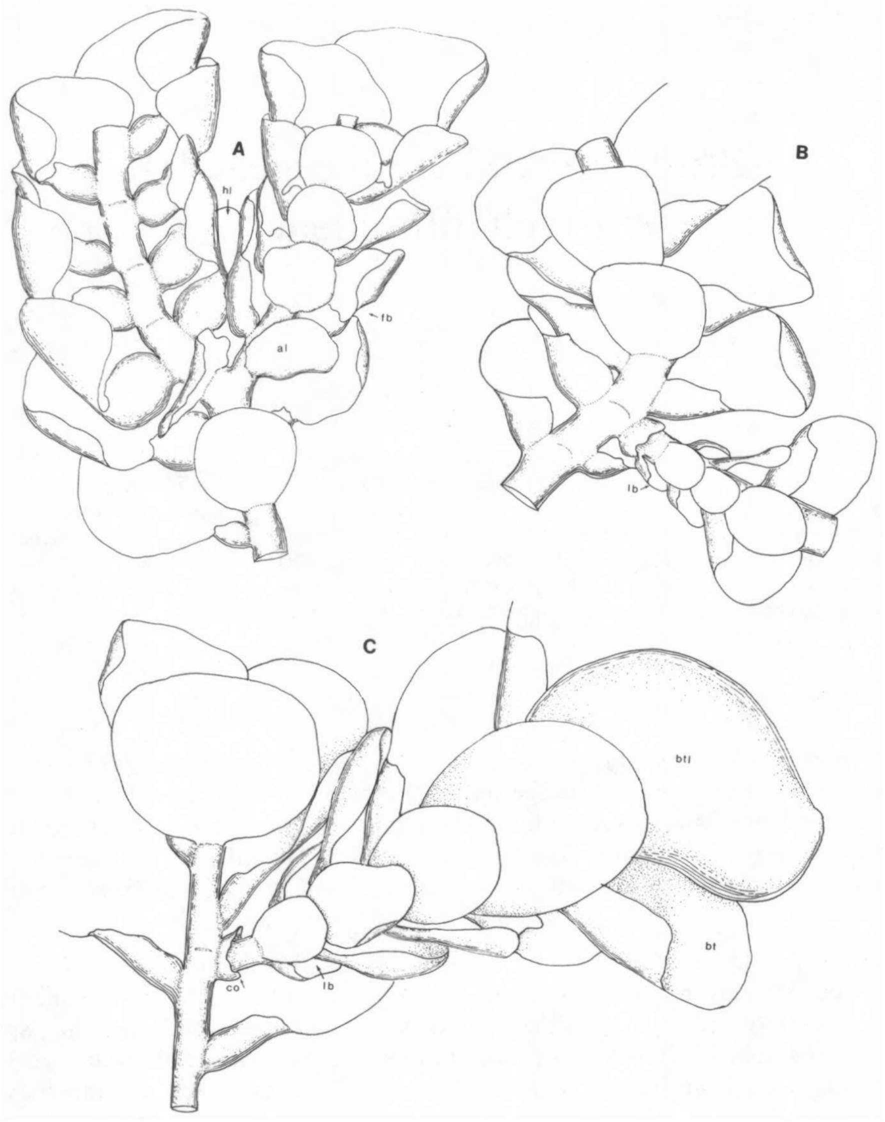


Fig. 1. Illustration of selected branch features in members of Lejeuneaceae subfamily Ptychanthoideae.

A. *Frullania*-type branch in *A. olivacea,* standard line = 250 μm. B. *Lejeunea*-type branch base in *Mastigolejeunea auriculata,* standard line = 250 μm. C. A short gynoecial branch in *Schiffneriolejeunea nymanii,* standard line = 450 μm. al = anomalous leaf; bt = bract; btl = bracteole; co = collar; fb = *Frullania*-type branch; hl = half leaf; lb = *Lejeunea*-type branch.

thorough description of branching in each genus, Crandall's survey did not highlight those characters most important to the taxonomy of Ptychanthoideae. Mizutani (1970) introduced an important new branch character concerning the arrangement of leaves on innovations, but the significance of this character in Ptychanthoideae was not noticed immediately by other workers. In my study, I found eight branch characters to be taxonomically important:

(1) Growth Habit

The growth habit of a plant is considered excurrent when main axes are consistently longer than secondary branches (Fig. 3c), but is termed deliquescent when secondary branches are as vigorous as primary ones (Fig. 3b). This character is most often useful at the species level. Although conceivably subject to environmental modification in some taxa, differences in growth habit are consistent in at least some species, e.g., those of *Bryopteris.*

(2) Ramification Pattern

This character pertains to the frequency of secondary branches along a main axis. When secondary branches are frequent and evenly spaced along a stem, the pattern is regularly pinnate (Fig. 3a); otherwise the pattern is irregularly pinnate (Fig. 3b). As with growth habit, ramification pattern is most useful at the species level.

(3) Branch Type

Lateral branches, i.e., branches that subtend vegetative lateral leaves, may be *Frullania*-type (Fig. 1a) or *Lejeunea*-type (Figs. 1b, c) in Ptychanthoideae. Most plants that produce *Frullania*-type branches usually produce *Lejeunea*-type branches as well. However, many taxa produce only *Lejeunea*-type branches. The most common distinction is between "branches of both *Lejeunea*- and *Frullania*-types" and "branches of *Lejeunea*-type only. " Applied in this way, the character may provide a useful distinction between genera. Mizutani (1970) and Gradstein (1980) typified the patterns of leaf arrangement at *Frullania*-type branch bases, and implied that this character might be important taxonomically. However, upon examination of *Frullania*-type branch bases in a variety of ptychanthoid taxa, I concluded that this character was quite variable within some species, and precise classification of the types and positions of leaf-like appendages at the branch base resulted in characters too complex for practical use.

(4) Gynoecial Position

Acrogynous taxa are those in which gynoecia terminate long or short branches (Fig. 4a), whereas cladogynous plants produce gynoecia only on short branches (usually less than five leaf cycles in length, Figs. 1c, 3a). This character most often shows significant variation at the generic rank.

(5) Innovation Presence

An innovational branch is one that subtends a gynoecial bract. Such branches may be lacking (Figs. 2c, 3a-c), but if present, they are usually *Radula*-type. *Frullania*-type innovations are found in *Trocholejeunea sandvicensis* (Figs 2c, 7h), and *Lejeunea*-type innovations may occur in *Caudalejeunea* or *Lopholejeunea*

(Figs. 8b, 8c). The presence or absence of gynoecial innovations is usually reliable for differentiating genera.

(6) Innovation Number

Innovational branches may subtend one or both bracts of a given gynoecium, and thus are referred to as single (Fig. 2a) or paired (2b). Although emphasized as a generic character in early treatments of the subfamily, (e.g., Schiffner 1895) this character is most useful when based on tendencies, i.e., with the contrasting character states "Innovations usually single" or "Innovations usually paired." The distinction may be important at generic, or more commonly, specific rank.

(7) Innovation Leaf Sequence

The order of leaf production on an innovational branch is most commonly lejeuneoid or pycnolejeuneoid in Ptychanthoideae (Grolle 1980, Thiers 1984). In the lejeuneoid sequence the first leaf of an innovation is a lateral leaf (Fig. 4a) and in the pycnolejeuneoid sequence the first leaf is an underleaf (Fig. 7e). Innovation leaf sequence is usually consistent at the genus level. However, pycnolejeuneoid as well as lejeuneoid species are found in *Archilejeunea, Thysananthus,* and *Dicranolejeunea.* In *Thysananthus evansii* Fulf. and *Tuzibeanthus chinensis* (Steph.) Mizut. leaf sequence varies on different innovations of the same plant.

(8) Inflorescence Pattern

This character, a composite one, refers to the spatial arrangement of gynoecia. The components of this character are: gynoecial branch length, presence or absence of innovations, innovation number and length, and the ability of innovations to bear gynoecia. The four inflorescence patterns found in Ptychanthoideae are: simple (Figs 3a-c), diffuse (Figs 5b-f), monochasial (Fig. 6f) and dichasial (Fig. 7f). As with innovation number, these character states (except "simple") are rarely absolutely consistent. The state "diffuse" is used when the positioning of gynoecia relative to other gynoecia appears to be random. Assessment of inflorescence pattern is usually made after observation of five or more stem systems.

Some incidental branch features are mentioned in the generic treatments when they may be potentially useful in differentiating species. These are: presence of microphyllous (i.e., reduced) branches, as found in *Spruceanthus polymorphus* (Sande Lac.) Verd. (Fig. 6h); upright, sometimes leafless branches known as flagella, as in *Acrolejeunea* (Gradstein 1975, Plate VIII, fig.1); and pseudoinnovations, found also in *Acrolejeunea* (Gradstein 1975, Plate III, fig. 8).

Branching in Individual Genera of Ptychanthoideae

In the generic synopses that follow, I include: (1) the disposition of the important branch characters in each genus; (2) the type of variation (if any) found among species of a given genus, and (3) the potential for taxonomic use of this variation;

Fig. 2. Illustration of selected branch features in members of Lejeuneaceae subfamily Ptychanthoideae.

A. Gynoecium on leading stem and single innovation in *Mastigolejeunea auriculata*, standard line = 275 μm. B. Gynoecium with paired innovations in *Oreolejeunea securifolia*, standard line = 250 μm. C. *Frullania*-type innovation in *Trocholejeunea sandvicensis*, standard line = 275 μm. al = anomalous leaf; hl = half leaf.

Table 1. Order of Generic Treatment

Bryopteris
Ptychanthus
Tuzibeanthus
Phaeolejeunea
Schiffneriolejeunea
Verdoornianthus
Thysananthus
Mastigolejeunea
Archilejeunea
Spruceanthus
Caudalejeunea
Acrolejeunea
Brachiolejeunea
Trocholejeunea
Oreolejeunea
Dicranolejeunea
Odontolejeunea
Lopholejeunea
Marchesinia
Symbiezidium
Stictolejeunea
Neurolejeunea

and (4) the similarity of the branch system to that found in other genera of Ptychanthoideae. The order in which genera are treated (Table 1) is modified from the subfamilial classiication by Gradstein (1975) to juxtapose genera with the most overall similar branch systems.

Bryopteris (Sw.) Nees (Fig. 3)

Features common to all species of *Bryopteris* are the predominance of *Frullania*-type vegetative branches, restriction of gynoecia to very short *Lejeunea*-type branches (upon which vegetative leaves intergrade with bracts), absence of gynoecial innovations, and a simple inflorescence pattern.

Within *Bryopteris*, species differ primarily in growth habit and ramification pattern. An excurrent growth habit characterizes *B. fruticulosa* T. Tayl., *B. filicina* (Sw.) Nees (Fig. 3c), most plants of *B. trinitensis* (Lehm. & Lindenb.) Lehm. & Lindenb. (Fig. 3a), *B. flaccida* (Lindenb.) Hampe and *B. liebmanniana* Lindenb. & Gott. *Bryopteris diffusa* (Sw.) Nees (Fig. 3b) exhibits a deliquescent growth habit. *Bryopteris fruticulosa* and *B. filicina* have a regularly pinnate ramification pattern, whereas the pattern in *B. diffusa* is irregular (pseudodichotomous). In *B. liebmanniana*, *B. flaccida* and *B. trinitensis*, the ramification pattern is usually irregular, although on some plants of all three species (especially *B. trinitensis*) the pattern is regularly pinnate. Microphyllous branches of the *Lejeunea*-type characterize *B. trinitensis*.

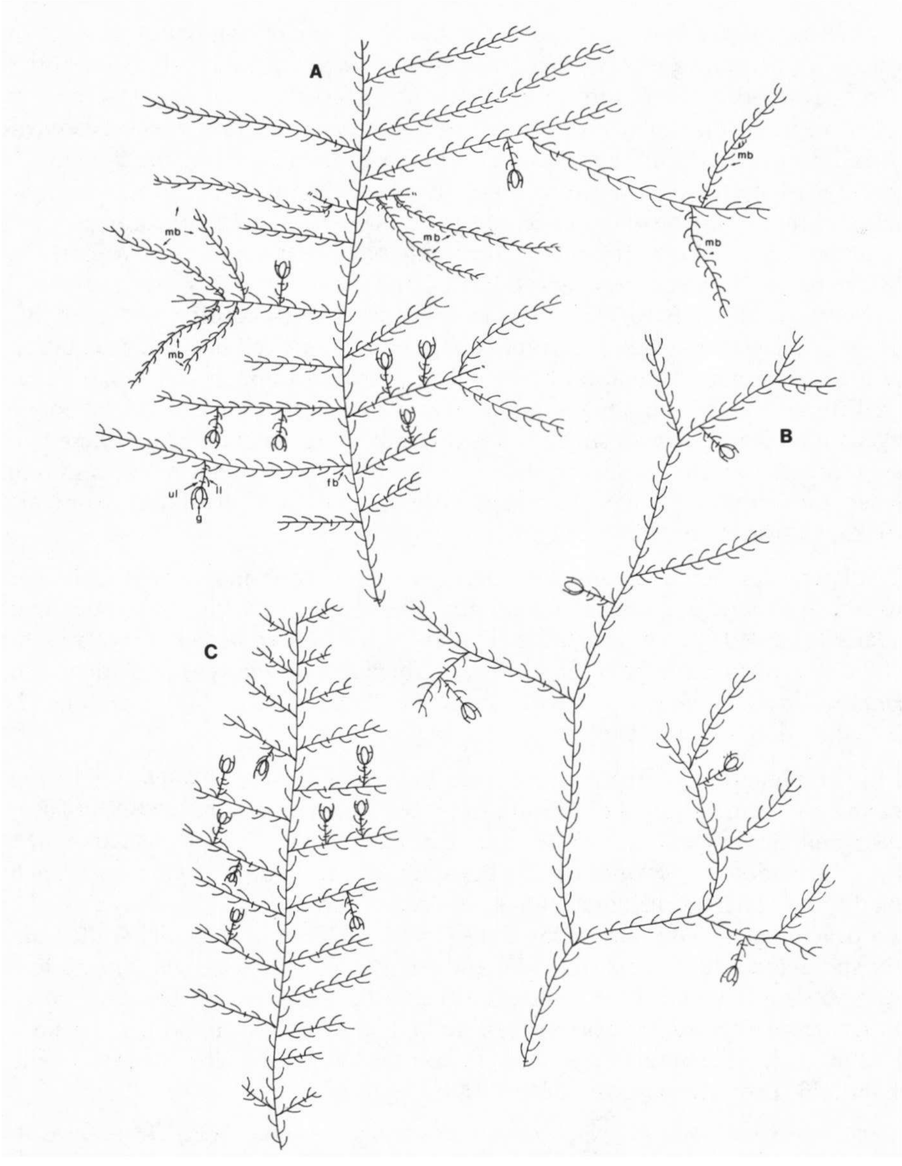


Fig. 3. Diagrams of branch systems in *Bryopteris*.

A. *B. trinitensis*. B. *B. diffusa*. C. *B. filicina*. g = gynoecium; ll = lateral leaf; mb = microphyllous (*Lejeunea*-type) branch; ul = underleaf. All branches terminating in gynoecia are *Lejeunea*-type branches. Unless otherwise indicated, all other lateral branches are *Frullania*-type.

Bryopteris has been monographed recently by Stotler and Crandall-Stotler (1974), and in this treatment, branching is described in detail. Although my observations on branching in *Bryopteris* match theirs in most repects, we differ in the categorization of collared branches. Stotler and Crandall-Stotler refer to such branches in

Bryopteris as "*Bryopteris*-type", but for the purposes of this study, I do not recognize this branch type as distinct from the *Lejeunea*-type. According to Stotler and Crandall-Stotler, the *Bryopteris*-type branch differs from the *Lejeunea*-type in the axial origin of the collar (as opposed to a leaf-derived collar in the *Lejeunea*-type), and the irregular, torn appearance of the collar at the base of a mature branch in *Bryopteris*-type (as opposed to a regularly four-lobed collar on *Lejeunea*-type branches). I remain unconvinced concerning the differences in the appearance of the collar at the branch base. Irregularly torn collars can be demonstrated easily in many members of Lejeuneaceae, and I did not find the frequency of irregularly torn collars any greater in *Bryopteris* than in other genera. According to Crandall's (1969) description, the two branch types differ in only one cell division orientation at the locus of branch formation below a lateral leaf. Although not denying that such a difference exists, I maintain that until branch development in a larger sample of Ptychanthoideae species is studied, it is difficult to tell whether or not these two patterns of cell divisions remain absolutely distinct, and because the resulting branches are virtually identical in appearance, I hesitate to attribute taxonomic significance to the *Bryopteris*-type branch.

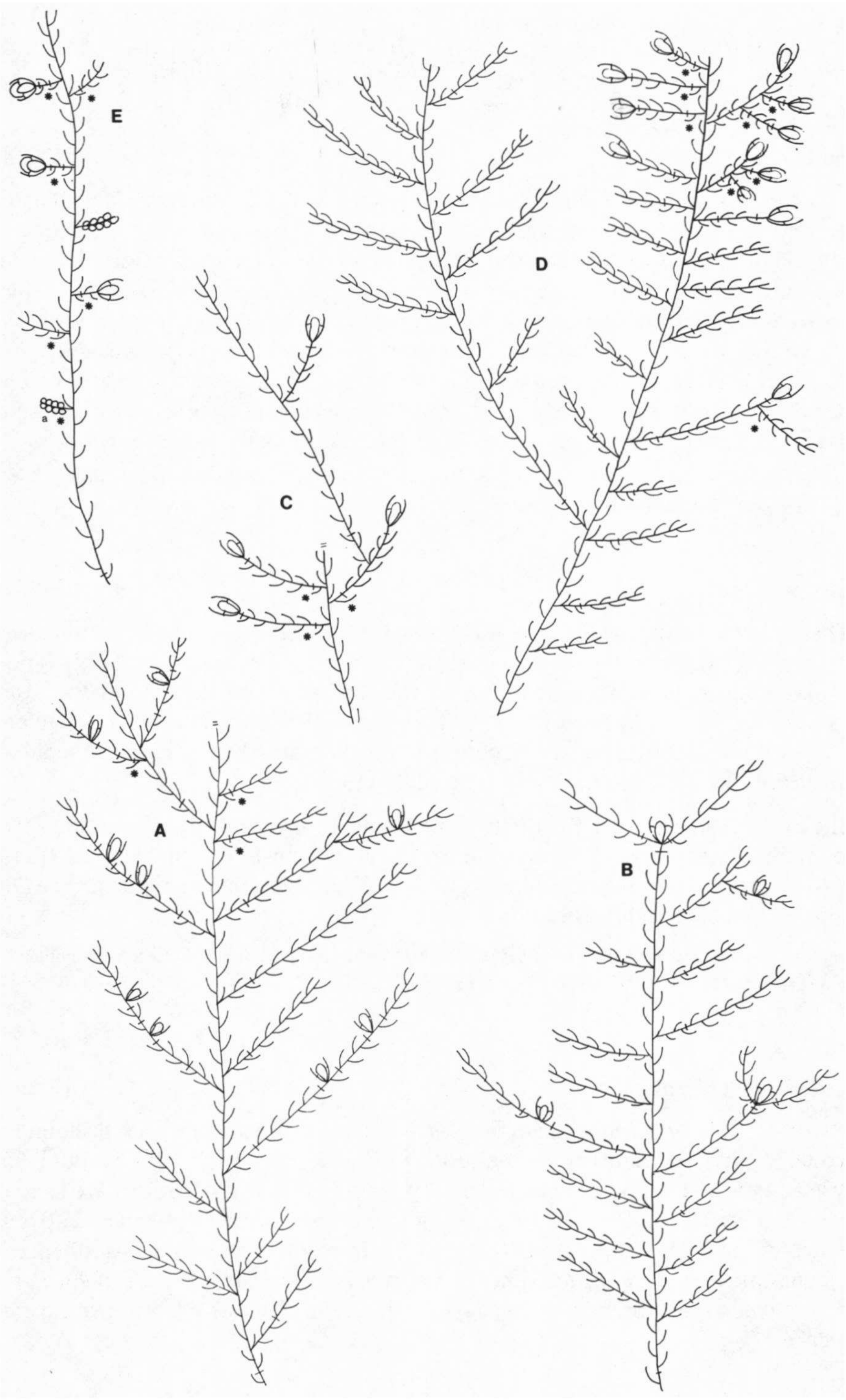
The differences noted among the species of *Bryopteris* in growth habit and ramification pattern are critical taxonomic characters according to Stotler and Crandall-Stotler (1974). They suggested that evolution in *Bryopteris* has involved the transition in growth form from the less well-defined *B. flaccida*-type (including also *B. trinitensis* and *B. liebmanniana*) to both the *B. fruticulosa*-type (including *B. filicina*) and the *B. diffusa*-type.

In the combination of regularly pinnate branching of the *Frullania*-type and cladogyny, the branch system of *Bryopteris* shows similarities to that of *Schiffneriolejeunea* and *Stictolejeunea*. Stotler and Crandall-Stotler (1974) erected a new family to accomodate *Bryopteris*, the Bryopteridaceae, based in part on branch system differences. This realignment has not been widely accepted, but based on the branch development data accumulated by Crandall (1969) and on the frullanioid type of spore and seta, Gradstein (1975) and Schuster (1980) placed *Bryopteris* in a separate subfamily within Lejeuneaceae. Because the main reason for removal of *Bryopteris* from Ptychanthoideae appears to be the differences in branch development that I have chosen here not to accept, I return *Bryopteris* to the Ptychanthoideae for the purposes of this study.

MATERIAL EXAMINED: *Bryopteris diffusa* (Sw.) Nees: TRINIDAD. Southern Watershed Preserve, *E. Britton 1115* (NY). *B. filicina* (Sw.) Nees: BRAZIL. [no further locality] *Weir s.n.* (NY). *B. flaccida* (Lindenb.) Hampe: GUATEMALA. Alta Verapaz, Coban, *Turckheim s.n.* (NY). *B. fruticulosa* T. Tayl.: DOMINICA. Morne Dialotins, *Schuster 67-740* (Herb. R.M. Schuster). *B. liebmanniana* Lindenb. & Gott.: ECUADOR. Galapagos Is., Santa Cruz, Mt. Crocker, *Gradstein & Weber H338*

Fig. 4. Diagrams of branch systems in *Verdoornianthus, Schiffneriolejeunea, Ptychanthus,* and *Tuzibeanthus.*

A. *Ptychanthus striatus.* B. *Tuzibeanthus chinensis.* C. *Schiffneriolejeunea nymanii.* D. *S. omphalanthoides.* E. *Verdoornianthus marsupiifolius.* a = androecial branch; i = innovation. All lateral branches are *Frullania*-type except those marked with asterisks.


E
a
D
C
A
B

(NY); "Andes Quitensis," *Jameson 368* (NY). *B. trinitensis* (Lehm. & Lindenb.) Lehm. & Lindenb.: MEXICO. Mt. Orizaba, banks of Rio Blanco, Jan-Feb 1892, *J.G. Smith s.n.* (NY); COSTA RICA. Prov. Puntarenas, Finca Las Cruces near San Vita de Java, 12 Apr 1973, *H.E. Moore s.n.* (NY).

Ptychanthus Nees (Fig. 4a)

Ptychanthus striatus (Lehm. & Lindenb.) Nees is characterized by an excurrent habit and a regularly pinnate ramification pattern. Lateral branching is predominantly of the *Frullania*-type, although *Lejeunea*-type branches also occur in some plants. Gynoecia are produced on main as well as secondary axes, and single or paired innovations are present consistently. Leaf arrangement on innovations is lejeuneoid. Innovations frequently terminate in gynoecia, and three to four fertile units may be produced in series, creating a monochasial inflorescence pattern. *Ptychanthus* is similar to *Tuzibeanthus* and *Phaeolejeunea* in the presence of *Frullania*-type branches, acrogyny, and a lejeuneoid innovation sequence.

MATERIAL EXAMINED: *Ptychanthus striatus* (Lehm. & Lindenb.) Nees: JAVA. Prov. Preanger, Mt. Salak, *Fleischer 177* (FH); [no further locality] *Motley s.n.* (NY).

Tuzibeanthus Hatt. (Fig. 4b)

The growth habit of the species studied is excurrent, and the ramification pattern is irregularly to regularly pinnate. Lateral branches are all *Frullania*-type in the plants examined. Gynoecia are borne on short or long branches, and innovations are present, one or two per gynoecium. The leaf sequence is lejeuneoid on innovations subtending the second-produced bract, but pycnolejeuneoid on innovations that subtend the first-produced bract.

The inflorescence pattern is diffuse. The branch system of *Tuzibeanthus* shows some similarity to that of *Ptychanthus* and *Phaeolejeunea*, but the combination of consistent *Frullania*-type branching and variable innovation leaf sequence was not observed elsewhere in the subfamily.

MATERIAL EXAMINED: *Tuzibeanthus chinensis* (Steph.) Mizut.: THAILAND. Payap, Chiangmai, Mt. Doi Chiangdao, *Tagawa & Kitagawa T4437* (NY); JAPAN. Miyazaki, Shiba, ca. 800 m, 23 Aug 1951, *Mayebara s.n.* (NY).

Phaeolejeunea Mizut. (Fig. 5c)

Phaeolejeunea latistipula (Schiffn.) Mizut. has a deliquescent growth habit, an irregularly pinnate ramification pattern, and branching of both *Frullania*- and *Lejeunea*-type. Gynoecia are borne on long branches, and innovations are present, single or paired. The leaf sequence on innovations is usually lejeuneoid (pycnolejeuneoid sequence found rarely), and the inflorescence pattern is diffuse to monochasial. *Phaeolejeunea* is similar to *Ptychanthus* in the presence of *Frullania*- and *Lejeunea*-type branches, acrogyny, and the lejeuneoid innovation leaf sequence.

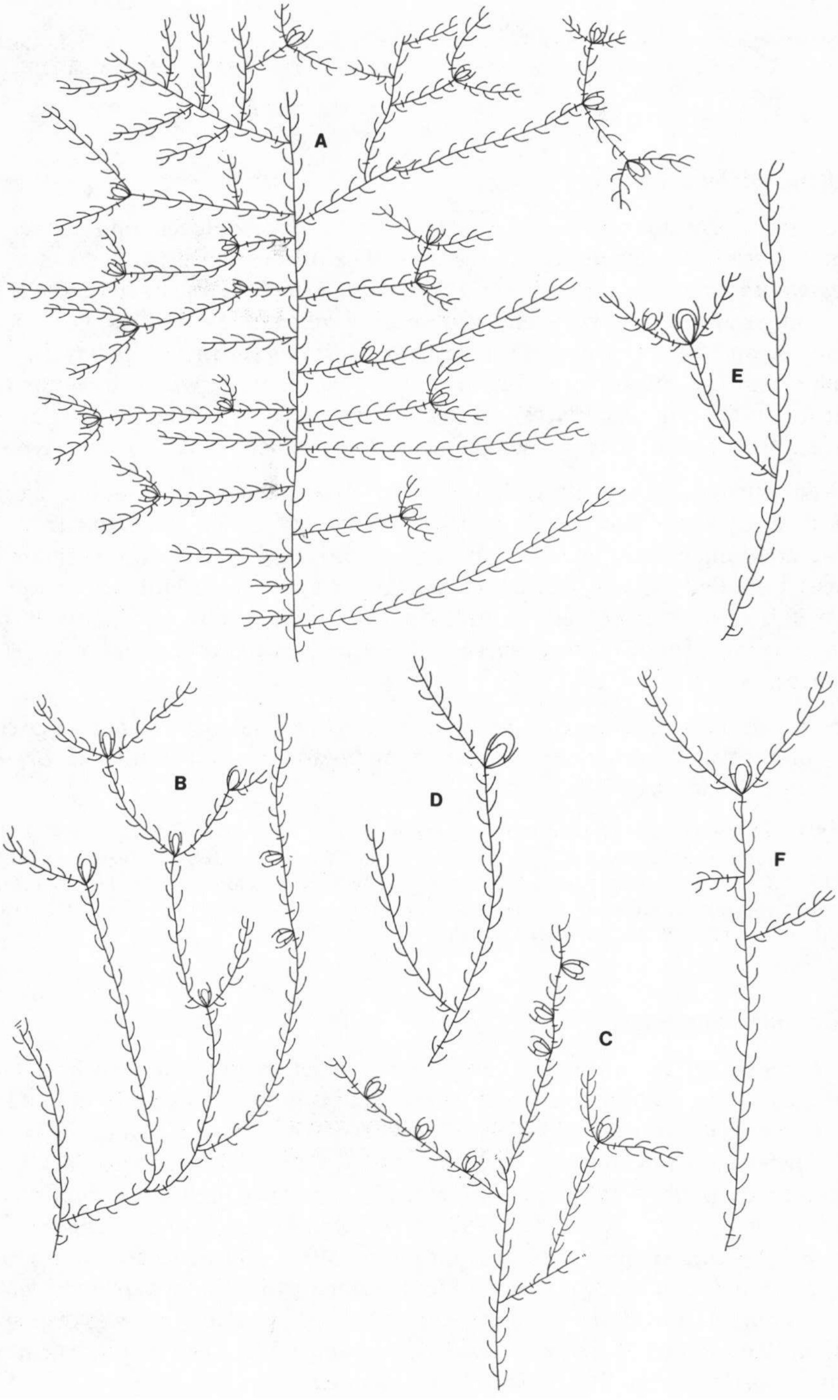


Fig. 5. Diagram of branch systems in *Thysananthus, Phaeolejeunea* and *Mastigolejeunea.*

A. *Thysananthus evansii.* B. *T. spathulistipus.* C. *Phaeolejeunea latistipula.* D. *Mastigolejeunea auriculata.* E. *M. humilis.* F. *M. nigra.* All lateral branches are *Lejeunea*-type.

MATERIAL EXAMINED: *Phaeolejeunea latistipula* (Schiffn.) Mizut.: PHILIPPINES. Sulu, Sibutu Is., *Merrill 52389* (NY); SAMOA. Shortlands Is., Paperang, *Rechinger 4781* (NY - ISOSYNTYPE of *Archilejeunea kaernbachii* Steph.).

Schiffneriolejeunea Verd. (Figs. 4c-d)

All species examined of *Schiffneriolejeunea* produce gynoecia on relatively short branches, and lack gynoecial innovations. The inflorescence pattern is simple. *S. omphalanthoides* Verd. (Fig. 5d) and *S. nymanii* (Steph.) Gradst. & Terken (Fig. 5c) have an excurrent growth habit and bear *Frullania*- as well as *Lejeunea*-type branches, and both types may bear gynoecia. *S. omphalanthoides* has a regularly pinnate ramification pattern, but that of *S. nymanii, S. pulopenangensis* (Gott.) Gradst., and *S. tumida* (Nees) Gradst. is irregularly pinnate. In the latter two species, the growth habit is deliquescent, and branching is *Lejeunea*-type only.

Gradstein and Terken (1981) did not utilize branch characters in their taxonomic treatment of three species of *Schiffneriolejeunea* section *Saccatae* from Asia. However, branch type, growth habit and ramification pattern are variable in the species I studied of *Schiffneriolejeunea,* and may prove useful within the genus when it is treated more fully (Gradstein and Terken indicated that *Schiffneriolejeunea* may contain fifteen species, but the identity of all has not yet been revealed).

In the absence of gynoecial innovations and the tendency toward an excurrent habit and pinnate ramification pattern, *Schiffneriolejeunea* is similar to *Bryopteris* and *Verdoornianthus.*

MATERIAL EXAMINED: *Schiffneriolejeunea nymanii* (Steph.) Gradst. & Terken: NEW GUINEA. Bernhard Camp, *Brass 12654* (FH). *S. omphalanthoides* Verd.: CELEBES. Bouthain, 1888, *Warburg s.n.* (FH). *S. pulopenangensis* (Gott.) Gradst.: JAVA. Batavia, Buitenzorg, 1893-1894, *Schiffner s.n.*, "Hepaticae Selectae et Criticae" (F. Verdoorn, ed.) ser. 6 no. 274 (NY). *S. tumida* (Nees) Gradst. CEYLON [no further locality] *Gardner s.n.* (NY).

Verdoornianthus Gradst. (Fig. 4e)

The collection examined of *Verdoornianthus marsupiifolius* (Spruce) Gradst. contained plants with an excurrent growth habit and an irregularly pinnate ramification pattern. Only *Lejeunea*-type branches were observed. Gynoecia are borne on branches two to three leaf cycles in length, and innovations are lacking. The inflorescence pattern is simple. A recently described genus, *Verdoornianthus* contains two species (Gradstein 1977). In addition to Spruce's species is one described by Gradstein, *V. griffinii.* Gradstein (1977) did not mention any branch differences between the two species. He described gynoecia in *Verdoornianthus* as "...terminal on short branches or on leading stems" but cladogyny was displayed by all plants I examined of *Verdoornianthus marsupiifolius.* The branch system of this genus is most similar to that of *Schiffneriolejeunea.*

MATERIAL EXAMINED: *Verdoornianthus marsupiifolius* (Spruce) Gradst. BRAZIL. Amazonas, Rio Uatuma, along Iguarapé Caititu, 0°45 'S 59°40 'W, *Buck 2956* (NY).

Thysananthus Lindenb. (Figs. 5a-b)

All species studied of *Thysananthus* are acrogynous and they consistently produce gynoecial innovations. Lateral branches are exclusively of the *Lejeunea*-type. *Thysananthus pterobryoides* (Spruce) Steph. is distinct from other species examined in its plumose appearance (strongly excurrent growth habit and regularly pinnate ramification pattern), consistently paired innovations and pycnolejeuneoid innovation leaf sequence (Fig. 5a). The inflorescence pattern is diffuse to dichasial. *T. evansii* Fulf. produces two innovations at each gynoecium, but has a deliquescent habit and an irregularly pinnate ramification pattern. Unlike other species studied, the innovation leaf sequence is variable: the innovation subtending the first bract is pycnolejeuneoid, but the sequence on the second innovation is lejeuneoid. The inflorescence pattern is diffuse. In the other species studied, single innovations predominate, the innovation leaf sequence is always lejeuneoid, and the inflorescence pattern is diffuse to monochasial or even dichasial in *T. spathulistipus* (Reinw. et al.) Lindenb. (Fig. 5b). Microphyllous branches were observed in *T. gottschei* (Steph. & Jack) Steph. and *T. amazonicus* (Spruce) Steph.

Fulford (1941) suggested a close relationship between *Thysananthus pterobryoides* and *T. evansii* on the basis of similarities in color, lateral and underleaf size, and shape of leaf cells, lobule size and the presence of consistently paired innovations. These two species are united also by the pycnolejeuneoid leaf sequence on at least some innovations, and the dichasial inflorescence pattern. Therefore, branching differences among species of *Thysananthus* may help to suggest a basis for a subgeneric classification of the genus. Presence of microphyllous branches is also potentially useful. Variation in innovation leaf sequence within a genus is rather rare in Ptychanthoideae, and even rarer is variation within two innovations of a pair. This phenomenon has been noted elsewhere only in *Tuzibeanthus,* and *Siphonolejeunea* Herz. of Tuyamaelloideae. Aside from the aberrant *T. pterobryoides* and *T. evansii, Thysananthus* is fairly uniform in its branch system, and is most similar to *Mastigolejeunea, Archilejeunea,* and *Spruceanthus* in the presence of *Lejeunea*-type branching, acrogyny, and the predominance of a lejeuneoid innovation sequence, single innovations, deliquescent growth habit and irregularly pinnate ramification pattern.

MATERIAL EXAMINED: *Thysananthus aculeatus* Herz.: JAPAN. Ryukyu, Okinawa, Oogimi, 28 Jan 1955, *T. Amano s.n.* "Hepaticae Japonicae" (A. Noguchi and S. Hattori, eds.) ser. 7 (1957) 349 (NY). *T. anguiformis* T. Tayl.: NEW ZEALAND. [no further locality] 1880, *W.T. Travers s.n.* (NY). *T. amazonicus* (Spruce) Steph.: TRINIDAD. Sange Grande, Mora forest, *E. Britton 2876* (NY). *T. convolutus* Lindenb.: SUMATRA. Eugano, 1894, *Modigliani s.n.* (NY). *T. evansii* Fulf.: COSTA RICA. Prov. de Limon, Tortuguero, *Steere 31* (NY). *T. gottschei* (Steph. & Jack) Steph. BORNEO, Sarawak, *Micholitz s.n.* (FH). *T. pterobryoides* (Spruce) Steph.: COLOMBIA. Dept. El Valle, Cordoba, *Killip 11776* (NY). *T. richardsianus* Verd.: BORNEO. Sarawak, *Richards 298* (FH - HOLOTYPE). *T. spathulistipus* (Reinw. et al.) Lindenb. INDIA. Perak, *Wray 1180* (FH).

Mastigolejeunea (Spruce) Steph. (Figs. 5d-f)

Common to all species studied of *Mastigolejeunea* is a deliquescent growth habit, an irregularly pinnate ramification pattern, lateral branches of the *Lejeunea*-type only, acrogyny, and the presence of gynoecial innovations (rarely occasionally lacking in *M. auriculata* (Wils. & Hook.) Schiffn.). In most species, single innovations predominate, but paired innovations are common in *M. nigra* (Steph.) Steph. (Fig. 5f), and *M. florea* Steph. The inflorescence pattern is diffuse in *M. atypos* (Gott.) Steph., *M. auriculata* (Wils. & Hook.) Schiffn. (Fig. 5d), *M. innovans* (Spruce) Steph., and *M. nigra,* but diffuse to monochasial in *M. humilis* (Gott.) Steph. (Fig. 5e), and diffuse to dichasial in *M. florea.* Microphyllous branches are found in *M. auriculata.*

Inflorescence number and pattern vary within *Mastigolejeunea,* but the variability does not correlate well with species delimitation as it now stands. However, species delimitation in *Mastigolejeunea* is very poor, and no accurate assessment of the significance of branch characters in this genus can be made until revisionary studies are completed. *Mastigolejeunea* is similar in its branch system to *Spruceanthus* and typical species of *Archilejeunea* and *Thysananthus.*

MATERIAL EXAMINED: *Mastigolejeunea atypos* (Gott.) Steph.: NEW GUINEA. [no further locality] 1899, *Naumann s.n.* (FH - Herb. Schiffner (3239). *M. auriculata* (Wils. & Hook.) Schiffn.: U.S.A. Florida, *Schuster 80-192* (Herb. R.M. Schuster); TANZANIA. Usagara Mts., *Hannington s.n.* (NY-HOLOTYPE of *M. carinata* (Mitt.) Steph.). *M. calcarata* (Mitt.) Steph.: FIJI. Ovalau, *Seemann s.n.* (NY-HOLOTYPE). *M. florea* Steph.: NIGERIA. [no further locality] *Richards 3410* (NY). *M. humilis* (Gott.) Schiffn.: JAVA. Buitenzorg, *Massart 235* (FH). *M. innovans* (Spruce) Steph.: CUBA. La Magdalena, Gayamas, *Baker 4603* (NY). *M. nigra* (Steph.) Steph.: TANZANIA. Usambara, *Fischer 39* (FH).

Archilejeunea (Spruce) Schiffn. (Figs. 6a-f)

All species examined of *Archilejeunea* have a deliquescent growth habit, an irregularly pinnate ramification pattern, and at least one innovation per gynoecium. However, all other characters surveyed are variable in *Archilejeunea.* Although the genus is usually described as producing lateral branches of the *Lejeunea*-type only (Crandall 1969), some *Frullania*-type branches were observed in *A. olivacea* (Hook. f. & T. Tayl.) Steph. (Figs. 6b-c). All species examined are acrogynous, with the exception of *A. rotalis* (T. Tayl.) Steph. (Fig. 6e), which is usually cladogynous. Innovation leaf sequence is lejeuneoid in all species studied except *A. porelloides* (Spruce) Steph. (Fig. 6d), which exhibits the pycnolejeuneoid sequence. Single innovations only were observed in *A. rotalis,* but in all other species, innovations may be single or paired. The inflorescence pattern is diffuse to monochasial in *A. abbreviata* (Mitt.) Vanden Bergh., *A. auberiana* (Mont.) Steph., *A. parviflora* (Nees) Steph. (Fig. 6f), and *A. porelloides.* In *A. olivacea* the pattern is dichasial.

As indicated by Gradstein & Buskes (this volume), innovation leaf sequence is important at the subgeneric level in *Archilejeunea.* At the specific level, gynoecial branch length and inflorescence pattern are the only branch characters that appear to have potential as taxonomic characters. In the branch systems of most species, *Archilejeunea* is most similar to *Spruceanthus, Mastigolejeunea* and *Thysananthus.*

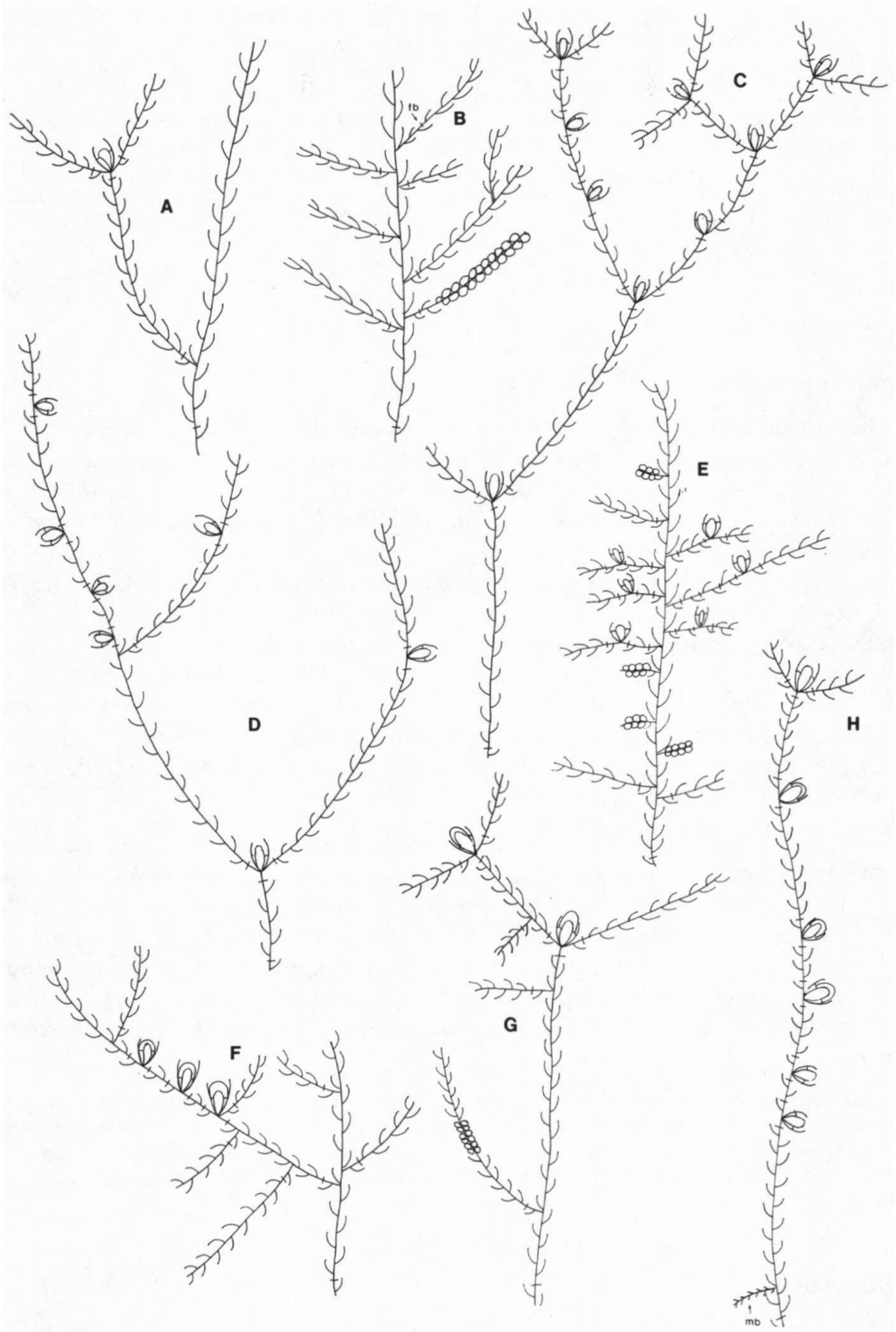


Fig. 6. Diagram of branch systems in *Archilejeunea* and *Spruceanthus*.

A. *Archilejeunea mariana*. B. - C. *A. olivacea*. D. *A. porelloides*. E. *A. rotalis*. F. *A. parviflora*. G. *Spruceanthus semirepandus*. H. *S. polymorphus*. mb = microphyllous branch. Unless otherwise indicated, all other lateral branches are *Lejeunea*-type.

Material Examined: *Archilejeunea abbreviata* (Mitt.) Vanden Bergh.: SIERRA LEONE. Bagru River, 1861, *Mann s.n.* (NY - HOLOTYPE). *A. auberiana* (Mont.) Steph.: BRAZIL. Pará, Rio Negro, "in arborum ramilis." *Spruce s.n.* "Hepaticae Spruceanae: Amazonicae et Andinae" (NY - as *A. florentissima* Spruce, NY). *A. mariana* (Gott.) Steph.: NEW GUINEA. Burai, *Kärnbach 13* (FH - as *Archi lejeunea falcata* Steph.). *A. olivacea* (Hook. f. & T. Tayl.) Steph.: NEW ZEALAND. Auckland, 1895, *Cheeseman s.n.* (FH). *A. parviflora* (Nees) Steph.: BRAZIL. Amazonas, "Obidos et Rio Caipuru," *Spruce s.n.*, "Hepaticae Spruceanae: Amazonicae et Andinae" (NY - as *A. leprieurii* Mont.); JAMAICA. Union Hill, 1908, *E. Britton 824* (NY - as *A. viridissima* (Lindenb.) Evans); COLOMBIA. Risaralda, Municipio de Santa Rosa de Cabal, El Pitel, *Gradstein 3607* (NY - as *A. viridissima*). *A. porelloides* (Spruce) Steph.: VENEZUELA. San Carlos del Rio Negro, *Spruce s.n.* "Hepaticae Spruceanae: Amazonicae et Andinae" (NY). *A. rotalis* (T. Tayl.) Steph. ST. HELENA. [no further locality] *Seemann s.n.* (NY).

Spruceanthus Verd. (Figs. 6g-h)

The branch system of *Spruceanthus* is characterized by a deliquescent growth habit, irregularly pinnate ramification pattern, acrogyny, a lejeuneoid innovation leaf sequence, and gynoecia subtended by vigorous innovations. *Frullania-* and *Lejeunea*-type branches characterize *S. sulcatus* (Nees) Gradst. and *S. theobromae* (Spruce) Gradst., but only *Lejeunea*-type branches are found in *S. polymorphus* (Sande Lac.) Verd. (Fig. 6h) and *S. semirepandus* (Nees) Verd. (Fig. 6g). The leaves on innovations are arranged according to the lejeuneoid sequence. Microphyllous branches were observed in *S. polymorphus,* but not in the other species studied. Both single and paired gynoecial innovations are found in *Spruceanthus.* Single innovations predominate in *S. polymorphus, S. sulcatus* and *S. theobromae,* and the inflorescence pattern in these species is diffuse or monochasial. Paired innovations are more common in *S. semirepandus,* and in this species, the inflorescence pattern may be a monochasium or a dichasium.

Probably the most significant branch difference among species of *Spruceanthus* is branch type. The presence of microphyllous branches in *S. polymorphus* may also be useful, but differences noted in innovation number are probably not reliable taxonomically. No infrageneric classification has been proposed for *Spruceanthus,* and therefore assessment of the importance of branch characters within the genus must await further revisionary studies. At the generic level, *Spruceanthus* is similar in its branch system to members of *Archilejeunea, Thysananthus,* and *Mastigolejeunea.*

Material Examined: *Spruceanthus polymorphus* (Sande Lac.) Verd.: U.S.A. Hawaii, Oahu, Manoa, *Heller 2886* (FH). *S. semirepandus* (Nees) Verd.: NEPAL. Khatmandu, 1900, *Rana s.n.* (FH). *S. sulcatus* (Nees) Gradst.: JAVA. Prov. Preanger, Mt. Salak, 1893, *Schiffner s.n.* (FH). *S. theobromae* (Spruce) Gradst.: ECUADOR. Guayaquil, Rio Ventranos, *Spruce s.n.* "Hepaticae Amazonicae et Andinae" (NY).

Caudalejeunea (Steph.) Schiffn. (Figs. 7a-c)

Five species of *Caudalejeunea* were examined in this study. The growth habit is deliquescent in all except *C. stephanii* Spruce ex Steph. (Fig. 7a), which exhibits an excurrent habit. The ramification pattern is basically irregularly pinnate, although plants with a regularly pinnate pattern were observed in collections of *C. stephanii* and *C. lehmanniana* (Lehm. & Lindenb.) Steph. Only *Lejeunea*-type branches were observed. *C. stephanii* and some plants of *C. lehmanniana* are cladogynous, but the remaining species are acrogynous. *Lejeunea*-type branches form innovations on some plants of *C. lehmanniana* (Fig. 7b). The leaf sequence on these innovations is lejeuneoid. Innovations are usually single, but paired ones were observed occasionally. The inflorescence pattern is simple or diffuse (rarely a weak taxilejeuneoid monochasium in *C. lehmanniana*). The branch system of *Caudalejeunea* is very similar to that of *Lopholejeunea* in that innovations are usually absent, but when present, they are *Lejeunea*-type branches.

MATERIAL EXAMINED: *Caudalejeunea africana* Steph.: CAMEROON. Bipinde, *Zenker 1244* (FH). *C. crescentiae* (Lindenb. & Gott.) Steph.: PUERTO RICO. Santurce, *Heller 838* (NY). *C. reniloba* (Gott.) Steph.: BORNEO. Mt. Kinabalu, Menetendok, *Verdoorn 406* (NY). *C. lehmanniana* (Lehm. & Lindenb.) Steph.: U.S.A. Florida, *Schuster 80-214* (Herb. R.M. Schuster). *C. stephanii* Spruce ex Steph.: ANDAMAN IS. Port Blair, 1899, *Man s.n.* (FH).

Acrolejeunea (Spruce) Schiffn. (Fig. 7d)

Acrolejeunea was monographed recently by Gradstein (1975) and in this treatment, branching was discussed in detail. My observations based on four species concur with those of Gradstein, convincing me that further study on my part would be superfluous. The following summary of branching in *Acrolejeunea* is based on my own and Gradstein's observations. The growth habit is deliquescent in *Acrolejeunea,* and the ramification pattern is irregularly pinnate. *Frullania*- and *Lejeunea*-type branches are both found in most species, with *Lejeunea*-type usually predominating. *Frullania*-type branches are entirely lacking in only the smallest species *A. pusilla* (Steph.) Grolle & Gradst. and *A. parvula* (Mizut.) Gradst. (branch data on *A. parvula* from Gradstein, 1975). An unusual feature of *Acrolejeunea* is the presence in some species of flagelliform branches, i.e., upright branches upon which leaves are caducous or reduced. Gynoecia are usually borne on leading branches, and are never subtended by true gynoecial innovations. A peculiar feature of *Acrolejeunea* is the presence of more than one cycle of gynoecial bracts. According to Gradstein, *Radula*-type branches may occasionally subtend one or more of these supernumerary bracts. Such branches are referred to as "pseudoinnovations" by Verdoorn (1934). The inflorescence pattern is diffuse. The branch system of *Acrolejeunea* is most similar to that of *Schiffneriolejeunea, Verdoornianthus, Caudalejeunea* and *Lopholejeunea* in the absence of innovations. *Acrolejeunea* and *Schiffneriolejeunea* share the additional feature of *Frullania*-type branching in some species.

MATERIAL EXAMINED: *Acrolejeunea fertilis* (Reinw. et al.) Schiffn.: BURMA. Arakan, Ramree Is., Kyaukpyu, Sep 1945, *Wallace s.n.* (NY). *A. heterophylla* (Evans) Grolle & Gradst.: COSTA RICA. near Turrialba, on *Hevea, Schultes 11885* (NY). *A. pusilla* (Steph.) Grolle & Gradst.: JAPAN. Prov. Higo, Kuma-gun, Watari, 8 Aug 1947, *Mayebara s.n.* (NY). *A. pycnoclada* (T. Tayl.) Schiffn.: SOLOMON IS. Buka, *Kärnbach s.n.* (FH).

Brachiolejeunea (Spruce) Schiffn. (Figs. 7e-f)

The growth habit is deliquescent in species studied of *Brachiolejeunea,* and the ramification pattern is irregular. Both *Lejeunea*- and *Frullania*-type branches were observed in *B. corticalis* (Lehm. & Lindenb.) Schiffn. (Fig. 7e), although *Lejeunea*-type branches were observed only in *B. bahamensis* Evans (Fig. 7f) and *B. insularis* Evans. All species studied are acrogynous, and the usually paired innovations have a pycnolejeuneoid leaf sequence. The inflorescence pattern is dichasial. Differences in branch type help distinguish the species of *Brachiolejeunea* studied. The branching system in *Brachiolejeunea* recalls that of *Marchesinia, Dicranolejeunea* and *Neurolejeunea* in the presence of acrogyny and predominately paired innovations. *Marchesinia* and *Dicranolejeunea* also produce both *Frullania*- and *Lejeunea*-type branches.

MATERIAL EXAMINED: *Brachiolejeunea bahamensis* Evans: PUERTO RICO. Mono Is., Ubero, *Britton, Cowell & Hess 1853* (NY). *B. corticalis* (Lehm. & Lindenb.) Schiffn.: TRINIDAD. North Post Rd., *Britton, Coker & Rowland s.n.* (NY). *B. insularis* Evans.: U.S.A. Florida, *Schuster 80-141* (Herb. R.M. Schuster).

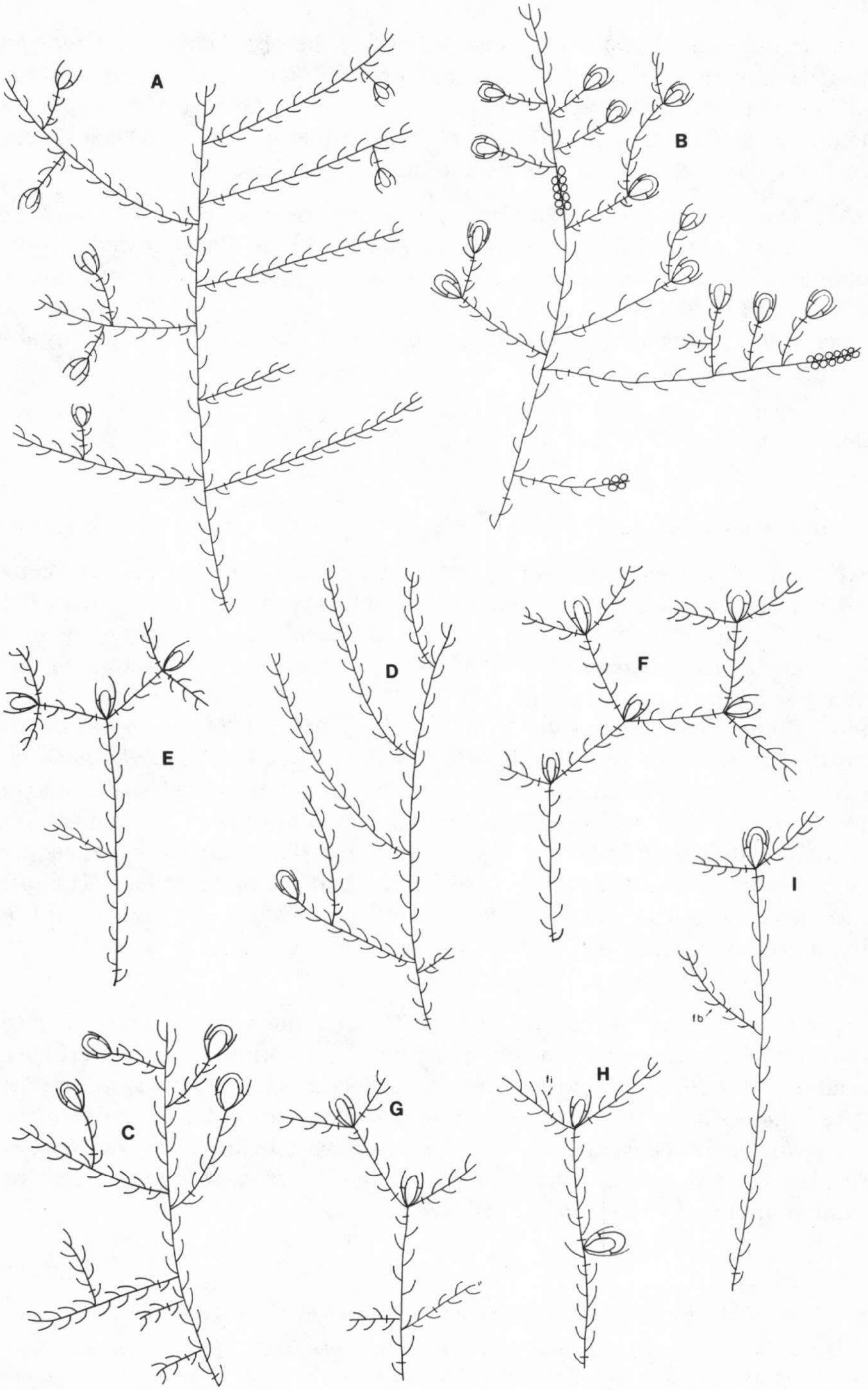
Trocholejeunea Schiffn. (Figs. 7g-h)

Plants in both species studied of *Trocholejeunea* have a deliquescent habit and an irregularly pinnate ramification pattern. Only *Lejeunea*-type lateral branches were observed in *T. sandvicensis* (Gott.) Schiffn. (Fig. 7h), but the *Frullania*-type predominates in *T. infuscata* (Mitt.) Verd. (Fig. 7g). All plants are acrogynous, and innovations are consistently present. As noted first by Verdoorn (1934) some gynoecial innovations in *T. sandvicensis* are *Frullania*-type branches, replacing the bracteal lobule. Where paired innovations occur in *T. sandvicensis,* one is *Frullania*-type, the other is *Radula*-type. However, innovations are usually single in both species. The leaf sequence on *Radula*-type innovations is pycnolejeuneoid. On *Frullania*-type innovations, the first appendage is anomalous, as in Fig. 1a, and the second is a basiscopically oriented lateral leaf, followed by an acroscopic leaf, then an underleaf. The inflorescence pattern is diffuse to mono- or dichasial. The two species studied have fairly distinctive branch systems, differentiated by branch type of both lateral and innovational branches. With the exception of the occasional *Frullania*-type innovations in *T. sandvicensis,* branching in *Trocholejeunea* is identical to that in *Brachiolejeunea.*

MATERIAL EXAMINED: *Trocholejeunea infuscata* (Mitt.) Verd.: INDIA. Chindupje [sic], on banks, *Griffith s.n.* (NY). *T. sandvicensis* (Gott.) Schiffn.: U.S.A. Hawaii, Kauai, *Degener 21609* (NY).

Fig. 7. Diagram of branch systems in *Caudalejeunea, Brachiolejeunea, Acrolejeunea, Trocholejeunea* and *Oreolejeunea.*

A. *Caudalejeunea stephanii.* B. *C. lehmanniana.* Innovations are *Lejeunea*-type branches. C. *C. africana.* D. *Acrolejeunea pycnoclada.* E. *Brachiolejeunea bahamensis.* F. *B. corticalis.* G. *Trocholejeunea infuscata.* H. *T. sandvicensis.* I. *Oreolejeunea securifolia.* fi = *Frullania*-type innovation. Unless otherwise indicated, all lateral branches are *Lejeunea*-type.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Oreolejeunea Schust. (Fig. 7i)

In *Oreolejeunea securifolia* (Spruce) Schust., the only species of *Oreolejeunea,* the growth habit is deliquescent, and the ramification pattern is irregularly pinnate. All lateral branches I observed were *Frullania*-type. Gynoecia usually terminate main axes, and are subtended by paired innovations. The innovation leaf sequence is pycnolejeuneoid, and the inflorescence pattern is diffuse.

According to Schuster (1980) *Oreolejeunea* is closely related to *Blepharolejeunea* S. Arn. and more distantly to *Brachiolejeunea.* Van Slageren and Kruijt (this volume) consider *Oreolejeunea* to be a synonym of *Blepharolejeunea. Oreolejeunea* has no distinctive branch features, and resembles *Brachiolejeunea* in the presence of *Frullania*-type innovations, paired innovations, and a dichasial inflorescence pattern.

MATERIAL EXAMINED: VENEZUELA. Estado de Merida, Sierra de Merida, *Schuster 76-1403b* (Herb. R.M. Schuster).

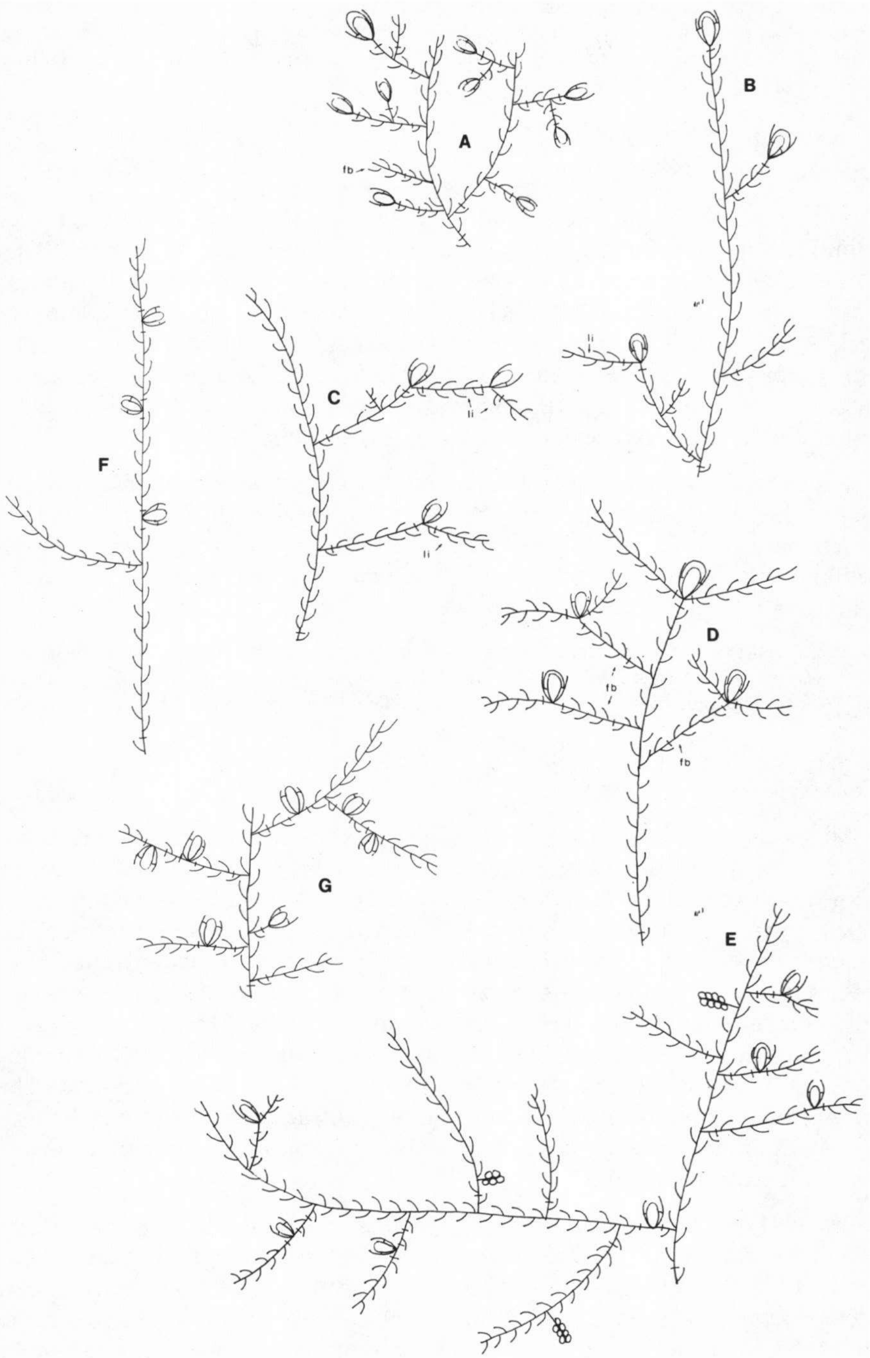
Dicranolejeunea (Spruce) Schiffn. (Figs. 8d-e)

In *Dicranolejeunea,* the growth habit is deliquescent and the ramification pattern is irregularly pinnate. Only *Frullania*-type lateral branches were observed in *D. axillaris* (Mont) Schiffn. (Fig. 8d), but both *Lejeunea*- and *Frullania*-type branches occur in *D. yoshinagana* (Hatt.) Mizut., *D. chrysophylla* (Steph.) Grolle, *D. madagascariensis* var. *obtusifolia* E. Jones (Fig. 8e), *D. javanica* Steph. and *D. gilva* Steph. (branch data on *D. gilva* from Mizutani 1980). In *D. madagascariensis* var. *obtusifolia,* gynoecia usually terminate short branches, but *D. axillaris, D. chrysophylla, D. javanica* Steph. and *D. yoshinagana* are acrogynous. Single innovations only were observed in *D. madagascariensis* var. *obtusifolia,* but innovations are predominantly paired in the other species studied. The innovation leaf sequence is lejeuneoid in *D. javanica,* but pycnolejeuneoid in the other species. The inflorescence pattern is diffuse in *D. yoshinagana* and *D. madagascariensis* var. *obtusifolia,* diffuse to monochasial in *D. javanica* Steph., and dichasial in *D. axillaris* and *D. chrysophylla.*

Species studied of *Dicranolejeunea* differ in branch type, gynoecial position, innovation leaf sequence, innovation number and inflorescence pattern. All this variation is potentially useful at some infrageneric rank. *D. madagascariensis* var. *obtusifolia* is similar in branch pattern to *Odontolejeunea,* but *D. yoshinagana, D. chrysophylla. D. gilva* and *D. axillaris* resemble species of *Brachiolejeunea* or *Marchesinia.* The branch pattern exhibited by *D. javanica* is reminiscent of that found in species of *Archilejeunea* or *Spruceanthus.*

Fig. 8. Diagram of branch systems in *Lopholejeunea, Dicranolejeunea,* and *Odontolejeunea.*

A. *Lopholejeunea hispidissima.* B. *L. subfusca.* C. *L. herzogiana.* D. *Dicranolejeunea axillaris.* E. *D. madagascariensis* var. *obtusifolia.* F. *Odontolejeunea lunulata.* G. *O. sieberiana.* li = *Lejeunea*-type innovation. Unless otherwise indicated, all other lateral branches are *Lejeunea*-type.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MATERIAL EXAMINED: *Dicranolejeunea axillaris* (Mont.) Schiffn.: ECUADOR. Pallutrango & Chimborazo, *Spruce s.n.* (NY). *D. chrysophylla* (Steph.) Grolle: SOUTH AFRICA. Cape Philippstown, *Ecklon s.n.* (FH). *D. javanica* Steph.: NEW GUINEA. Morobe Prov., Slate Creek and Gumi Creek Divide, 17 km W of Bulolo, 30 Jan 1981, *Streimann 13993* (NY). *D. madagascariensis* var. *obtusifolia* E. Jones: UGANDA. Mpanda, *Jones 619* (NY). *D. yoshinagana* (Hatt.) Mizut. JAPAN. Saitama Pref., Chichibu Montane area, Ochigawa ravine, *Mizutani 521* (NY).

Odontolejeunea (Spruce) Schiffn. (Figs. 8f-g)

The growth habit in species studied of *Odontolejeunea* is deliquescent, and the ramification pattern is irregularly pinnate. Lateral branches are *Lejeunea*-type, and gynoecia are borne on short or long branches. Innovations subtended all gynoecia observed in *O. lunulata* (Web.) Schiffn. (Fig. 8f) and *O. longispica.* Evans but were lacking occasionally in the specimen examined of *O. sieberiana* (Gott.) Steph. (Fig. 8g). Innovations are single and leaves follow the pycnolejeuneoid sequence in all three species. I observed fertile innovations in *O. lunulata,* and the inflorescence pattern in the genus can be described as diffuse to monochasial.

The occasional absence of innovations in *Odontolejeunea sieberiana* may be helpful in distinguishing it from the other two species when used in concert with other characters. Although possessing no unusual branch traits, *Odontolejeunea* is similar only to *Dicranolejeunea obtusifolia* var. *madagascariensis* in branch features.

MATERIAL EXAMINED: *Odontolejeunea lunulata* (Web.) Schiffn.: CUBA. [no further locality] *Wright s.n.* (NY). *O. sieberiana* (Gott.) Steph.: CUBA. [no further locality] *Wright s.n.* (FH). *O. longispica* Evans: JAMAICA. Lapland, near Catadupa, 1900 ft., 14 Feb 1906, *Harris 11, 119 p.p.* (NY-ISOTYPE).

Lopholejeunea (Spruce) Steph. (Figs. 8a-c)

All species examined of *Lopholejeunea* exhibit a deliquescent growth habit, and an irregularly pinnate ramification pattern. Both *Frullania*- and *Lejeunea*-type branches occur in *L. hispidissima* Steph. (Fig. 8a) and *L. macroloma* Steph. *Lejeunea*-type branching only characterized the other species examined. *Lopholejeunea asiatica* Steph. and *L. hispidissima* are primarily cladogynous, but other species produce gynoecia on short or long branches. Although the genus is predominantly innovation-free, *Lejeunea*-type innovations were found occasionally in *L. subfusca* (Nees) Steph. (Fig. 8b) and *L. herzogiana* (Fig. 8c). These innovations are occasionally paired in *L. herzogiana* and may bear gynoecia. The leaf arrangement on innovations is lejeuneoid. The inflorescence pattern is diffuse in all species examined of *Lopholejeunea* excepting *L. hispidissima* and *L. asiatica* in which the pattern is simple.

Branch type, innovation presence, gynoecial position and inflorescence pattern are all variable within *Lopholejeunea,* and thus are potentially useful taxonomic tools within the genus. Some sections and subgenera have been recognized within *Lopholejeunea* (Verdoorn 1934, Schuster 1980, Thiers 1983) but branch characters are not used to delimit them. Although exhibiting a distinctive array of branch characters, *Lopholejeunea* most closely resembles *Caudalejeunea* in the type of variation found within the genus.

MATERIAL EXAMINED: *Lopholejeunea asiatica* Steph.: PHILIPPINES. Baguio, *Robinson 14011* (FH). *L. ceylanica* Steph.: CEYLON. [no further locality] 1900, *Willis s.n.* (FH - ISOTYPE). *L. eulopha* (T. Tayl.) Steph.: SUMATRA. Res. Sum., Westk. [sic], Aneh, Jul 1894, *Schiffner s.n.* "Hepaticae Selectae et Criticae 244" (F. Verdoorn, ed.) (NY). *L. herzogiana* Verd.: JAVA. Prov. Preanger, Tjibodas, Mt. Pangerango, 1894, *Schiffner s.n.* (FH - ISOTYPE). *L. hispidissima* Steph.: NEW CALEDONIA. [no further locality] *Franc s.n.* (FH). *L. macroloma* Steph.: AUSTRALIA. Queensland, Mt. Bidwell, collector unknown (NY). *L. subfusca* (Nees) Steph.: BRAZIL. Amazonas, Rio Negro, *Spruce s.n.* "Hepaticae Spruceanae: Amazonicae et Andinae," as *L. sagraeana* (Mont.) Steph. (NY); U.S.A. Florida, *Schuster 80-122* (Herb. R.M. Schuster). *L. subnuda* Steph.: INDIA. Madras, Madura, Palni Hills, Kodackanal, Perumal Mt., 1923, *Foreau s.n.* (NY).

Marchesinia S.F. Gray (Figs. 9a-c)

Branching was studied in six species of *Marchesinia*. The growth habit is deliquescent in all, and the ramification pattern is irregularly pinnate. Lateral branches may be *Frullania-*, *Lejeunea-*, or *Radula*-type in *M. brachiata* (Sw.) Nees (Fig. 9c) but only *Lejeunea*-type branches were observed in the remaining species (although Crandall, 1969, reported *Frullania*-type branches in *M. mackayi* S.F. Gray). All species are acrogynous, and innovations, usually two per gynoecium, are present in all (single innovations predominate in *M. acutiloba* T. Tayl.). The leaf sequence is pycnolejeuneoid. The inflorescence pattern is dichasial in *M. longistipula* Steph. (Fig. 9b) and *M. mackayi*, but diffuse in the other species studied.

Differences in branching among species studied of *Marchesinia* are minor, and probably do not have any taxonomic significance. The branch system of *Marchesinia* shows similarities to that of *Brachiolejeunea, Dicranolejeunea* and *Neurolejeunea.*

MATERIAL EXAMINED: *Marchesinia acutiloba* T. Tayl.: ST. HELENA. [no further locality, collector unknown] (FH - ISOTYPE). *M. brachiata* (Sw.) Nees: CUBA. Prov. de Havana, Ariganabo, 1915, *Leon s.n.* (FH). *M. fuscescens* (Hampe) Hampe: ECUADOR. Gualaquiza, 1909, *Allioni s.n.* (FH). *M. galapagoana* Steph.: ECUADOR. Galapagos Is., Charles Is., *Andersson s.n.* (FH - ISOTYPE). *M. longistipula* Steph.: ECUADOR. Prov. Azuay, Gualaquiza, 1909, *Allioni s.n.* (FH - ISOTYPE). *M. mackayi* S.F. Gray: IRELAND. Killarney, 1885, *Stewart & Holt s.n.* (FH).

Symbiezidium Trevis. (Fig. 9d)

Symbiezidium has an excurrent growth habit, an irregularly pinnate ramification pattern, gynoecial branches consisting of one leaf cycle only, and single innovations that are usually rather short. Only *Lejeunea*-type lateral branches are found. The innovation leaf sequence is pycnolejeuneoid, and inflorescence pattern is simple.

Branch systems are identical in *Symbiezidium barbiflorum* (Lindenb.) Evans and *S. transversale* (Sw.) Trevis., and thus branch patterns do not elucidate relationships within the genus. *Stictolejeunea* is similar to *Symbiezidium* in the presence of an excurrent growth habit, cladogyny, and short, single innovations. *Symbiezidium* differs from *Stictolejeunea* in lacking *Frullania*-type branches.

MATERIAL EXAMINED: *Symbiezidium barbiflorum* (Lindenb.) Evans: CUBA. [no further locality, collector unknown] (FH). *S. transversale* (Sw.) Trevis.: TRINIDAD, Valencia, Toco Rd., *Britton 1859* (FH - as *S. granulatum* (Nees) Trevis.): PUERTO RICO, Luquillo Mts., El Yunque, *Evans 25* (NY).

Stictolejeunea (Spruce) Schiffn. (Fig. 9e)

Stictolejeunea squamata (Willd.) Schiffn. and *S. balfourii* (Mitt.) E. Jones are characterized by an excurrent growth habit, and a regularly pinnate ramification pattern. Elongate lateral branches are all *Frullania*-type in *S. squamata,* but may be *Frullania*- or *Lejeunea*-type in *S. balfourii.* Gynoecia are restricted to very short *Lejeunea*-type branches, and the gynoecia are usually subtended by very short, weak innovations (often androecial in *S. balfourii*) that are hidden by the perianth. The sequence of leaves on innovations is pycnolejeuneoid, and the inflorescence pattern is simple.

Branch type of elongate lateral branches is the only important difference between the species studied of *Stictolejeunea.* Mizutani (1978) used branch type as a fundamental criterion to separate species of *Stictolejeunea.* He characterized *S. squamata* and *S. kunzeana* (Gott. et al.) Schiffn., (a synonym of *S. squamata* according to Gradstein, this volume) as having "vegetative branching usually of th *Frullania*-type," and *S. balfourii, S. richardsii* Herz. and *S. iwatsukii* Mizut. as having "vegetative branches of the *Lejeunea*-type." My observations indicate that the differentiation in branch type is not as clear as Mizutani indicated, because both *Lejeunea*- and *Frullania*-type elongate lateral branches are found with approximately equal frequency in the two collections examined of *S. balfourii.* Because of similarities in growth habit, ramification pattern, and gynoecial position, the branch system of *Stictolejeunea* is reminiscent of that found in *Bryopteris,* although these two genera are very dissimilar in other respects.

MATERIAL EXAMINED: *Stictolejeunea balfourii* (Mitt.) E. Jones: NIGERIA. Benin Prov., Ehor Forest Reservation, *Jones 870* (NY - as *S. africana* Vanden Bergh.); MAURITIUS. [collector unknown] (NY). *S. squamata* (Willd.) Schiffn.: BOLIVIA. [no further locality] *Buchtien s.n. & s.d.* (FH): PANAMA. Prov. Chiriqui, Boquota, *Helion 1906* (FH).

Neurolejeunea (Spruce) Schiffn. (Figs. 9f-g)

Common to all three species of *Neurolejeunea* is a deliquescent growth habit, an irregularly pinnate ramification pattern, *Lejeunea*-type branching, acrogyny, and paired innovations. Innovation leaf sequence is pycnolejeuneoid and the inflorescence pattern is diffuse to dichasial. Branch differences are not useful in delimiting species within *Neurolejeunea.* Branching in *Neurolejeunea* is reminiscent of that in *Marchesinia, Dicranolejeunea* and *Brachiolejeunea,* although *Frullania*-type branches are entirely lacking in *Neurolejeunea.*

MATERIAL EXAMINED: *Neurolejeunea breutelii* (Gott.) Schiffn.: U.S.A. Florida, Liberty Co., Camel Lake Recreation Area, *Breil 2411* (NY). *N. catenulata* (Nees) Schiffn.: PUERTO RICO, Luquillo Mts., El Yunque, *Evans 119* (NY). *N. seminervis* (Spruce) Steph.: VENEZUELA. San Carlos del Rio Negro, *Spruce s.n.* "Hepaticae Spruceanae: Amazonicae et Andinae." (FH - ISOTYPE).

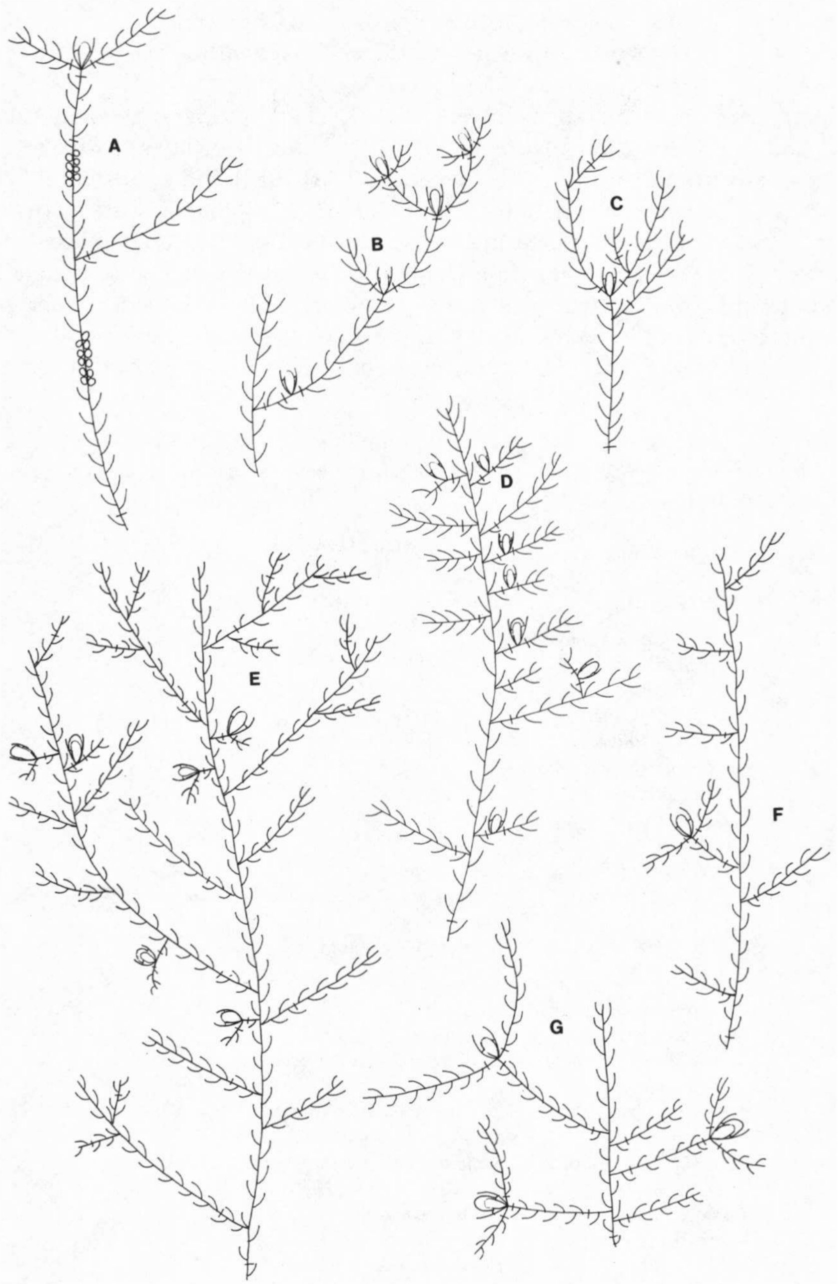

Fig. 9. Diagrams of branch systems in *Marchesinia, Symbiezidium, Stictolejeunea* and *Neurolejeunea.*

A. *Marchesinia fuscescens.* B. *M. longistipula.* C. *M. brachiata.* D. *Symbiezidium barbiflorum.* E. *Stictolejeunea squamata.* All branches terminating in gynoecia are *Lejeunea*-type. All others are *Frullania*-type. F. *Neurolejeunea breutelii.* G. *N. seminervis.* ri = *Radula*-type branch. Unless otherwise indicated, all other lateral branches are *Lejeunea*-type.

Taxonomic Significance of Branch Characters in the Subfamilial Classification of Ptychanthoideae

A summary of branch systems in genera of Ptychanthoideae is given in Tables 3 and 4, and the distribution of branch character states is compared with the subfamilial classifications proposed by Schuster (1963, 1980) and Gradstein (1975) in Table 2. Arrangements of genera by Schuster (1963, 1980) and Gradstein (1975) are similar in that both group genera into informal categories called complexes. These classifications are phenetic, based on similarities in features such as stem anatomy, oil body morphology, trigone structure, perianth morphology, ventral merophyte width, presence of ocelli, setal articulations, leaf cell shape, and position of leaves in the dried condition. Branch features such as branch type and innovation presence

Table 2. Comparison between classification schemes of Gradstein and Schuster for Lejeuneaceae subfamily Ptychanthoideae.

Gradstein (1975):	Schuster (1963, 1980):
PTYCHANTHEAE	tribal rank not used
Ptychanthus complex	
Ptychanthus	
Thysananthus	
Mastigolejeunea	(*Ptychanthus* complex
Schiffneriolejeunea	also includes *Tuzibeanthus*)
Caudalejeunea complex	
Caudalejeunea	
Brachiolejeunea complex	
Acrolejeunea	
Brachiolejeunea	(*Trocholejeunea* considered
Trocholejeunea	a subgenus of *Brachiolejeunea*)
ARCHILEJEUNEAE	tribal rank not used
Dicranolejeunea complex	
Dicranolejeunea	
Odontolejeunea	placement uncertain
Lopholejeunea complex	contains only *Lopholejeunea*
Lopholejeunea	
Symbiezidium	autonomous complex
Marchesinia	autonomous complex
Archilejeunea complex	contains only *Archilejeunea*
Archilejeunea	
Phaeolejeunea	not treated
Spruceanthus	autonomous complex
Tuzibeanthus	*Ptychanthus* complex
[*Verdoornianthus*]*	not treated
Stictolejeunea complex	
Stictolejeunea	
Neurolejeunea	

*Described by Gradstein, 1977.

Table 3. Comparison of salient branch features in genera with a lejeuneoid innovation leaf sequence (predominantly), and related genera lacking innovations (indicated by asterisks).

1 = growth habit; 2 = ramification pattern; 3 = lateral branch type; 4 = gynoecial position; 5 = innovation presence; 6 = innovation number; 7 = inflorescence pattern.

	1	2	3	4	5	6	7
	excurrent (+) deliquescent (-)	regularly pinnate (+) irregularly pinnate (-)	*Frullania*-type (+) *Lejeunea*-type (-)	acrogyna (+) cladogyny (-)	present (+) absent (-)	paired (+) single (-)	simple (1) diffuse (2) monochasial (3) dichasial (4)
*Bryopteris**	±	±	±	-	-	NA	1
Ptychanthus	+	+	±	+	+	±	2-3
Tuzibeanthus	+	±	+	+	+	±	2
Phaeolejeunea	-	-	±	+	+	±	2-3
*Schiffneriolejeunea**	±	±	±	-	-	NA	1
*Verdoornianthus**	+	-	-	-	-	NA	1
Thysananthus	±	±	-	+	+	±	2-4
Mastigolejeunea	-	-	-	+	+	±	2-3
Archilejeunea	-	-	±	±	+	±	2-4
Spruceanthus	-	-	-	+	+	±	2-4
*Caudalejeunea**	-	-	-	±	±	-	1-2

Table 4. Comparison of salient branch features in genera with a pycnolejeuneoid innovation leaf sequence (predominantly), and related genera lacking innovations (indicated by asterisks).

1 = growth habit; 2 = ramification pattern; 3 = lateral branch type; 4 = gynoecial position; 5 = innovation presence; 6 = innovation number; 7 = inflorescence pattern.

	1 excurrent (+) deliquescent (-)	2 regularly pinnate (+) irrgularly pinnate (-)	3 *Frullania*-type (+) Lejeunea-type (-)	4 acrogyny (+) cladogyny (-)	5 present (+) absent (-)	6 paired (+) single (-)	7 simple (1) diffuse (2) monochasial (3) dichasial (4)
*Acrolejeunea**	-	-	±	+	-	NA	1
Brachiolejeunea	-	-	±	+	+	+	4
Trocholejeunea	-	-	±	+	+	±	2-3
Oreolejeunea	-	-	+	+	+	+	2
Dicranolejeunea	-	-	±	±	+	±	4
Odontolejeunea	-	-	-	±	+	-	2-3
*Lopholejeunea**	-	-	±	±	±	±	2
Marchesinia	-	-	±	+	+	+	2, 4
Symbiezidium	+	-	-	-	+	-	1
Stictolejeunea	+	+	±	-	+	-	1
Neurolejeunea	-	-	-	+	-	+	2, 4

were also used. Gradstein (1975) united his complexes into two tribes, Ptychantheae and Archilejeuneae, based on trigone shape and leaf position in the dried condition. Constitution of generic complexes is fairly similar in the estimation of both Schuster and Gradstein, but their classifications differ primarily in placement of four controversial genera. Branch data may help resolve some of these differences. Placement of the four genera is discussed below:

(1) Tuzibeanthus. Placed in Gradstein's *Archilejeunea* complex, *Tuzibeanthus* held subgeneric rank within *Mastigolejeunea* in Schuster's original (1963) classification. Later (1980) Schuster recognized it as a genus in the *Ptychanthus* complex. Based on growth habit, ramification pattern, branch type and innovation leaf sequence, *Tuzibeanthus* has more features in common with members of the *Ptychanthus* complex than with the *Archilejeunea* complex. *Phaeolejeunea* (not treated by Schuster) also fits the *Ptychanthus* complex better on the basis of branch characters.

(2)*Trocholejeunea.* Schuster (1963, 1980) regarded *Trocholejeunea* as a subgenus of *Brachiolejeunea,* whereas Gradstein (1975) accorded it generic rank in the *Brachiolejeunea* complex. Branching in *Trocholejeunea* does not support the autonomy of the genus.

(3)*Dicranolejeunea.* Gradstein's classification placed *Dicranolejeunea* in a complex with *Odontolejeunea,* but Schuster (1980) aligned *Dicranolejeunea* with *Lopholejeunea.* The branch system of *Dicranolejeunea* is more similar to that of *Odontolejeunea* than *Lopholejeunea.*

(4)*Spruceanthus.* A member of the *Archilejeunea* complex in Gradstein's (1975) scheme, *Spruceanthus* forms an autonomous generic complex according to Schuster (1963). Because *Spruceanthus* is very similar to *Archilejeunea* in salient branch features, Gradstein's grouping of the two genera is supported.

Innovation leaf sequence shows the best correlation with the emended complex classification. In the other characters, similar character state transitions occur in all the larger generic complexes, e.g., eliminiation of *Frullania*-type branching, reduction of gynoecial branches and innovations, and transition from indistinct to distinct inflorescence patterns. The most logical interpretation of branch character state distribution is that generic complexes, whose delimitation is confirmed by innovation leaf sequence, represent natural units in which parallel evolution has occurred in other branch characters.

Unresolved remains the question of interrelationship of generic complexes. Unlike many aspects of his generic complex scheme, Gradstein's (1975) tribal classification is not confirmed by a consideration of branch systems, because members of his *Archilejeunea* complex (in the Archilejeuneae) agree in innovation leaf sequence with members of the *Ptychanthus* complex (in the Ptychantheae). Although cognizant that I may overemphasize the importance of innovation leaf sequence in the classification of Ptychanthoideae, I suggest that the question of generic complex interrelationships remains open to interpretation, and that although informal, the generic complex is still the most useful supergeneric unit within Ptychanthoideae.

References

CRANDALL, B.J. 1969. Morphology and development of branches in the leafy Hepaticae. Beih. Nova Hedwigia 30: 1-261.

EVANS, A.W. 1907. Hepaticae of Puerto Rico. 7. *Stictolejeunea, Neurolejeunea, Omphalanthus,* and *Lopholejeunea.* Bull. Torrey Bot. Club 34: 1-34.

EVANS, A.W. 1907a. Hepaticae of Puerto Rico. 8. *Symbiezidium, Marchesinia, Mastigolejeunea, Caudalejeunea* and *Bryopteris.* Bull. Torrey Bot. Club 34: 533-568.

EVANS, A.W. 1908. Hepaticae of Puerto Rico. 9. *Brachiolejeunea, Ptychocoleus, Archilejeunea, Leucolejeunea* and *Anoplolejeunea.* Bull. Torrey Bot. Club 35: 155-179.

FULFORD, M. 1941. Studies on American Hepaticae, I. Revision of the genus *Thysananthus.* Bull. Torrey Bot. Club 68: 32-42.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea* with an arrangement of the genera of Ptychanthoideae. Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. 1977. Studies on Lejeuneaceae subfam. Ptychanthoideae (Hepaticae) IV: *Verdoornianthus,* a new genus from Amazonas, Brazil. Bryologist 80: 606-611.

GRADSTEIN, S.R. 1980. Genera of the Lejeuneaceae: Past and Present. In: Clarke, G.S.C. and J. Duckett (eds.), Bryophyte Systematics. Academic Press, London, pp. 83-100.

GRADSTEIN, S.R. & TERKEN, L. 1981. Studies on Lejeuneaceae subfam. Ptychanthoideae VI. A revision of *Schiffneriolejeunea* section Saccatae from Asia. Occas. Pap. Farlow Herb. 16: 71-81.

GROLLE, R. 1980. Über *Harpalejeunea* in Australasien. J. Hattori Bot. Lab. 47: 237-244.

MIZUTANI, M. 1970. Branching types of Lejeuneaceae. Miscnea Bryol. Lichenol. 5: 81-90.

MIZUTANI, M. 1978. Lejeuneaceae from Ishigaki and Iriomote Islands of Ryukyu Archipelago. J. Hattori Bot. Lab. 44: 121-136.

MIZUTANI, M. 1980. Notes on the Lejeuneaceae 4. Asiatic species of the genus *Dicranolejeunea.* J. Hattori Bot. Lab. 48: 235-242.

SCHIFFNER, V. 1895. Hepticae (Lebermoose). pp. 2-141. In: A. Engler and K. Prantl (eds.), Die natürlichen Pflanzenfamilien 1, 3: 2-141.

SCHUSTER, R.M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae. I. Introduction: Annotated keys to the subfamilies and genera. Beih. Nova Hedwigia 9: 1-203.

SCHUSTER, R.M. 1980. The Hepaticae and Anthocerotae of North America, vol. 4. Columbia University Press, New York.

SPRUCE, R. 1884-1885. Hepaticae Amazonicae et Andinae. Trans. & Proc. Bot. Soc. Edinburgh 15: 1-590.

STOTLER, R. & CRANDALL-STOTLER, B. 1974. A monograph of the genus *Bryopteris* (Sw.) Nees von Esenbeck. Bryophyt. Bibl. 3: 1-159.

THIERS, B.M. 1983. Type studies in the Lejeuneaceae. II. *Pteryganthus,* a new subgenus of *Lopholejeunea.* Brittonia 35: 81-86.

THIERS, B.M. 1984. Branch characters significant to subfamilial classification of Lejeuneaceae (Hepaticae). Syst. Bot. 9: 33-41.

VERDOORN, F. 1934. De Frullaniaceis XV: Die Lejeuneaceae Holostipae der Indomalaya unter Berücksichtigung sämtlicher aus Asien, Australien, Neu-Seeland und Ozeanien angeführten Arten. Ann. Bryol. Suppl. 4: 40-192.

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3 A Chemotaxonomic Survey of Terpenoids and Aromatic Compounds in the Lejeuneaceae (Hepaticae)

by

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ABSTRACT: Gaschromatography-mass-spectrometry of 55 samples of Lejeuneaceae (40 species) and literature data revealed the presence in most taxa of large quantities of various sesquiterpenoids and/or diterpenoids, many of them unidentified. Only few taxa elaborate monoterpenes and aromatic compounds. Striatene-type and pinguisane-type sesquiterpenes are characteristic for Ptychanthoideae and Bryopteridoideae and striatene-type sesquiterpenes were also detected in some members of the Lejeuneoideae (*Omphalanthus* complex only). The distribution of these compounds coincides to some extent with generic complexes. Drimane-, calamenane-, chamigrane-type sesquiterpenes and phenylpropanoids were detected as major components in a limited number of taxa only and proved useful as chemical characters of individual genera or species. Other compounds show more puzzling distributions. Data obtained on infraspecific chemical variation are suggestive of large differences in the amount of variation among species.

Introduction

Hepaticae are able to synthesize large quantities of terpenoids - especially sesquiterpenes and diterpenes - and lipophilic aromatic compounds, which are stored in oil bodies. The study of these compounds has long been neglected, largely due to the difficulty of obtaining quantities of pure material sufficiently large for chemical analysis. Very frequently species grow intermingled and to separate and purify them is time-consuming and troublesome. However, recent improvements of the analytical apparatus have made it possible to determine chemical structures of even millimicron-sized samples and have led to an enormous increase in the number of reports dealing with the phytochemistry of the Hepaticae (see Asakawa 1982).

The Lejeuneaceae are the largest family of the Hepaticae (ca. 80 genera and hundreds of species) and are mainly tropical in distribution. Most species are epiphytes and confined to the rainforest. In previous papers (Asakawa et al. 1980a, 1980b, 1981a, Asakawa 1982a, Gradstein et al. 1981, Inoue et al. 1981) we have reported data on the terpenoids and aromatic compounds of about twenty species of Lejeuneaceae and have suggested that some of these substances are taxonomic markers for members of the family. For instance, species of *Brachiolejeunea* subg. *Plicolejeunea, Trocholejeunea* and *Acrolejeunea* (*Brachiolejeunea* complex) synthesize large quantities of pinguisane-type sesquiterpenes (Gradstein et al. 1981) and the species of the genus *Nipponolejeunea* seem characterized by the presence of borneol and bornyl-acetate (Inoue et al. 1981). However, due to the scarcity of chemical data these conclusions should be considered premature.

This paper presents the results of chemical analysis of about 40 species of Lejeuneaceae and reviews our present information on terpenoids and aromatic compounds in the family from a taxonomic point of view.

Material and Methods

Fifty-five samples of Lejeuneaceae, collected by the senior author and others in Papua New Guinea, Japan, New Zealand and South America (Table 1), were identified, purified, air-dried and extracted with ether. Dried voucher specimens were deposited in the Herbarium of the University of Utrecht (U) and chemical analysis of the samples was carried out at the Institute of Pharmacognosy of Tokushima Bunri University. The crude extracts were filtered through a glass column packed with silica gel. After evaporation of the solvent, the extracts were analysed by thin layer chromatography (TLC), gaschromatography (GC) and gaschromatography-mass spectrometry (GC/MS). The mass spectra obtained by GC/MS equipped with a computer were identified by direct comparison with those of authentic specimens and/or published information.

Comparative Survey

The identified and unidentified components of the 55 investigated samples are shown in Table I. Major components are italicized. Known chemical structures are shown in Fig. 1. The distribution of mono-, sesqui-, di- and triterpenes and aromatic compounds in all present and previously investigated species, as well as the possible chemical markers for each of them, are summarized in Tables II and III.

Table I. Terpenoids and aromatic compounds in 55 samples of Lejeuneaceae. Major components are italicized. Bold numbers refer to figures (Fig. 1). Gr. = S.R. Gradstein (collector).

No.	Species and Source	Compounds detected
1	*Acrolejeunea pusilla* (Japan Hattori s.n.)	α-humulene (**22**), bicyclogermacrene (**9**), ?(43)SA, 232(107), *pinguisanin* (**38**), *dehydropinguisanin* (**39**), pinguisenol (**44**), 232(97), 234(97), pinguisanolide (**41**),278(68), 264(108) pinguisane-type, 264(108) pinguisane-type, pinguisenal (**43**), campesterol, stigmasterol, sitosterol, 426(69)sterol.
2	*Acrolejeunea pycnoclada* (Papua New Guinea, Gr. 3830)	204(123)SH, β-elemene (**14**), 204(135)SH, 204(105)SH, α-humulene (**22**), *eremophilene* (**13**), 220(137)SA, 220(107) SA, pinguisanin (**38**), dehydropinguisanin (**39**), 234(41),

		220 (43) [SA with dimethyl carbinol)], ?(109)pinguisane-type, ?(95), *pinguisanolide* (41), isopinguisanolide (42), ?(108)pinguisane-type, *pinguisenal* (43), ?(107), ?(57) paraffin, ?(57)paraffin, ?(351), ?(55), ?(189).
3	*Acrolejeunea pycnoclada* (Papua New Guinea, Gr. 3812)	
4	*Acrolejeunea torulosa* (Suriname, Bekker 1575)	α-pinene (1), β-pinene (3), limonene (5), 128(43), β-elemene (14), 204(107)SH, γ-cadinene (16), 202, 204 (107)SH), *trans-β-farnesene* (17), 220 (82)SA, 232(59), 220(109)SA, *dehydropinguisanin* (39), 218(163), 220(109) pinguisane-type, 230(43), 262(97)pinguisane-type, *pinguisanolide* (41), isopinguisanolide (42), 278(109), *236*(121), 236(108) pinguisane-type, 288(119)DA, 304(95), 288(135)DA, ?(71)paraffin, ?(69), campesterol, stigmasterol, sitosterol.
5	*Archilejeunea mariana* (Papua New Guinea, Gr. 3831)	striatene (18), β-elemene, α-barbatene (34), β-barbatene (35), 204(105)SH, 204(81)SH, bazzanene (36), ?(123)SH, 220(91)SA, 220(119)SA, 236(109)pinguisane-type, 3 α-acetoxygermacrene (12), 272(109), 268(135), 278(68), 278(81), 272(93), *232*(175), *272*(135), 300(135), 286(135), *300*(122), 304(95), 304(137), 318(179), ?(59)diterpene with dimethyl carbinol, ?(113), ?(43)DAc, campesterol, stigma*sterol*, sitosterol.
6	*Archilejeunea olivacea* (New Zealand, Mues 80c)	*204*(148)SH, β-caryophyllene (21), *202*(187)SH, 204(91)SH, spathulenol (28), 220(146)SA, 220(119)SA, 236(95), *236* (43), 5-hydroxycalamenene (33), 278(68), 278(177), 290(95), 304(279), 326(219), ?(109), 378(363), 346(107), 380(117), campesterol, stigmasterol, sitosterol.
7	*Archilejeunea olivacea*	*204*(148)SH, 204(81)SH, 204(81)SH, *202*(187)SH, spatulenol, 220(146)SA, 236(43), 236(43), 278(68), 232(71), 278 (177), 290(95), 304(177), 380(57), 346(107), campesterol, stigmasterol, sitosterol.
8	*Archilejeunea parviflora* (Suriname, Bekker 1671)	β-pinene (3), limonene (5), 164(43)M, 180(109)M, β-elemene (14), β-caryophyllene (21), 204(161)SH, 202 (133)SH, 204(161)SH, 202(134)SH, 220(109)SA, *204*(123) striatene-type, *206*(109)pinguisane-type, 220(43)SA, *222* (109)pinguisane-type, 220(109)SA, 236(109)pinguisane-type, 238(109)pinguisane-type, 220(43)SA, *222*(109) pinguisane-type, 278(68), 278(81), 250(175), 258(107), 272 (175)DA, 272(95)DH, 314(95), ?(67), ?(279)DAc, 328(95) DAc, 330(149), 372(95), ?(43)DAc, 360(163), *410*(235), 430(175), campesterol.
9	*Blepharolejeunea incongrua* (Colombia, Aguirre 1326)	*trans-β*-farnesene (17), 208(137)SH, 206(109)SH, 222 (152)SA, 220(195)SA, 260(159), 272(109)DH, 272(109), 278 (68), 292(121), *272*(135), 292(176)DA, 290(161)DA, phytol (45), 304(95), *306*(233), 304(235), *316*(219), 316(163), 368 (255), *334*(43)DAc, 334(43)DAc, ?(57) paraffin, 410(69), 386(386), campesterol, stigmasterol, sitosterol.
10	*Brachiolejeunea densifolia* (Peru, Bryotrop 1001)	292(109), ?(57)paraffin, 272(135)DH, 286(43), 304(147), ?(57)paraffin, ?(57)paraffin, campesterol, stigmasterol, sitosterol.
11	*Bryopteris diffusa* (Suriname, van Slageren 404)	*204*(161)SH, ?(189)SH, *striatene*(18), 206(109)pinguisane-type, 202(82)SH, 236(109) pinguisane-type, 220(43)SA, 272

		(109), 278(68), 278(82), 286(124), *272*(135), phytol (**45**), 286 (150) *304*(95), *304*(147), 304(243), 368(245), 304(179), 322 (95), *?*(199), *300*(43)DAc, *408*(43)DAc, ?(43)DAc, 430(199), campesterol, stigmasterol, sitosterol.
12	*Bryopteris trinitensis* (Suriname, van Slageren 403)	138(105)MH, 154(III)M, 154(68)M, 154(57)M, ?(83), ?(137), 206(109)SH, 222(109)SA, 238(139), ?(109), 220(41) SA, *232*(43), *272*(109), ?(43)278(95), ?(237), 278(175), 284(135), 304(95), 304(147), 302(245), ?(95), 392(392), stigmasterol.
13	*Cheilolejeunea excisula* (Papua New Guinea, Gr. 3949)	*β*-chamigrene (**31**), *β*-caryophyllene (**21**), *striatene* (**18**), striatol (**19**), *β-monocyclonerolidol* (**20**), ?(123)striatene-type.
14	*Cheilolejeunea imbricata* (Japan, Gr. 3339)	striatene (**18**), *?*(97)SA, 248(43), ?(97).
15	*Diplasiolejeunea patelligera* (Papua New Guinea, Gr. 3946)	204(105)SH, 204(161)SH, *β-caryophyllene* (**21**), striatene (**18**), 204(123)SH, spathulenol (**28**), cyclocolorenone (**27**), 272(68), 272(275)kaurene-type, 274(124), 272(135), 290 (285), *288*(255)DA, 312(88)methyl ester, 306(79)DA, 306 (291), 304(137), 412(255), hop-22-ol (**47**).
16	*Lejeunea albescens* (Papua New Guinea, Gr. 3887, det. M. Mizutani)	*δ*-elemene (**15**), 204(105), *β*-elemene (**14**), *204*(107), germacrene-D (**8**), *bicyclogermacrene* (**9**), spathulenol (**28**), 218(91), 272(229)DH, 272(135)DH, 270(135), 272(135)DH, 274(93), 274(124), *272*(135), *290*(95), 290(43), 304(43)DAc, 374(95), 318(275)DAc, campesterol, stigmasterol.
17	*Lejeunea* aff. *albescens* (Papua New Guinea, Gr. 4119)	164(55)M, *α*-barbatene (**34**), *β-barbatene* (**35**), 204(94)SH, bazzanene (**36**), ?(95), 236(95), 234(176), *272*(229), 250(43), 288(157), 272(135)DH, 286(286), 288(95), *304*(147), 316 (243), 304(137), *304*(81), 304(179), ?olefin, 368(88), ?(57) paraffin, ?(57)paraffin, 380(380), 392(392), ?(275), campesterol, stigmasterol.
18	*Lejeunea discreta* (Papua New Guinea,Gr. 3906a, det M. Mizutani)	204(105)SH, *204*(107), *germacrene-D*, bicyclogermacrene, spathulenol, cyclocolorenone, norpinguisone methyl ester (**40**), 270(135)DH, 286(DA), 286(137), 274(124), *272*(135), 288(59) diterpene with dimethyl carbinol, 286(133), 290(59) diterpene with dimethyl carbinol, 306(43)DAc, 304(43)DAc, 318(43)DAc, 318(135) (diterpene with dimethyl carbinol, *356*(137), *318*(275), campesterol, stigmasterol.
19	*Lejeunea discreta* (Papua New Guinea, Gr. 3801, det. M. Mizutani)	204(105)SH, 204(107)SH, 204(161)SH, 204(119)SH, striatol, 220(109)SA, 220(153)SA, 272(229)DH, *?*(87), 278 (68), *272*(135), 286(121), ?(275), 318(43), ?(43)DAc, *320* (43)DAc, 318(43)DAc, ?(43)DAc, campesterol, stigmasterol.
20	*Lejeunea discreta* (Japan, Gr. 3342)	204(93)SH, 278(68), *?*(123), 290(137), *286*(43), ?(57) paraffin, 294(70), ?(43)DAc, 322(70), stigmasterol.
21	*Lejeunea* aff. *discreta* (Papua New Guinea, Gr. 3991)	?(70), 204(105)SH, *204*(107)SH, 208(134)SH, 222(199)SA, 236(112), 218(218), 272(229), 270(270), 284(88), 288(137), 290(275), 310(88), *304*(207), *306*(207), 320(207), *322*(207), 322(207), 368(88), 306(57)paraffin, campesterol, stigmasterol.
22	*Lejeunea flava* (Japan, Gr. 3340)	?(85), 236(221), *cinnamolide* (**23**), 310(58).

23	*Lejeunea glaucescens* Gott. (Suriname, Bekker 1676, det. R. Grolle)	myrcene(4), 204(121)SH, 220(204)SA, ?(136)SA, spathulenol (28), 220(95)SA, 220(161)SA, 272(229)DH, 272(135) DH, 272(229)DH, 286(68), 278(82), 278(81), *272*(93)DH, 272(135)DH, 286(93)DA, 294(43), *290*(95)DA, 304(59)DA with dimethyl carbinol, 288(135)DA, 314(95), 304(142), 314 (59), 316(214), 304(137), 304(164), 318(149), *318*(234), 318 (43)DAc, 408(135) bibenzyl, stigmasterol, 468(204).
24	*Lejeunea lumbricoides* (Papua New Guinea, Gr. 3892, det M. Mizutani)	β-elemene, *germacrene-D*, acoradiene (31), *alloaromadendrene* (25), 204(41)SH, 270(135), 272(149), 272(81), 274 (136), 274(124), *272*(135), 252(95), *272*(95), 280(59).
25	*Lejeunea* aff. *lumbricoides* (Papua New Guinea, Gr. 3901a)	204(105)SH, 204(68)SH, *204*(197), 204(105), *alloaromadendrene* (25), striatene, spathulenol, 272(175), 270(135), 272 (135), 286(93), 274(124), *272*(81), ?(69), 314(88)methyl ester, ?(43), 358(95), *362*(43).
26	*Lejeunea* spec. a (Papua New Guinea, Gr. 3761)	*δ-elemene, β-elemene, eremophilene, β-selinene* (10), germacrene-D, 220(43)SA, 272(43), norpinguisone methyl ester, 272(135), 272(135), 286(93), 274(137), ?(93), *272*(135), 280(93), 304(93), *272*(69), *304*(43)DAc, 304(43) DAc, 304(95), campesterol, stigmasterol.
27	*Lejeunea* spec. b (Papua New Guinea, Gr. 3852)	β-elemene, eremophilene, spathulenol, 222(43)SA, 272 (229)DH, 270(68), 274(137), 274(124), 272(135), *272*(69), phytol, 304(69), 304(43)DAc, 304(41), *304*(147), campesterol, stigmasterol, sitosterol.
28	*Lepidolejeunea ornata* (Suriname, Bekker 1729, det. R. Grolle)	138(95)MH, camphene(2), limonene (5), spathulenol, ?(161)SA, 220(43)SA, 278(68), 278(82), 278(81), 272(149), 272(135), kaurene (46), 288(245)kaurene-type, ?(81), ?(81), ?(84), 286(91)DA, 330(255), 300(137), 302(274), *344*(137), *374*(179), 314(300), 318(43)DAc, 316(189), stigmasterol.
29	*Leucolejeunea* aff. *decurrens* (Papua New Guinea, Gr. 3843)	β-chamigrene (32), 222(137)SA, striatene, *204*(189), 204 (189)SH, ?(123)striatene-type, 220(41)SA, 220(192)SA, cyclocolorenone, 326(108), stigmasterol.
30	*Leucolejeunea* aff. *decurrens* (Papua New Guinea, Gr. 3950)	204(189), striatene, *204*(189), striatol (19), ?(41), ?(123) striatene-type, campesterol, stigmasterol, sitosterol.
31	*Lopholejeunea eulopha* (Papua New Guinea, Gr. 3760)	β-caryophyllene, 204(105)cadinene-type, *alloaromadendrene*, cuparene (37), 220(109)SA, *5-hydroxycalamenene* (33), 278(68), 272(107), 260(145), 244(161), ?(57)paraffin, ?(55) olefin, ?(461).
32	*Lopholejeunea howei* (Antilles, Saba, van Slageren 277)	limonene, 138(95)MH, 154(III)M, 154(68)M, 204(161)SH, 204(165)SH, 204(161)SH, *cuparene*, 200(157), 220(81)SA, 188(183), *5-hydroxycalamenene* (33), 244(59), 244(244), 278 (68), 286(145), 278(81), 260(145), *248*(163), ?(177), *260* (163), campesterol, stigmasterol.
33	*Lopholejeunea subfusca* (Papua New Guinea, Gr. 3790)	α-gurjunene (26), β-guainene (29), germacrene-D, spathulenol, 220(95), *5-hydroxycalamenene*, 290(247), ?(81), 274(124), *272*(135)DH, 290(85), 304(147), 290(175), ?(57) paraffin, stigmasterol.
34	*Marchesinia brachiata* (Suriname, van Slageren 400)	138(95)MH, 154(III)M, 154(68)M, β-caryophyllene, 3-hydroxy-4,5-dimethoxyallylbenzene or 4-hydroxy-3,5-dimethoxyallylbenzene, 208(208)aromatic, 208(208) aromatic, 220(136)SA, ?(109), ?(57)paraffin, ?(82), 220(43) SA, 240(43), ?(95), 284(88)methyl ester, 264 and 266(55),

		?(57) paraffin, ?(194) aromatic, *?*(194) aromatic, 314(193) aromatic, ?(194) aromatic, 344(151), 386(328), ?(147), campesterol, stigmasterol, sitosterol.
35	*Mastigolejeunea humilis* (Papua New Guinea, Gr. 3833)	striatene, 218(137), 238(109)pinguisane-type, *250*(109) pinguisane-type, 250(43), 232(175), 282(95), ?(149), campesterol, stigmasterol, sitosterol.
36	*Mastigolejeunea humilis* (Papua New Guinea, Gr. 3836)	*alloaromadendrene*, striatene, ?(275), 362(43)DAc, 420(43)DAc, campesterol, stigmasterol, sitosterol.
37	*Mastigolejeunea undulata* (Papua New Guinea, Gr. 4136)	204(189)SH, 204(135)SH, 204(95)SH, 204(161)SH, ?(109) pinguisane-type, *108*(108)pinguisane-type, 210(109) pinguisane-type, 5-hydroxycalamenene, *?*(109)pinguisane-type, *?*(109)pinguisane-type, 276(257), 264(81), ?(331)DAc, ?(331)DAc, 362(347), *420*(43)DAc, campesterol, stigmasterol.
38	*Schiffneriolejeunea nymannii* (Papua New Guinea, Gr. 3759)	*β*-chamigrene, striatene, 204(123)striatene-type, *striatol*, 220(123)SA, 238(95), *272*(229), 278(68), 294(237), ?(95), 272(135), 306(277), 306(41), 304(95), 304(147), 304(137), 304(179), campesterol, stigmasterol.
39	*Schiffneriolejeunea omphalanthoides* (Papua New Guinea, Gr. 3887)	*striatene*, striatol, spathulenol, 252(132), cyclocolorenone, *272*(229), 278(68), *272*(257), 272(99), 272(135), 288(146), 272(135), 302(135), 304(277), 304(95), 320(243), 326(95), *304*(137), ?(179), campesterol, stigmasterol.
40	*Schiffneriolejeunea omphalanthoides* (Papua New Guinea, Gr. 3799)	alloaramadendrene, 220(123)SA, 220(123)SA, *272*(229), 278(68), *272*(272), *272*(135), 288(84), *304*(95), *304*(147), 302(243), 304(137), 304(279), campesterol, stigmasterol, 426(204), 424(124), 410(55).
41	*Stictolejeunea balfourii* var. *bekkeri* (Suriname, Bekker 1713)	138(95)SH, limonene, *p*-cymene(6), 1-methyl-4-isopropylbenzenen (7), 152(84)M, 204(161)SH, 204(161)SH, 204(161)SH, 204(161)SH, *α*-humulene (22), 222(109)SA, spathulenol, *222*(43)SA, 222(109)SA, 220(43)SA, 220(82)SA, 220(43)SA, 218(134), 278(68), 278(82), 278(81), *232*(93), 272(93)DH, ?(133), ?(134), ?(135), 248(135), 294(67), 308(81), 274(121) dihydroxy-dimethoxybibenzyl (48), *314*(193)bibenzyl, ?(69), 372(121)bibenzyl, stigmasterol.
42	*Stictolejeunea squamata* (Suriname, Bekker 1060)	204(148)SH, 204(91)SH, *204*(147)SH, 204(107) selinene-type, spathulenol, 222(43)SA, 220(81)SA, 278(68), 278(81), 278(81), 270(74), 254(79), 294(67), phytol, *234*(234), ?(224), 300(134), campesterol, stigmasterol.
43	*Symbiezidium barbiflorum* (Suriname, Bekker, 1063)	*α*-pinene, 202(109)SH, 220(139)SA, 220(109)SA, *232*(164) sesquiterpene lactone?, ?(109), 250(179), 278(68), 278(81), 278(81), 278(175), 284(88)methyl ester, 312(88)methyl ester, ?(57)paraffin, stigmasterol.
44	*Symbiezidium transversale* var. *hookeriana* (Suriname, van Slageren 401)	138(95)MH, 154(111)M, 154(68)M, 232(131), 232(131), ?(57)paraffin, 278(68), 278(81), 232(273), *?*(173), *246*(95), 262(167), 264(69), campesterol, stigmasterol.
45	*Thysananthus amazonicus* (Suriname, Bekker 1175)	?(43)olefin, striatene, germacrene-D, spathulenol, 220(43), 220(43), 278(68), 278(81), 278(81), 284(81), phytol, 312(88) methyl ester, ?(43)DAc, 326(221), 316(221), 346(331), ?(57) paraffin, ?(43)olefin, *316*(187), ?(57)paraffin, *campesterol, stigmasterol, sitosterol.*

46	*Thysananthus amazonicus* (Suriname, Bekker, 1494)	138(95)MH, limonene, β-elemene, anastreptene (24), *204*(161)cadinene-type, 204(121)SH, 204(161)cadinene-type, striatol, spathulenol, *?*(82)SA, ?(107)SA, 236(109), 218(79), 220(43)SA, 220(43)SA, 220(43)SA, 278(68), 278(81), 278(81), 272(107), ?(221), 316(221), 330(107), 316(187)DA, *316*(187), 316(187), 376(133), stigmasterol, 412(69) sterol?
47	*Thysananthus amazonicus* (Suriname, Bekker 1555)	camphene, limonene, 128(43), β-elemene, 202(159)SH, *204*(161) cadinene-type, 204(121)SH, 204(161)cadinene-type, spathulenol, *220*(109)SA, 220(159)SA, 236(109)furanosesquiterpene, 236(43), ?(82), *236*(43), ?(43), 238(81), 278(68), 278(81), 272(83), ?(221), 292(138), ?(43)DAc, 316(221), 322(138), 316(187), 316(187), *?*(43)DAc, 376(133), stigmasterol, ?(111).
48	*Thysananthus convolutus* (Papua New Guinea, Gr. 3931)	δ-elemene, β-elemene, 204(105)SH, *bicyclogermacrene*, spathulenol, β-eudesmol (11), 272(43), 272(229), 286(135), 272(257), 286(95), 274(124), *272*(135), ?(43)DAc, ?(95)diterpene with dimethyl carbinol, *304*(95)DAc, 390(95), 304(107), *304*(137), 304(95), campesterol, stigmasterol.
49	*Thysananthus convolutus* (Papua New Guinea, Gr. 3894)	δ-elemene, *204*(105(SH), *germacrene-D*, *eremophilene*, spathulenol, β-eudesmol, 272(43), 272(229), 270(149), 272(257), 274(124), *272*(135), ?(229), 290(275), phytol, 304(43)DAc, 304(147), 302(43)DAc, 304(137), 316(138), campesterol, stigmasterol, sitosterol.
50	*Thysananthus convolutus* (Papua New Guinea, Gr. 3796)	β-caryophyllene, *eremophilene*, spathulenol, 218(41), 220(107), 290(275), *290*(203), 394(394), stigmasterol.
51	*Thysananthus convolutus* (Papua New Guinea, Gr. 3779)	β-selinene, alloaromadendrene, 222(122)SA, 220(43)SA, 272(229), 278(68), *272*(257) rimuene?, *272*(135), 272(135), 272(135), 298(275), 288(245), 304(95), 304(243), 304(137), 304(179), 392(187), 394(394), stigmasterol, 414(43).
52	*Thysananthus fruticosus* (Papua New Guinea, Gr. 3963)	striatene, 204(148)SH, β-caryophyllene, *204*(95)SH, 206(109)pinguisane-type, pinguisenene (30), 208(137), *222*(109) pinguisane-type, 220(206)SA, ?(109)pinguisane-type, 286(68), 234(109)pinguisane-type, 272(121), *232*(175), 272(135), 256(109)pinguisane-type, ?(95), 304(147), 290(187), ?(187), 324(223), 314(187), 326(55), campesterol, stigmasterol.
53	*Thysananthus mollis* (Papua New Guinea, Gr. 3884)	β-caryophyllene, eremophilene, spathulenol, 218(41), 220(93)SA, 272(43), 278(68), 286(93), 274(124), *272*(135), ?(43)DAc, 302(95)diterpene with dimethyl carbinol, *304*(95), ?(147), 304(43)DAc, *304*(138), *304*(137), 330(298), campesterol, stigmasterol, sitosterol.
54	*Thysananthus mollis* (Papua New Guinea, Gr. 3792)	alloaromadendrene, 272(229), 278(68), *272*(135), 272(135), 288(245), 304(43)DAc, 288(245), 304(43)DAc, 288(245), 304(95), 304(147), 304(137), 316(43), ?(179), ?(57) paraffin, campesterol, stigmasterol.
55	*Thysananthus mollis* (Papua New Guinea, Gr. 3795)	β-caryophyllene, eremophilene, 220(43)SA, 272(229), 278(68), 274(124), *272*(135), 288(121), 304(135), 304(245), 288(245), 304(95), 304(147), 304(243), 304(137), ?(43)DAc, 304(179), 308(207), campesterol, stigmasterol.

Bryopteridoideae

A monotypic family, containing only the genus *Bryopteris*. On morphological grounds, the group is most closely related to the Ptychanthoideae (see Thiers, this volume).

Three species have thus far been checked (one sample each): *B. diffusa* (Sw.) Nees, *B. fruticulosa* Tayl. and *B. trinitensis* (Lehm. & Lindenb.) Lehm. & Lindenb. In *B. diffusa* striatene (Fig. 1:18) and a few unidentified acetates have been detected as the major components, along with a small quantity of a few unidentified pinguisane-type sesquiterpenes. *B. trinitensis* produces a few unidentified oxygenated monoterpenes as minor components. The main components are an oxygenated sesquiterpene and a diterpene, whose structures remain to be identified. Colombian *B. fruticulosa* contains a large quantity of sesqui- and diterpenes, in which pinguisane-type sesquiterpenes and diterpene-acetates have been detected (Gradstein et al. 1981). The gaschromatograms of the three species are quite different from each other and show little chemical affinity.

Ptychanthoideae

The genera of this subfamily are placed in complexes (Schuster 1963, Gradstein 1975) and sometimes in tribes as well (Gradstein 1975). We shall discuss the chemical results for each complex. The following generic complexes remain largely uninvestigated: *Caudalejeunea* complex (*Caudalejeunea*) and *Dicranolejeunea* complex (*Dicranolejeunea, Odontolejeunea, Lindigianthus*).

Ptychanthus complex

(*Ptychanthus, Tuzibeanthus, Thysananthus, Mastigolejeunea, Schiffneriolejeunea)*

Four species of *Thysananthus* have been investigated: *T. amazonicus* (Spruce) Steph. (3 samples), *T. convolutus* Lindenb. (4 samples), *T. fruticosus* (Lindenb. & Gott.) Schiffn. and *T. mollis* Steph. *T. convolutus* is a rather polymorphic species with respect to the dentation of leaves, underleaves and bracts, which varies from strongly dentate to ± edentate. Edentate forms are sometimes called *T. gottschei* (Jack & Steph.) Steph., which we consider a synonym of *T. convolutus* (cf. Grolle and Piipo 1984). Variation is also seen in the gaschromatograms of the four samples, which are heterogeneous as to sesquiterpene content. Samples 48 and 49 biosynthesize various aromadendrene-type sesquiterpenes, including germacrene-D (49 only) and spathulenol (both samples). Nr. 48 contains bicyclogermacrene (Fig. 1:9), a compound widely spread in the Hepaticae, which may be considered a precursor of this group of sesquiterpenes (Asakawa 1982). Sample nr. 51 has a more simplified gaschromatogram, mainly containing alloaromadendrene and some diterpenes. The three samples are somewhat similar in diterpene content by the common presence of the unidentified diterpenes M^+ 272 (135) and M^+ 304 (137), which may be chemical markers for *T. convolutus*. Sample nr. 50 is chemically aberrant, showing a very much simplified GC lacking almost all the compounds found in the other sample.

The samples of *T. mollis* are chemically more uniform. They are rather poor in sesquiterpenes (mainly caryophyllene- and alloaromadendrene-type) and rich in diterpene content. The diterpenes are rather similar to those of *T. convolutus*, indicating a rather close chemical affinity among the two species. Morphologically, the two species are not so close, however, and are sometimes placed in different sections (Verdoorn 1934).

Major components of *T. amazonicus* include a cadinane-type sesquiterpene hydrocarbon and a few diterpene acetates of which M^+ 316 (187) is the most abundant. The total chemical constitution of each of the three investigated samples differs considerably, however, and one of them (nr. 45) lacks cadinane-type sesquiterpenes altogether. Morphologically, the three samples are fairly uniform.

T. fruticosus shows no obvious chemical relationship to the other *Thysananthus* species investigated. It is poor in diterpenes but produces striatene (Fig. 1: 18) and several pinguisane-type sesquiterpenes (Fig. 1: 38-44), like other members of the *Ptychanthus* complex (*Pt. striatus, Tuz. chinensis, Mastigolej.* spp. and *Schiffneriolej.* spp. - the latter genus producing striatene only, no pinguisane-type sesquiterpenes). The chemical data seem supportive of the morphology, because *T. fruticosus* is morphologically rather different from the other *Thysananthus* species investigated (branching, strong vitta). Some authors place *T. mollis* close to *T. fruticosus* (Verdoorn 1934) but we believe that *T. mollis* is more close to the generitype, *T. spathulistipus* (not investigated). Chemically, the genus *Thysananthus* is apparently linked to the other members of the *Ptychanthus* complex via *T. fruticosus.*

The two investigated species of *Mastigolejeunea, M. humilis* (Gott.) Steph. (2 samples) and *M. undulata* Grolle & Gradst. (one sample) produce a large quantity of sequi- and diterpenoids (not very many components, though). The chemical markers of *M. undulata* are pinguisane-type sesquiterpenes and a few unknown diterpene acetates. The two samples of *M. humilis* show no apparent chemical similarity, except for the common presence of striatene (Fig. 1: 18). Both are chemically related to *M. undulata*, however, because one of them contains pinguisane-type sesquiterpenes like *M. undulata* whereas the other has the same diterpene acetates as found in *M. undulata*. The chemical dissimilarity of the two samples of *M. humilis* is reflected in the morphology, as the sample lacking pinguisanes (nr. 35) has a long and curved lobule tooth, whereas the other sample (nr. 36) approaches *Mastigolejeunea auriculata* by its possession of a short, straight tooth (cf. Gradstein and Inoue 1980).

The chemical markers of *Ptychanthus striatus* (Lehm. & Lindenb.) Nees and *Tuzibeanthus chinensis* (Steph.) Mizut. (monotypic genera) are striatene- and pinguisane-type sesquiterpenes, and labdane-type diterpenes (Asakawa et al. 1980b). Both chemistry and morphology suggest a close relationship between the two genera. Inoue (1976) reduced *Tuzibeanthus* to subgeneric rank under *Ptychanthus* but morphologically the groups seem distinct enough (leaf areolation and shape) to be kept as separate genera (Gradstein 1975). The *Mastigolejeunea* species and *Thysananthus fruticosus* are chemically related to *Ptychanthus* and *Tuzibeanthus.*

Schiffneriolejeunea nymannii (Steph.) Gradst. & Terken (one sample) and *S. omphalanthoides* Verd. (2 samples) produce the same unidentified diterpenes as those found in *Thysananthus convolutus* and *T. mollis,* but their sesquiterpene constitution is different. Striatene-type sesquiterpenes are common in *S. nymannii* and in one of the two samples of *S. omphalanthoides.*

In conclusion, it seems that the *Ptychanthus* complex is chemotaxonomically rather diverse (morphologically rather well-defined and homogeneous, though), although high contents of diterpenes, striatenes and, sometimes, pinguisanes seem to be fairly characteristic.

Brachiolejeunea complex

(*Acrolejeunea, Trocholejeunea, Brachiolejeunea, Blepharolejeunea*)

Three species of *Acrolejeunea* have been investigated: *A. pusilla* (Hatt.) Grolle & Gradst. (one sample), *A. pycnoclada* (Tayl.) Schiffn. (2 samples) and *A. torulosa* (Lehm. & Lindenb.) Schiffn. (one sample). Morphologically, the three species are quite distinct and placed in different subgenera or sections (Gradstein 1975). Chemically, they are remarkably similar, though, producing pinguisane-type sesquiterpenes (Fig. 1: 38-44) as major components and very little diterpene. Mass spectra for the two samples of *A. pycnoclada,* which are morphologically uniform but were collected in different localities (near Wau, Papua New Guinea), are completely identical. Apparently, the genus *Acrolejeunea* has undergone little infrageneric chemical evolution.

Trocholejeunea sandvicensis (Gott.) Mizut. produces the same pinguisane-type sesquiterpenes as those detected in the above three species of *Acrolejeunea,* as the main components (Asakawa et al. 1980b). Thus, *Trocholejeunea* is chemically very close to *Acrolejeunea.*

In a previous paper (Gradstein et al. 1981) we reported chemical constituents for three species of *Brachiolejeunea: B. chinantlana* Schiffn. (subgenus *Plicolejeunea*), *B. laxifolia* (Tayl.) Schiffn. (subgenus *Brachiolejeunea*) and *B. securifolia* (Spruce) Steph. The latter species is now placed in *Blepharolejeunea,* as *B. securifolia* (Spruce) Schust., on morphological grounds (see van Slageren and Kruijt, this volume).

Brachiolejeunea chinantlana Schiffn. produces the same pinguisane-type sesquiterpenes (major components) as *Trocholejeunea* and *Acrolejeunea,* confirming the close morphological relationship between the three taxa. *B. laxifolia* is chemically completely different from *B. chinantlana* and *Blepharolejeunea securi-*

folia, but the latter species shows a weak chemical relationship to *B. chinantlana* by its ability to biosynthesize pinguisone (related pinguisane-type compounds in *B. chinantlana* and its allies).

We have investigated two further species of this group: *Brachiolejeunea densifolia* (Raddi) Evans (one sample) and *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt (one sample). Unfortunately, the sample of *B. densifolia* was so dry that no conclusive results could be obtained. *B. incongrua* contains many diterpenoids, whose structures remain to be clarified. The species shows no apparent chemical affinity to *B. securifolia,* nor to the investigated species of *Brachiolejeunea.*

Dicranolejeunea complex

(*Lindigianthus;* not investigated: *Dicranolejeunea, Odontolejeunea)*

Previously, we recorded the chemical constitution of *Dicranolejeunea cipaconea* (Gott.) Steph. (Gradstein et al. 1981). This species is now placed in a new, monotypic genus, *Lindigianthus,* as *L. cipaconeus* (Gott.) Kruijt & Gradst. (Kruijt and Gradstein, this volume). The gaschromatogram of *Lindigianthus cipaconeus* is very complex and shows the presence of some diterpenes (minor components) also found in *Thysananthus convolutus* and *T. mollis.* Otherwise, the sample does not show chemical affinity to any other species of Ptychanthoideae investigated.

Lopholejeunea complex

(*Lopholejeunea, Symbiezidium, Marchesinia)*

Three species of *Lopholejeunea* have been checked (one sample each): *L. eulopha* (Tayl.) Schiffn., *L. howei* Evans and *L. subfusca* (Nees) Steph. Each of them produces much 5-hydroxycalamenene (Fig. 1: 33), which may be the significant chemical marker for this genus. The rather small content of diterpenoids in each of the species seems another important chemical character.

Gradstein et al. (1981) reported GC/MS data for *Symbiezidium barbiflorum* (Gott.) Evans collected in Colombia. We have reexamined the chemistry of this species as well as of *S. transversale* (Sw.) Trevis. var. *hookeriana* (Gott.) Gradst. & van Beek (one sample each), based on material from Suriname. The chemical constitution of each of the three samples is different and shows no obvious chemical affinity. In the Suriname sample of *S. barbiflorum* we detected an unidentified sesquiterpene-lactone like compound. Sesquiterpene-lactones are rare in Lejeuneaceae and have thus far only been recorded for *Omphalanthus* (Gradstein et al. 1981). *S. transversale* var. *hookeriana* produces a few unknown diterpenes as major components. The species of *Symbiezidium* are morphologically very plastic (Gradstein and van Beek, this volume), which seems reflected in the chemical diversity observed in the three samples.

Previous investigations of *Marchesinia mackaii* (Hook.) S.F. Gray (Asakawa et al. 1980a) and *M. brachiata* (Sw.) Schiffn. (Gradstein et al. 1981) indicated that eugenol-type aromatic compounds are the chemical markers for this genus. However, Gradstein et al. (l.c.) could detect these components only in fresh plants of *M. brachiata* from the Antilles whereas in poorly preserved, dead material of the same species from Colombia they were found lacking. We have reexamined the chemistry of *M. brachiata* based on fresh material from Suriname and found the same eugenol-type aromatic compounds as in the material from the Antilles. Thus, we assume that their absence in the Colombian material was due to the bad state of preservation of the material.

Summing up, it appears that the *Lopholejeunea* complex is chemically very heterogeneous. Morphologically, the genera are quite distinct. The chemical data would not conflict with a placement of the individual genera in complexes of their own, as was done by Schuster (1963).

Archilejeunea complex

(*Archilejeunea, Spruceanthus;* not investigated: *Phaeolejeunea, Verdoornianthus*).

We have checked the chemistry of three species of *Archilejeunea* belonging to the subgenus *Dibrachiella* (see Gradstein and Buskes, this volume): *A. mariana* (Gott.) Steph. (one sample), *A. olivacea* (Hook. & Tayl.) Schiffn. (2 samples) and *A. parviflora* (Nees) Schiffn. (one sample). The sample of *A. mariana* was previously identified and published as *Spruceanthus polymorphus* (Sande Lac.) Verd. (Grolle and Piipo 1984), which may be a synonym of *A. mariana. A. mariana* produces a lot of sesqui- and diterpenoids, including striatene- and pinguisane-type sesquiterpenes as minor components. Pinguisane-type sesquiterpenes are present in much greater quantity in the sample of *A. parviflora* from Suriname, where they are the obvious chemical markers. The GC of the latter species is very complex. *A. parviflora* was previously checked by Gradstein et al. (1981), based on material from Colombia and identified as *A. viridissima* Lindenb., which is now considered a synonym of *A. parviflora* (Gradstein and Buskes, this volume). The chemical constitution of each of the two samples of *A. parviflora* is entirely different and no pinguisane-type sesquiterpenes have been detected in the Colombian sample. The observed chemical diversity of *A. parviflora,* which is paralleled by a marked morphological plasticity (Gradstein and Buskes, this volume) deserves further study.

The two samples of *Archilejeunea olivacea* from New Zealand are rich in sesquiterpene but poor in diterpene content. They are chemically almost identical; one of them contains 5-hydroxycalamene (as a minor component), which is the chemical marker of *Lopholejeunea* species. Chemical markers of *A. olivacea* are an unknown sesquiterpene hydrocarbon M^+ 202 (187) and an unknown oxygenated sesquiterpene M^+ 236 (43); their chemical constitution is fairly simple. *A. olivacea* is chemically unrelated to the other *Archilejeunea* species. In morphological respect, the species is also quite distinct (Gradstein and Buskes, this volume).

Stictolejeunea complex

(*Stictolejeunea*; not investigated: *Neurolejeunea*)

Two species of *Stictolejeunea* have been investigated (one sample each): *S. squamata* (Willd.) Schiffn. and *S. balfourii* (Mitt.) E.W. Jones var. *bekkeri* Gradst. *S. balfourii* is chemically quite distinct from *S. squamata*, which is supportive of the apparently remote morphological affinity between the two species (see the revision by Gradstein, this volume). Chemical markers of *S. balfourii* var. *bekkeri* are three unidentified bibenzyl derivatives, whereas an oxygenated sesquiterpene M^+ 234 (234) is the most abundant component of *S. squamata*.

Nipponolejeuneoideae

A monotypic subfamily, containing only the endemic Japanese genus *Nipponolejeunea* Hatt. with two species: *N. pilifera* (Steph.) Hatt. and *N. subalpina* (Horik.) Hatt. Inoue et al. (1981) investigated the chemical constitution of the two species and found that both contained the monoterpenes borneol and bornyl acetate, responsible for the fragrant odour of the plants. The odour was strongest in the sample of *N. subalpina*, which indeed produced these monoterpenes in much larger quantity than the other species. Differences in sesqui- and diterpene content could also be detected, but as a whole the two species proved chemically related. Borneol and bornyl acetate have not yet been detected in other members of the Lejeuneaceae and are therefore good chemical markers of the genus *Nipponolejeunea*.

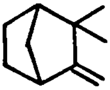
Lejeuneoideae

The Lejeuneoideae are the largest subfamily and taxonomically the poorest known. For that reason several taxa recorded here could be named only provisionally. Most of them are very small plants, growing so strongly intermingled that isolation and purification, even under the microscope, is troublesome. The genera are sometimes placed in complexes, like Ptychanthoideae, but the circumscription of these complexes is still rather provisional. As a rather broad approach, we have grouped the investigated taxa in three complexes: the *Omphalanthus* complex (characterized by the large oil bodies, frequent holostipous condition, reduction of first lobule tooth (hence hyaline papilla distal), usually distinct trigones and coarse texture; not all included taxa would fit the entire circumscription!), the *Lejeunea* complex (see Schuster 1963) and the *Leptolejeunea* complex (see Schuster 1963).

Omphalanthus complex

(*Omphalanthus, Aureolejeunea* (not investigated), *Evansiolejeunea* (not investigated), *Leucolejeunea, Cheilolejeunea, Anoplolejeunea*; should probably also contain *Amblyolejeunea, Amphilejeunea* and *Cyrtolejeunea* (not investigated)).


(1)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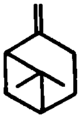
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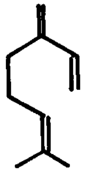
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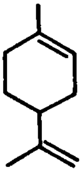
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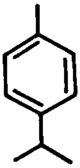
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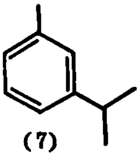
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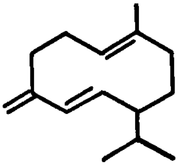
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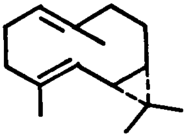
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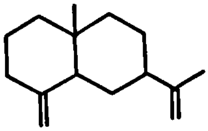
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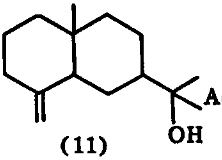
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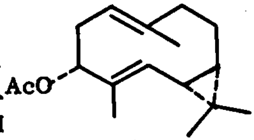
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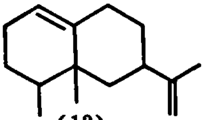
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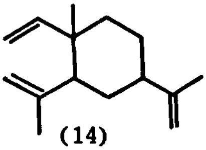
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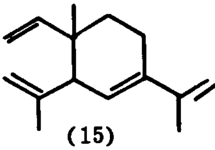
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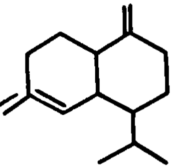
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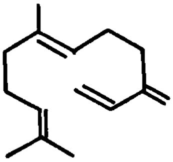
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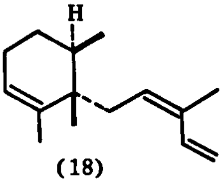
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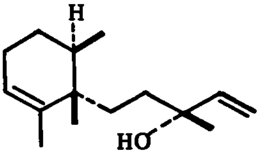
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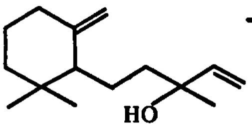
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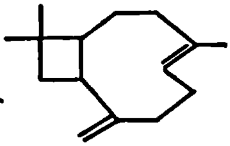
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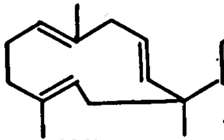
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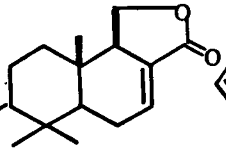
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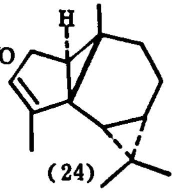
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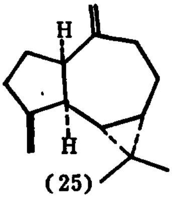
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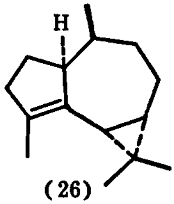
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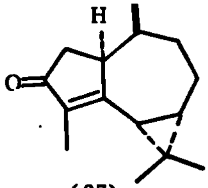
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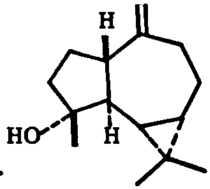
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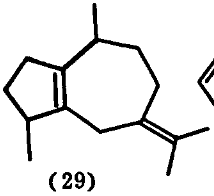
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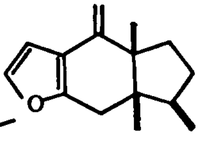
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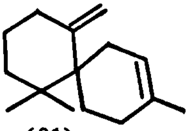
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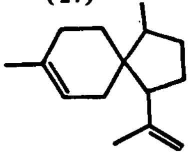
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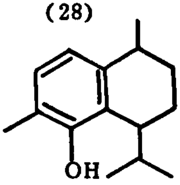
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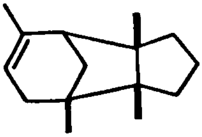
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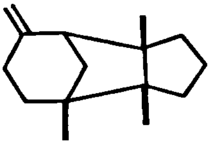
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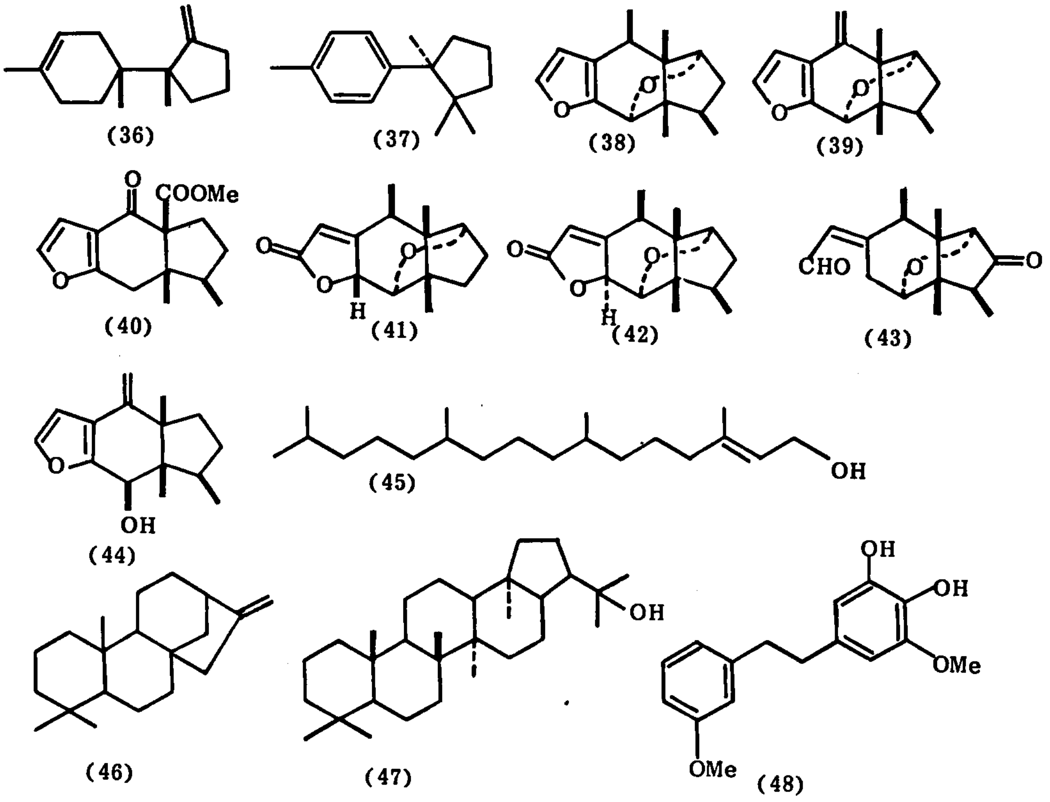

Fig. 1. The chemical structures of monoterpenes (1-7), sesquiterpenes (8-44), diterpenes (45, 46), triterpene (47) and bibenzyl derivative (48) detected in the Lejeuneaceae.

(1): α-pinene. (2): β-pinene. (3): camphene. (4): myrcene. (5): limonene. (6): *p*-cymene. (7): *m*-cymene. (8): germacrene-D. (9): bicyclogermacrene. (10): β-selinene. (11): β-eudesmol. (12): 3α-acetoxybicyclogermacrene. (13): eremophilene. (14): β-elemene. (15): δ-elemene. (16): γ-cadinene. (17): *trans-β*-farnesene. (18): striatene. (19): striatol. (20): β-monocyclonerolidol. (21): β-caryophyllene. (22): α-humulene. (23): cinnamolide. (24): anastreptene. (25): alloarmadendrene. (26): α-gurjunene. (27): cyclocolorenone. (28): spathulenol. (29): β-guaiene. (30): pinguisenene. (31): β-chamigrene. (32): acoradiene. (33): 5-hydroxycalamenene. (34): α-barbatene. (35): β-barbatene. (36): bazzanene. (37): cuparene. (38): pinguisanin. (39): dehydropinguisanin. (40): norpinguison methyl ester. (41): pinguisanolide. (42): isopinguisanolide. (43): pinguisenal. (44): dehydropinguisenol. (45): phytol. (46): kaurene. (47): hop-22-ol. (48): 3,3 '-dimethoxy-4,5-dihydroxybibenzyl.

The chemical constituents of two species of *Omphalanthus, O. platycoleus* (Herz.) Gradst. and *O. paramicola* (Herz.) Gradst. have been reported by Gradstein et al. (1981). Both species are rich in sesquiterpene content and produce *β*-chamigrene (Fig. 1: 31) as chemical marker, but otherwise they are chemically different. A dihydrosesquiterpene-lactone (unidentified) has been detected in *O. platycoleus.* We have checked two samples of an undescribed species of *Leucolejeunea* from Mt. Kaindi, Papua New Guinea (nrs. 29 and 30), related to *L. decurrens* (Steph.) Mitt. The species produces a large quantity of an unidentified sesquiterpene, together with striatene-type sesquiterpenes. The diterpene content is remarkably poor. On the other hand, in *L. xanthocarpa* (Lehm. & Lindenb.) Evans from Colombia (Gradstein et al. 1981) two unidentified diterpene-like compounds are the most abundant constituents. Thus, chemically, *L.* aff. *decurrens* is quite distinct from *L. xanthocarpa.*

From the large genus *Cheilolejeunea* we have investigated two species (one sample each): *C. excisula* (Steph.) Mizut. (subgenus *Tegulifolium* Schust.) and *C. imbricata* (Nees) Hatt. (subgenus *Cheilolej.* ?). The gaschromatograms of the crude extracts of the two species are quite simple. *C. excisula* contains striatol (Fig. 1: 19) as major component whereas in *C. imbricata* an unidentified sesquiterpene alcohol constitutes the only major peak. Although *C. imbricata* biosynthesizes striatene (Fig. 1: 18) as minor component, it is chemically not closely related to *C. excisula.* Striatene-type sesquiterpenes, including striatene and striatol, are also the major components of *Anoplolejeunea conferta* (Meissn.) Schiffn. from Colombia (Gradstein et al. 1981).

Summing up, the available data suggest that members of the *Omphalanthus* complex are mainly characterized by the presence of striatene-type sesquiterpenes (except *Omphalanthus*). Their chemical constitution in general resembles that of members of the Ptychanthoideae, but pinguisane-type sesquiterpenes have not been detected in the *Omphalanthus* complex.

Lejeunea complex

(Genus *Lejeunea* and allies, see Schuster 1963; only few taxa investigated)

Besides the recording of unidentified sesquiterpene alcohols in Japanese *Lejeunea aquatica* Horik. (Asakawa et al. 1981a), no data on terpenoids were as yet available for members of the large *Lejeunea* complex. We have investigated 13 samples of the genus *Lejeunea,* belonging to *L. albescens* (Steph.) Mizut. (one sample), *L. discreta* Lindenb. (3 samples), *L. flava* (Sw.) Nees (one sample), *L. glaucescens* Gott. (one sample), *L. lumbricoides* (Nees) Nees (one sample) and to some provisionally named taxa. In addition, one sample of *Lepidolejeunea ornata* (Robins.) Schust. (= *Kingiolejeunea ornata* Robins.) was checked. This species produces a large quantity of diterpenes, among which kaurene (Fig. 1: 46) and its analogues have been detected. The major components of *Lepidolejeunea ornata* are other unidentified diterpenes.

Except for *Lejeunea flava,* all investigated *Lejeunea* species elaborate both sesquiterpenes and diterpenes. *L. albescens* (nr. 16) and *L.* aff. *albescens* (nr. 17) are chemically different. The major components of *L. albescens* are bicyclogermacrene (Fig. 1: 9), two unknown diterpenes and a sesquiterpene hydrocarbon. Also the three samples of *L. discreta* are each chemically different. Nr. 18 from Papua New Guinea produces germacrene-, aromadendrene- and one pinguisane-type sesquiterpenes, along with a few diterpenoids with a dimethyl-carbinyl group. These compounds have not been detected in sample nr. 19 from Papua New Guinea, nor in the sample from Japan. The GC/MS of the latter sample is rather simple and is characterized by the abundant presence of two unidentified diterpenes, which have not been found in the other *Lejeunea* species. *L.* aff. *discreta* from Papua New Guinea produces an unknown sesquiterpene hydrocarbon M + 204 (107) as the main component, which is also detected in *L. discreta* (sample nr. 18).

L. flava is chemically the most isolated *Lejeunea* species investigated, since it contains mainly cinnamolide (Fig. 1: 23). This drimane-type sesquiterpene lactone constitutes about 85% of the total yield in the GC! Cinnamolide is one of the significant chamical markers of *Porella* species (Asakawa 1982a).

L. lumbricoides and *L.* aff. *lumbricoides* mainly elaborate the sesquiterpene hydrocarbon alloaromadendrene (Fig. 1: 25), which has not been detected in the other *Lejeunea* species so far examined. Thus, alloaromadendrene is a useful chemical marker of *L. lumbricoides.*

Two species were provisionally identified as *Lejeunea* sp. *a* and *Lejeunea* sp. *b*. *Lejeunea* sp. *a* is particularly rich in the common sesquiterpenes β-elemene (Fig. 1: 14), δ-elemene (Fig. 1: 15), eremophilene (Fig. 1: 13) and β-selinene (Fig. 1: 10) and the common diterpene M + 272 (135), whereas the diterpene M + 304 (147), found in *Lejeunea* aff. *albescens,* has been detected in *Lejeunea* sp. *b* as the major component.

In conclusion, our data on the chemistry of the *Lejeunea* complex indicate the presence of a rich variety of diterpenoids in this group, including many unique compounds. On the other hand, sesquiterpene contents are less diversified and usually consist of common compounds, widespread in the Hepaticae. Notable is the almost lack of striatene- and pinguisane-type sesquiterpenes, so common in other generic complexes of the Lejeuneaceae. The terpenoid constitution of *Lejeunea flava,* consisting largely of the single compound cinnamolide, is unique for Lejeuneaceae.

Leptolejeunea complex

(one species of *Leptolejeunea* investigated)

Nakayama et al. (1979) reported that the strong odour of *Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn. is due to the presence of large amounts of the aromatic compound *p*-ethylanisole. This substance has not been isolated from or detected in the other Lejeuneaceae species and thus serves to characterize this taxon quite well.

Table II

Species	Monoterpenes	Sesquiterpenes	Diterpenes	Triterpenes	Sterols	Aromatic compounds
Acrolejeunea pusilla[1]		+ + + + +			+ +	
A. pycnoclada[1]		+ + + + +			+	
A. torulosa[1]	+	+ + + + +	+		+ +	
Anoplolejeunea conferta[6]		+ + + + +	+		+	
Archilejeunea mariana[1]		+ + +	+ +		+	
A. olivacea[1]		+ + + + +	+		+	
A. parviflora[1] [6]		+ + + +	+ + +		+	
Blepharolejeunea incongrua[1]		+ +	+ + + +		+	
B. securifolia[6]		+ + +	+ + +		+	
Brachiolejeunea densifolia[1]		?	+ +		+ +	
B. chinantlana[6]		+ + + +	+		+	
B. laxifolia[6]		+ + +	+ + +		+	
Bryopteris diffusa[1]		+ +	+ + + +		+	
B. fruticulosa[6]		+ + +	+ + +		+	
B. trinitensis[1]	+	+ +	+ +		+	
Cheilolejeunea excisula[1]		+ + + + +			+	
C. imbricata[1]		+ + + + +				
Diplasiolejeunea patelligera[1]		+ + +	+ + + +	+	+	
Lejeunea albescens[1]		+ + +	+ + + +		+	
L. aquatica[4]		+ + +	+ + + +		+	
L. aff. *albescens*[1]		+ + +	+ + + +		+	
L. discreta[1]		+ +	+ + + +		+	
L. aff. *discreta*[1]		+ +	+ + + +		+	
L. flava[1]		+ + + + +				
L. glaucescens[1]		+	+ + + +		+ +	
L. lumbricoides[1]		+ +	+ + + +			
L. aff. *lumbricoides*[1]		+ +	+ + +			
L. sp. a[1]		+ +	+ + + +		+	
L. sp. b[1]		+	+ + + +		+	
Lepidolejeunea ornata[1]		+ + +	+ + + +		+	
Leptolejeunea elliptica[6]	+					+ + + + +

Leucolejeunea aff. *decurrens*[1]		+ + + + +	+	+	
L. xanthocarpa[6]		+ +	+	+	+ + + +
Lindigianthus cipaconeus[6]		+ +	+	+	
Lopholejeunea eulopha[1]		+ + + + +			
L. howei[1]		+ + + + +		+	
L. subfusca[1]		+ + + +	+ + +	+	
Marchesinia brachiata[1], [6]	+	+	+	+	+ + +
M. mackaii[2]	+	+		+	+ + + +
Mastigolejeunea humilis[1]		+ + +	+ + +		
M. undulata[1]		+ + +	+ + +	+	
Nipponolejeunea pilifera[7]	+	+ + + +	+	+	
N. subalpina[7]	+ +	+ +	+ + + +	+	
Omphalanthus paramicola[6]		+ + + +	+ +	+	
O. platycoleus[6]		+ + + + +	+	+	+
Ptychanthus striatus[3]	+	+ + + +	+ +	+	
Schiffneriolejeunea nymannii[1]		+ +	+ + + +	+	
S. omphalanthoides[1]		+ +	+ + + +	+	
Spruceanthus semirepandus[2]		+ + + + +	+	+	
Stictolejeunea balfourii[1]	+	+ + +	+ +	+	+ +
S. squamata[1]		+ + +	+ + +		
Symbiezidium barbiflorum[1], [6]	+	+ + + +		+	
S. transversale[1]	+	+ + + + +		+	
Thysananthus amazonicus[1]	+	+ + +	+ +	+ +	
T. convolutus[1]		+ +	+ + +	+	
T. fruticosus[1]		+ + + +	+ +	+	
T. mollis[1]		+	+ + + +		
Trocholejeunea sandvicensis[3]	+	+ + + + +		+	
Tuzibeanthus chinensis[3]		+ + + +	+ +	+	

Table II. The distribution of mono-, sesqui-, di- and triterpenes, sterols and aromatic compounds in the Lejeuneaceae (from this paper[1] and from Asakawa et al. 1980a[2], Asakawa et al. 1980b[3], Asakawa et al. 1981a[4], Asakawa 1982a[5], Gradstein et al. 1981[6], Inoue et al. 1981[7] and Nakayama et al. 1979[8]). The symbols +, + +, + + +, etc. are relative concentrations estimated by GC/MS.

Table III

Subfamily	Complex	Species	Chemical Markers
Bryopteridoideae	--	Bryopteris diffusa[1]	striatenes, diterpenes (unidentified)
		B. fruticulosa[6]	bicyclogermacrene, bazzanene
		B. trinitensis[1]	oxygenated sesqui- and diterpenes (unidentified)
Ptychanthoideae	Ptychanthus c.	Ptychanthus *striatus*[3]	pinguisanes, striatenes, labdanes
		Tuzibeanthus *chinensis*[3]	pinguisanes, striatenes, labdanes
		Thysananthus amazonicus[1]	cadinane-type sesquiterpenes
		T. convolutus[1]	M^+ 272(135), 304(137) diterpenes
		T. fruticosus[1]	pinguisanes
		T. mollis[1]	M^+ 272(135), 304(137) diterpenes
		Mastigolejeunea humilis[1]	pinguisanes
		M. undulata[1]	pinguisanes
		Schiffneriolejeunea nymannii[1]	striatenes, diterpenes (unidentified)
		S. *omphalanthoides*[1]	striatenes, diterpenes (unidentified)
	Brachiolejeunea c.	Acrolejeunea pusilla[1, 5]	pinguisanes
		A. pycnoclada[1]	pinguisanes
		A. *torulosa*[1]	pinguisanes
		Trocholejeunea sandvicensis[3]	pinguisanes
		Brachiolejeunea chinantlana[6]	pinguisanes
		B. densifolia	?
		Blepharolejeunea incongrua[1]	M^+ 272(135), 334(43) diterpenes
		B. securifolia[6]	striatenes, pinguisanes
		Brachiolejeunea *laxifolia*[6]	sesquiterpenes (unidentified)
	Lopholejeunea c.	Lopholejeunea eulopha[1]	alloaromadendrene, 5-hydroxycalamenene
		L. howei[1]	cuparene, 5-hydroxycalamenene
		L. *subfusca*[1]	5-hydroxycalamenene
		Symbiezidium barbiflorum[1,6]	sesquiterpenes (unidentified)
		S. *transversale*[1]	sesquiterpenes (unidentified)
		Marchesinia *mackaii*[2]	dimethyl-eugenol
		M. brachiata[1, 6]	eugenol, monohydroxy-dimethoxy-allylbenzene

	Dicranolejeunea c.	Lindigianthus *cipaconeus*[6]	sesquiterpenes (unidentified)
	Archilejeunea c.	Archilejeunea mariana[1]	striatenes, pinguisanes
		A. olivacea[1]	sesquiterpenes (unidentified)
		A. parviflora[1, 6]	striatenes, pinguisanes, sesqui- and diterpenes (unidentified)
		Spruceanthus semirepandus[2]	striatenes, pinguisanes
	Stictolejeunea c.	Stictolejeunea balfourii[1]	bibenzyls
		S. *squamata*[1]	sesquiterpenes (unidentified)
Nipponolejeuneoideae	- -	Nipponolejeunea *pilifera*[7]	sesquiterpenes (unidentified)
		N. subalpina[7]	bornyl acetate
Lejeuneoideae	Omphalanthus c.	Omphalanthus paramicola[6]	chamigrene, sesqui- and diterpenes (unidentified)
		O. platycoleus[6]	chamigrene, widdrene, bazzanene
		Leucolejeunea xanthocarpa[6]	chamigrene, striatenes
		L. aff. decurrens[1]	striatenes
		Cheilolejeunea excisula[1]	striatenes
		C. imbricata[1]	striatenes, sesquiterpenes (unidentified)
		Anoplolejeunea conferta[6]	striatenes
	Lejeunea c.	Lejeunea albescens[1]	bicyclogermacrene, diterpenes (unidentified)
		L. aquatica[4]	diterpene alcohols (unidentified)
		L. discreta[1]	germacrene-D, selinene, diterpenes (unidentified)
		L. flava[1]	cinnamolide
		L. glaucescens[1]	diterpenes (unidentified)
		L. lumbricoides	alloaromadendrene
		L. aff. lumbricoides[1]	alloaromadendrene
		L. sp. a[1]	elemenes, selinene
		Lepidolejeunea ornata[1]	diterpenes (unidentified)
	Leptolejeunea c.	Leptolejeunea elliptica[8]	*p*-ethylanisole
Cololejeuneoideae	Diplostipae	Diplasiolejeunea patelligera[1]	β-caryophyllene, M^+ 288(255) diterpene (unidentified)

Table III. Chemical markers of the Lejeuneaceae. Subfamilies are according to Gradstein (1979), generic complexes according to Schuster (1963) and Gradstein (1975) with some modifications. Species references (1, 2 etc.) are given with Table II. Type species of genera are italicized.

Cololejeuneoideae

This subfamily contains the smallest members of the family, including many epiphylls. No chemical data were as yet available. We have been able to investigate one sample of this group, belonging to *Diplasiolejeunea patelligera* Herz. (= *D. neobrachyclada* Hatt., fide Grolle and Piipo 1984). The species produces β-caryophyllene (Fig. 1: 21) and an unknown diterpene alcohol M^+ 288 (255) as the major components. The latter diterpene has not been found in any other Lejeuneaceae species so far examined. *D. patelligera* furthermore elaborates a small quantity of the triterpene hop-22-ol (Fig. 1: 47). Triterpenes are quite rare in the Hepaticae (Asakawa 1982) and have not yet been found in other members of the Lejeuneaceae. Lejeuneaceae.

Conclusions

The results (Tables II, III) indicate that most species of Lejeuneaceae elaborate large quantities of sesquiterpenes and/or diterpenes, whereas only few synthesize monoterpenes or aromatic compounds. Triterpenes are very rare - found only in *Diplasiolejeunea patelligera* as minor component - which corroborates results obtained for other groups of Hepaticae (Asakawa 1982). Although many compounds detected by means of gaschromatography remain unidentified, especially diterpenes, the outlines of the chemical characteristics of several taxonomic groups within this large family are becoming apparent.

Pinguisane-type sesquiterpenes, known from e.g. Ptilidiaceae and Porellaceae (Asakawa 1982), are chemical markers for several genera and species of the subfamily Ptychanthoideae, in particular members of the *Ptychanthus* complex, the *Archilejeunea* complex and the *Brachiolejeunea* complex. The genera *Thysananthus* and *Brachiolejeunea* are heterogeneous as to pinguisane-type sesquiterpene content, however, as some species elaborate them whereas others do not. Pinguisane-type sesquiterpenes are ± lacking in the other subfamilies investigated, except in the closely allied Bryopteridoideae.

Striatene-type sesquiterpenes are more widespread in the family and were also found in the Bryopteridoideae and the members of the *Omphalanthus* complex (Lejeuneoideae), but not in Nipponolejeuneoideae, Cololejeuneoideae (only one species checked!) or members of the *Lejeunea* complex (Lejeuneoideae). As Bryopteridoideae and the *Omphalanthus* complex are morphologically closer to Ptychanthoideae than the other investigated groups, the distribution of striatene-type sesquiterpenes apparently corroborates morphological evidence and seems indicative for major evolutionary relationships.

On the other hand, the distribution of a number of compounds is still puzzling and does not coincide with morphological findings. For instance, by its diterpene constitution the monotypic genus *Lindigianthus* is somewhat similar to members of the genus *Thysananthus*, to which it otherwise bears no relationship.

Drimane-, calamenane-, chamigrane-type sesquiterpenes and phenylpropanoids were detected as major components in a limited number of taxa and for that reason seem characteristic on the genus or species level. For instance, 5-hydroxy-calamenene is elaborated almost exclusively by the three species of *Lopholejeunea* investigated and *Marchesinia* exclusively synthesizes aromatic eugenol-type compounds. Labdane-type diterpenes are the chemical markers for *Ptychanthus* and *Tuzibeanthus,* which coincides with the close morphological relationship between these two genera, and the genus *Nipponolejeunea* seems well-defined by the exclusive presence of the odorous monoterpenes borneol and bornyl-acetate.

Sesquiterpene lactones, characteristic for the allied family Frullaniaceae, are very rare in Lejeuneaceae and have been found in a few unrelated species only, usually as a minor component. However, the terpenoid constitution of *Lejeunea flava* is almost entirely made up of large amounts of the drimane-type sesquiterpene lactone cinnamolide, which has not been detected in the other investigated members of the family. As *Lejeunea flava* is a widespread, pantropical species and morphologically rather variable, it would be interesting to investigate the chemical constitution of this species using many samples from throughout its range.

Data on infraspecific chemical variation are available for a limited number of species only and are rather inconclusive, being based on maximally four samples per species only. In *Acrolejeunea pycnoclada, Archilejeunea olivacea* and *Thysananthus mollis* the different samples of each species are fairly homogeneous, both qualitatively and quantitatively, but in *Lejeunea discreta, Archilejeunea parviflora, Mastigolejeunea humilis* (s.l.) and *Symbiezidium barbiflorum* large chemical differences among the samples were found. To what extent these differences coincide morphological and geographical differentiation, as well as what causes this variation, remain to be investigated. The chemical interrelationships between the various members of the Lejeuneaceae will become better understood when more samples are analysed and when the hitherto unknown major constituents, paticularly the many diterpenoids, become structurally elucidated.

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References

ASAKAWA, Y., TOKUNAGA, N., TAKEMOTO, T., HATTORI, S., MIZUTANI, M. & SUIRE, C. 1980a. Chemosystematics of Bryophytes IV. J. Hattori Bot. Lab. 47: 153-164.

ASAKAWA, Y., SUIRE, C., TOYOTA, M., TOKUNAGA, N., TAKEMOTO, T., HATTORI, S. & MIZUTANI, M. 1980b. Chemosystematics of Bryophytes V. J. Hattori Bot. Lab. 48: 285-303.

ASAKAWA, Y., MATSUDA, R., TAKEMOTO, T., HATTORI, M., MIZUTANI, M., INOUE, H., SUIRE, C. & HUNECK, S. 1981a. Chemosystematics of Bryophytes VII. J. Hattori Bot. Lab. 50: 107-122.

ASAKAWA, Y. 1982. Chemical constituents of the Hepaticae. In: Herz, W. et al. (ed.), Progress in the Chemistry of Organic Natural Products 42: 2-285. New York.

ASAKAWA, Y. 1982a. Terpenoids and aromatic compounds as chemosystematic indicators in Hepaticae and Anthocerotae. J. Hattori Bot. Lab. 53: 282-293.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae). Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. 1979. The Genera of the Lejeuneaceae: Past and Present. In: Clarke, G.C.S. and Duckett, J.G. (eds.), Bryophyte Systematics, p. 83-107. Acad. Press, London and New York.

GRADSTEIN, S.R. & INOUE, H. 1980. Studies on Lejeuneaceae subfam. Ptychanthoideae V. A review of the species from Ceylon. Bull. Nat. Sci. Mus. Ser. B, 6: 23-32.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

GROLLE, R. & PIIPO, S. 1984. Annotated catalogue of Western Malesian bryophytes. I Hepaticae and Anthocerotae. Acta Bot. Fenn. 125: 1-86.

INOUE, H. 1976. Illustrations of Japanese Hepaticae 2. Tokyo.

INOUE, H., ASAKAWA, Y. & GRADSTEIN, S.R. 1981. A biosystematic study of *Nipponolejeunea* Hatt. (Hepaticae). Bull. Nat. Sci. Mus. Ser. B, 7: 136-143.

NAKAYAMA, M., MATSUO, A., KAMI, T. & HAYASHI, S. 1979. Volatiles from *Leptolejeunea elliptica.* Phytochemistry 18: 328.

SCHUSTER, R. 1963. An annotated sysnopsis of the genera and subgenera of Lejeunecaeae. Beih. Nova Hedwigia 9: 1-203.

VERDOORN, F. 1934. Studien über Asiatische Jubulae. Ann. Bryol. Suppl. 4: 40-192.

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Section two

Taxonomic Revisions

BEIHEFT 80 ZUR NOVA HEDWIGIA

4 A Revision of Neotropical Archilejeunea (Spruce) Schiffn.

by

S.R. Gradstein and G.M.C. Buskes

ABSTRACT: *Archilejeunea* (Spruce) Schiffn. is a common epiphytic element of the lowland rain forests of tropical America. Four neotropical species are accepted in this revision: *A. crispistipula* (Spruce) Steph., *A. juliformis* (Nees) Gradst. and *A. porelloides* (Spruce) Schiffn. in the subgenus *Archilejeunea*, and *A. parviflora* (Nees) Schiffn. in the subgenus *Dibrachiella* (Spruce) Schiffn. The latter species is treated in a broad sense and is subdivided into two varieties: var. *parviflora* and var. *florentissima* (Spruce) comb. nov. (= *A. auberiana* (Mont.) Evans).

The subgenus *Archilejeunea* is largely restricted to Amazonia and the Guianas, where *A. juliformis* is one of the most common liverwort species. *A. parviflora* occurs throughout the neotropics yet is rare in Amazonia. The two subgenera are redefined on the basis of lobule morphology (a tendency for lobule reduction is found characteristic for subg. *Dibrachiella*), innovation type and some further trends. It is suggested that the African, Asiatic and Australasiatic *Archilejeunea* species belong in the subgenus *Dibrachiella*, including the widespread *A. mariana* (Gott.) Steph. (= *Mastigolejeunea paradoxa* Verd. syn. nov.) and the Australasian endemic *A. olivacea* (Hook f. & Tayl.) Steph. (= *A. scutellata* (Tayl.) Steph. syn. nov). Over twenty binomina are excluded from *Archilejeunea* and several new synonyms, lectotypes and new combinations are proposed.

Introduction

Archilejeunea (Spruce) Schiffn. is a pantropical genus of about 10 species (Gradstein 1975; this revision). The Asiatic species have been studied by Verdoorn (1934), Mizutani (1961) and Udar & Awasti (1981, 1982), the African species by Vanden Berghen (1951). The neotropical species, however, have not been examined critically since Spruce (1884) established the generic concept and described the Amazonian species, and since Evans (1908) examined the West Indian representatives. About 10 neotropical species were recognised in the early 1900's: *A. auberiana, A. cruegeri, A. florentissima, A. leprieurii, A. viridissima,* and especially from Amazonia *A. porelloides* (the lectotype species), *A. badia, A. crispistipula, A. recurvans* and *A. rufa.* Two further species placed by Spruce in *Archilejeunea, A. clypeata* and *A. unciloba,* were transferred to *Leucolejeunea* by Evans (1907). About 20 neotropical binomina were added by Stephani (1911), but most of these do not belong in *Archilejeunea* as our study shows

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*Studies on Lejeuneaceae subfam. Ptychanthoideae IX. Also appearing as STUDIES ON THE FLORA OF THE GUIANAS 8.

The genus *Archilejeunea* as currently understood, is characterized in the gametophyte by 1) the possession of isodiametric leaf cells, non-convoluted leaves, segmented oil bodies*, 1-2 innovations, hypostatic male bracts and a 3-5(-6) keeled perianth, and 2) by the *absence* of enlarged cortical cells, secondary pigmentation in the cell walls, gemmae or ocelli. Branching is predominantly of the *Lejeunea*-type and leaves are entire except in the Asiatic *A. mariana*, which may develop toothed margins. The sporophyte, as described for *Archilejeunea mariana* by Udar & Awashti (1982) and Crandall-Stotler & Geissler (1983, under *Spruceanthus marianus*) has the usual fenestrate inner valve thickenings, spiralled elaters and spores with rosettes as in many other Ptychanthoideae.

Archilejeunea was subdivided by Spruce into two groups, sect. *Monotropella* Spruce and sect. *Dibrachiella* Spruce, but this subdivision has been neglected by later authors after Schiffner (1893) had formally elevated these sections to subgeneric rank. As our study shows, these two subgenera are in fact natural groups fully deserving recognition; one of them (subg. *Monotropella* = subg. *Archilejeunea*) is probably entirely restricted to tropical America.

Among Ptychanthoideae *Archilejeunea* is related to the Amazonian genus *Verdoornianthus* (Gradstein 1978), which has no innovations and is only known from dried gametophytic material, and to *Spruceanthus,* which differs by its homogeneous oil bodies, its coarser texture and more robust stem, and its perianth which tends to become pluriplicate. By lack of oil bodies, the difference between the two genera is critical, however.

In the present study all neotropical binomina in *Archilejeunea* are revised, except for *A. argentinica* Herz. and *A. ovata* Herz. Four species are recognized, three in subg. *Archilejeunea* and one variable species in subg. *Dibrachiella.* Our study was based on examination of types and other material from BM, COLO, FH, FLAS, G, MACH, L, NY, PC, SP, STR, U, W and YU. Of particular value were the large amounts of new material from the Amazon basin collected by Griffin, Vital & Yano (1974), Prance et al. (1971-), Reese (1978) and others.

Key to neotropical Archilejeunea

1. Plants ± glossy brownish. Lobule never reduced, the apex truncate, with 0-1 teeth. Underleaves imbricated (spatiated only in weak plants), (3-)4-7 × stem width. Innovations of the *Radula-Jubula* type (first appendage an underleaf). Dioicous, rarely paroicous. Common in tropical South American lowland forests.. Subg. *Archilejeunea* ... 3

1. Plants green to greenish-brown or blackish. Lobule tending to become reduced, sometimes entirely lacking, the apex oblique, with 0-2 teeth. Underleaves

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*Reports of homogeneous oil bodies in *Archilejeunea* - including our recent recording in *A. viridissima* (Gradstein et al. 1981) - should all be considered doubtful and in need of verification, in view of the rapid degeneration of the segmentation of the oil body in this genus (Gradstein 1975: 144; Crandall-Stotler & Geissler 1983).

spatiated or (robust plants) imbricate, 2-4(-4,5) × stem width. Innovations of the *Radula-Lejeunea* type (first appendage a lateral leaf). Monoicous. Throughout tropical America but rare in Amazonia................. 4. *A. parviflora* ... 2
....(Subg. *Dibrachiella*)

2. Lobules up to 1/3 × lobe length, ovate, with 0-1 obscure teeth, often smaller, sometimes lacking entirely........................... 4a. var. *parviflora*

2. Lobules mostly larger, up to ½ × lobe length, rectangular, with (1-)2 distinct teeth of 2-5 cells long............................. 4b. var. *florentissima*

3. Underleaf margins undulate. Ventral leaf margin auriculate at the junction with the keel... 3. *A. crispistipula*

3. Underleaf margins plane. Ventral leaf margin not auriculate............... 4

4. Plants robust, 5-10 cm long, 2-3 mm wide. Underleaves longer than wide to orbicular. Lobule apex triangular, lacking a distinct tooth.. 2. *A. porelloides*

4. Plants less robust, 2-4(-6) cm long, 1-2 mm wide. Underleaves wider than long or (in small plants) orbicular. Lobule apex with 1 tooth. Very common species
.... 1. *A. juliformis* ... 5

5. Perianth inflated, the ventral surface with 2 distinct keels...................
.... *A. juliformis* var. *juliformis*

5. Perianth flattened, the ventral surface ± swollen and smooth or with 2 very low keels in the upper most portion................ *A. juliformis* var. *unicarinata*

ARCHILEJEUNEA subgenus **Archilejeunea**

Lejeunea subg. *Archilejeunea* Spruce sect. *Monotropella* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 89 (1884).

Archilejeunea subg. *Monotropella* (Spruce) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1, 3: 130 (1893).

Lectotype (Evans 1908): *Lejeunea porelloides* Spruce. As pointed out by Grolle (1983), the above citation is correct only when *Archilejeunea* (Spruce) Schiffn. is conserved against *Archilejeunea* Steph. 1888, with *A. erronea* Steph. as type. We have examined the holotype of *A. erronea* Steph. (South Africa, Cape Province, Ecklon s.n., G), and found that it represents a species of *Leucolejeunea* Evans, probably *L. rotundistipula* (Lindenb.) Steph. Peculiar in this plant are the small, ± evenly thickened, hexagonal leaf cells resembling the leaf areolation of *Sticto-lejeunea* and *Lepidolejeunea* (yet lacking ocelli).

In South America, *Archilejeunea* subg. *Archilejeunea* is represented by three species: the widespread *A. juliformis* and the more restricted, inner Amazonian endemics *A. crispistipula* and *A. porelloides.* All three species are corticolous epiphytes and inhabitants of the moist or mesic lowland forests. They are easily recognized by their glossy brownish appearance, their *Radula-Jubula* innovation and dioicous inflorescence. The truncate lobule with only one tooth (or none) and almost without any tendency for reduction (as contrary to subgenus *Dibrachiella*) is another characteristic feature of this group.

The sporophyte in *Archilejeunea* subg. *Archilejeunea* (observed in *A. juliformis* and *A. porelloides*, Fig. 4) has the usual characteristics of the ptychanthoid sporophyte (Mizutani 1961, Gradstein 1975): seta 16:4, capsule valves spreading after dehiscence, cells of the outer valve layer with nodulose thickenings, cells of the inner valve layer covered by a brownish, plurifenestrate sheet of thickening, elaters attached to the margin and the upper surface of the valves in a regular fashion, with one spiral, spores ± isodiametrical, their surface spinose and with rosettes.

Archilejeunea subg. *Archilejeunea* is not yet known from outside the Neotropics and within that area it is mainly restricted to Amazonia. *A. juliformis*, however, should be expected in other neotropical areas; outside South America it has thus far only been recorded from Cocos Island.

1. **Archilejeunea juliformis** (Nees) Gradst. Fig. 1

Bryophyt. Biblioth. 4: 126 (1975). *Jungermannia juliformis* Nees, in Martius, Fl. Bras. 1,1: 351 (1833) "*filiformis*".

Type: Colombia, Mt. Arara Coara, Martius s.n. (STR holo, FH, M, PC, S, W.).

Heterotypic synonyms:

Archilejeunea badia (Spruce) Steph., Spec. Hep. 4: 711 (1911) syn. nov. *Lejeunea badia* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 89 (1884).

Type: Rio Vaupés, "in caatingas, ad ramulos foliaque", Spruce L104, IX. 1852 (MANCH 15051 holo).

Archilejeunea fuscescens (Hampe ex Lehm.) Fulf., Bryologist 45: 174 (1942) syn. nov. *Lejeunea fuscescens* Hampe ex Lehm., Pugillus 7: 16 (1838).

Type: Peru (?), "in cortic. Chinae reg.", hb. Hampe (BM holo, W).

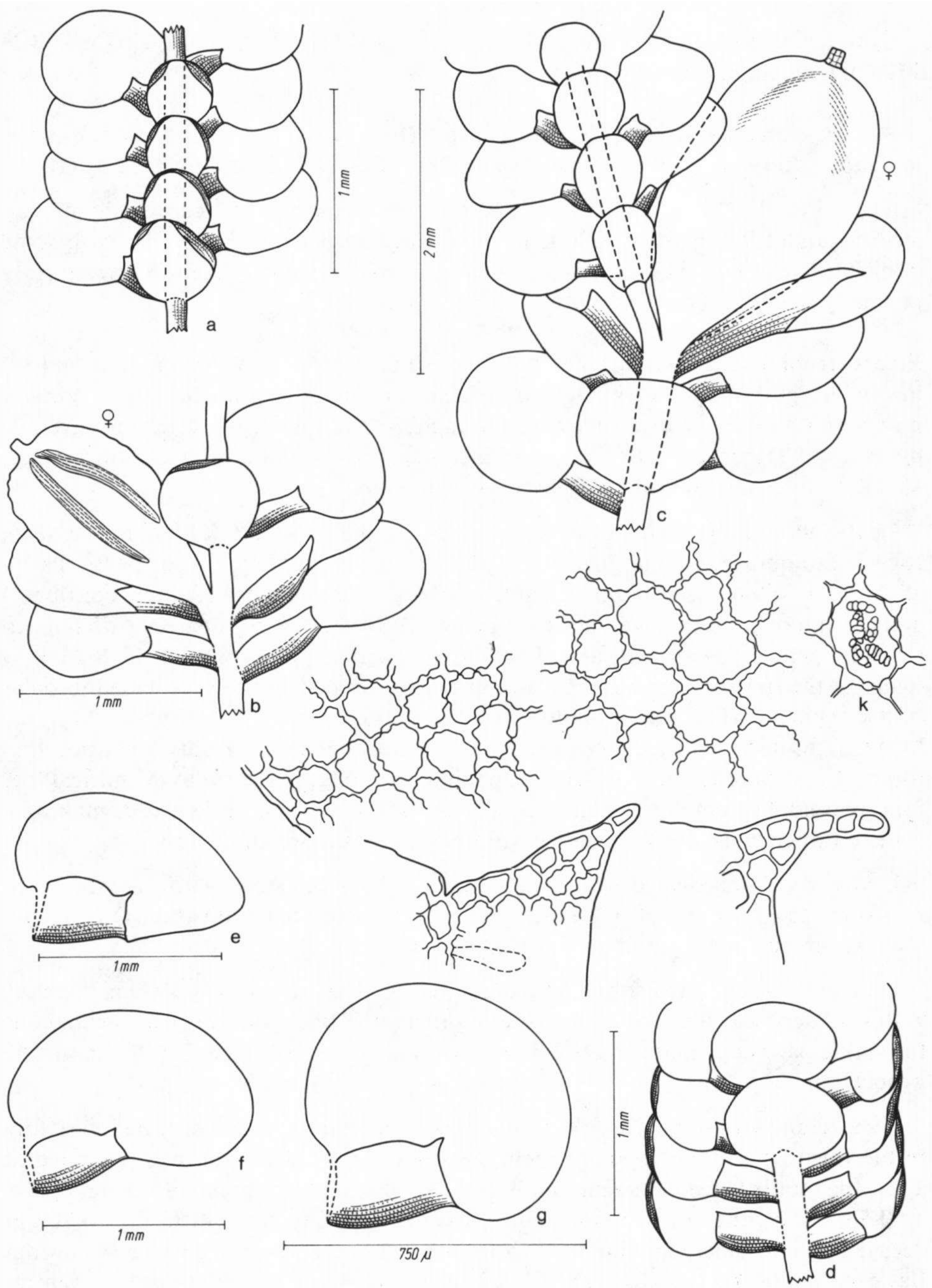
Archilejeunea recurvans (Spruce) Steph., Spec. Hep. 4: 718 (1911) syn. nov. *Lejeunea recurvans* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 89 (1884).

Lectotype (nov.): Brazil, Rio Negro, Sao Gabriel, Spruce L462 (MANCH 15154; ibid. 15155 iso).

Fig. 1. *Archilejeunea juliformis* (Nees) Gradst.

a-d. habitus. c. specimen with flattened perianth: *A. juliformis* var. *tricarinata* (Spruce) Gradst. & Buskes. e.-g. leaves. k. oil bodies and lobule apex

a from Griffin 489. b, f from Griffin 591. c from Griffin 168. d, g from Hegewald 6360. e from the type of *Lejeunea badia* Spruce. k. from Nelson 19a, Griffin 591 and Bekker 1165.


a
1 mm
2 mm
♀
c
♀
b
1 mm
k
e
1 mm
f
1 mm
g
750 µ
1 mm
d

Archilejeunea rufa (Spruce) Steph., Spec. Hep. 4: 719 (1911). *Lejeunea rufa* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 94 (1884).

Syntypes: Brazil, Pará, Santarem, Spruce L91 (MANCH 15161), L250 (MANCH 15162); Obidos, Spruce L57 (BM).

Archilejeunea spruceana Steph., Spec. Hep. 4: 720 (1911). *Archilejeunea unciloba* non typus, sensu Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 91 (1884).

Type: Brazil, "Silva Amazonica", leg. Spruce (lectotype not chosen; many collections under this name available in the Spruce herbarium, MANCH, with some duplicates in YU). All records of *Leucolejeunea unciloba* from Amazonia are probably *Archilejeunea juliformis.*

Plants creeping to ascending when fertile, medium-sized, up to 4(-6) cm long and 1-2 mm wide, glossy olive to golden to reddish-brown, little branched to irregularly pinnate with purely (?) *Lejeunea*-type branching. Stem in cross section in average made up of 15 cortical cells and ca. 18 medullary cells of equal size and thickening, 18-25 × 10-15 µm; ventral merophyte 4-6 cells wide.

Leaf lobes imbricated, ovate-orbicular, ca. 0.8-1 × 0.6-0.8 mm, the apex rounded to obtuse, the margins entire, plane or recurved towards the apex; cells ca. 25-35 µm in diam., with bluntly triradiate trigones (sometimes becoming confluent) and 1-3 intermediate thickenings (one per wall); oil bodies segmented, *Calypogeia*-type, 4-6 per cell in mid-leaf, at leaf base up to 9 per cell, bluntly ellipsoid, 8-16 × 4-6 µm, at the time of observation (ca. one week after collection) subdivided into 4-8 coarse segments (Fig. 1k). Lobule short ovate to (sub)rectangular, about ¼-½ × lobe length, never reduced, the apex truncate, with one erect or outwardly pointing tooth of 1-3(-5) cells long, the hyaline papilla very long, pyriform to cylindrical (ca. 5:1), marginal or entally displaced 2 cells below the margin; keel curved, making a wide to rather sharp (90-150°) angle with the ventral margin of the lobe.

Underleaves imbricated, rarely spatiated, (3-)4-7× stem with, orbicular to reniform, ca. 0,5-1 × 0,4-0,6 mm, the apex rounded, recurved (usually) or plane, the margins entire, the insertion line shallowly curved.

Dioicous, rarely paroicous. Androecia terminal or intercalary, when dioicous with 6-12 series of diandrous, hypostatic bracts, the bracteoles present throughout the spike; paroicous plants have 2-3 series of male bracts situated directly below the gynoecium.

Gynoecium with single *Radula-Jubula* type innovations, which may be repeatedly fertile forming a monotropous system; bracts about as large as leaves, rounded at apex, the lobule lanceolate-acuminate, ca 2/3 × lobe length; bracteole ovate, 0,75-1 × 0,5-0,6 mm, the apex rounded-entire to emarginate to short-bifid (up to 70 µm deep); perianth emerged, flattened to inflated, 3-5 keeled with 2 narrow or wide-flattened lateral keels, 0-1 (weak) dorsal keels and 1-2(-3) ventral keels, the ventral keels variable and sometimes almost lacking (var. *unicarinata*), the keels irregularly toothed to almost smooth. Sporophyte: see under subg. *Archilejeunea.*

DISTRIBUTION AND ECOLOGY: Costa Rica, French Guiana, Suriname, Guyana, Brazil, Venezuela, Columbia, Peru, Bolivia; 0-600 m. Very common in moist or mesic, primary or secondary Amazonian lowland forests on terra firme, in campina forests and, also, in riparian forests (igapó) near Manaus. On trunks, buttresses, branches or twigs of living trees, on lianas and vines, bases of palms and on rotten logs. Moderately drought-tolerant, may grow on trunks at forest edges in sunny locations.

Archilejeunea juliformis is the most common species of the genus in South America and abundant in Amazonia, where many collectors have gathered it. The species varies considerably in size and growth habit. Small plants were described by Spruce as *A. rufa*, while *A. badia* Spruce represents a large form.

Sterile plants are always creeping whereas fertile plants may obtain an ascending to subpendulous habit, especially when growing on small twigs. The female bracteole varies from entire to short-bifid; forms with bifid bracteoles and sharp lobule teeth were misidentified by Spruce as *A. unciloba* (= *Leucolejeunea unciloba*), a species which is probably lacking in inner South America. *A. juliformis* is normally dioicous but an occasional paroicous inflorescence was found in copiously fertile, subpendulous specimens (e.g. Griffin et al. I-84a, campus INPA, Manaus). The inflated male bracts in the paroicous specimen are in 2-3 series, situated directly below the gynoecium on the same shoot, with enlarged lobules which are hypostatic yet not overlapping. Since no other differentiating character could be found for these paroicous plants, we have refrained from introducing a formal name for their inception.

The perianth in *A. juliformis* is usually narrowly inflated with 4-5 distinct keels (Fig. 1b), but plants with wider, flattened perianths may also be found. In such plants the ventral perianth surface is convex and almost smooth or provided with 2 low plicae in the uppermost portion (Fig. 1c). The form with the flattened perianth and reduced ventral keels was described by Spruce as *Lejeunea unciloba* var. *unicarinata* Spruce, and seems distinct enough to stand as separate variety: **Archilejeunea juliformis** (Nees) Gradst. var. **unicarinata** (Spruce) comb. nov. (*Lejeunea unciloba* Lindenb. var. *unicarinata* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 92. 1884).

Specimens examined (*A. juliformis*): COSTA RICA: Cocos Island, Weber 580, III.1964 (COLO, U). TRINIDAD: Valencia, Toco Rd., E.G. Britton et al. 1883, IV.1920 (YU); East of Sangre Grande, E.G. Britton 2878, VI.1921 (YU). FRENCH GUIANA: Cayenne, Moen s.n. (MANCH). SURINAME: Pleike, Laura river, McGillavry s.n., XI.1971 (U); Kabalebo area, Bekker 1104, 1163, 1164a & 1165, X.1981 (BBS, U). GUYANA: Pomeroon river, Bartlett 8052, IX.1904 (BM); near Bartica, Richards 189, 201, 439, 473, 494, 515 & 812 (YU). BRAZIL: *Pará*, Santarem and Obidos, leg. Spruce (several colls.), syntypes of *Lejeunea rufa* Spruce (MANCH); *Roraima*, Mucajai airstrip, Prance et al. 10951, III.1971 (NY, U); *Amazonas*, Maués, Nelson 5, 9, 12, 19a & 29, IV.1974 (FLAS, U); Manaus, campus INPA, Griffin et al. I-69, I-83, I-84a, I-99, I-100 & I-100 AB, VII.1974 (FLAS, U); Manaus, Mauá, Griffin et al. 133 & 136, VII.1974 (FLAS, U) Manaus, Ponta Negra, Griffin et al. 294, 297 & 299, VII.1974 (FLAS,U); ibid., Prance et al. 11698 & 11706, III.1971 (NY, U); Manaus-Itacoatiara, Ducke Forest Reserve, Griffin et al. 168, 210, 313, 327, 340 & 354, VII.1974 (FLAS, U); ibid., Berg et al. P17596, XI.1973 (NY); ibid., Reserva Egler, Griffin et al. 489, 490, 496 & 519, VII.1974 (FLAS, U); Manaus-Caracarai km 60, Campina forest, Griffin et al. 20bc, 21, 88, 89, 585, 587, 591, 941, 977 & 982, VII.1974 (FLAS, U); ibid.

km 115, Rio Urubu, Griffin et al. 851, 871, 887 & 902, VII.1974 (FLAS, U); ibid. km 130, Rio Lages, Griffin et al. 361, 364, 371, 414, 462, VII.1974 (FLAS, U); Manaus-Velho km 240, Lieras et al. P19575 & P19580, XI.1973 (NY, U); Rio Vaupés, Spruce L104, type of *Lejeunea badia* Spruce (MANCH); upstream Rio Negro, many colls. from various locs, leg. Spruce sub *Lej. unciloba, Lej. recurvans* etc. (MANCH, YU); Sao Gabriel de Rio Negro, Spruce L46, lectotype of *L. recurvans* Spruce (MANCH); *Acre,* Rio Branco-Brasileia km 33, Reese & McPherson 13246, II.1978 (NY, U); Cruz do Sul, Estrada Alemanha, Prance et al. 11868, 11870, 11900, 11901, 11905 & 11951, IV.1971 (NY, U); VENEZUELA: Upper Orinoco, Caridad S. of Isla Cotua, Mägdefrau 138, I.1958 (hb. Mägdefrau, U); ibid., between Maricapure and Isla Quiritare, Mägdefrau 164, I.1958 (hb. Mägdefrau, U); Casiquiare, mouth of Rio Paciba, Mägdefrau 224, I.1958 (hb. Mägdefrau, U). COLOMBIA: Mt. Arara Coara, Martius s.n., type (FH, M, PC, S, STR, W); *Meta*, Rio Gayabero, 10 km S. of caño Lozáda, Bischler 1595 & 1616, I.1959 (COL, PC, U); Cord. la Macarena (extrem. NE), Schultes 11175 (FLAS, U); *Boyacá*, Casanáre, van der Hammen 1717 (COL, U). PERU: Iquitos, Laguna Quistrococha, Hegewald 630, VII.1973 (hb. Hegewald, U). BOLIVIA: *Beni,* Guayaramerín, Reese 1247, 12771, 12791, 12926 & 13100, II.1978 (NY, U).

2. **Archilejeunea porelloides** (Spruce) Schiffn. Fig. 2

Hedwigia 33: 181 (1894); Stephani (1911) 717. *Lejeunea porelloides* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 90 (1884).

Lectotype (nov.): Venezuela, San Carlos, Spruce L44 (MANCH 15139 female, 15137 male). In his original description Spruce gave details on the male and female plant. Since L44 is the only collection which has both sexes (kept in two different convolutes in MANCH), we have chosen this number as the lectotype.

Heterotypic synonyms:

Lejeunea porelloides var. *andina* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 91 (1884) syn. nov.

Lectotype (nov.): Ecuador, Mt. Guayrapurina, "in cortice", Spruce L180 (MANCH 15138 female; 15141 iso).

Lejeunea porelloides var. *longiflora* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 91 (1884) syn. nov.

Lectotype (nov.): Venezuela, San Carlos, "ad ramulos in caatingas", Spruce s.n. 1853 (MANCH 15127 female).

Plants ascending, mostly free from the substrate, rather robust, 5-10 cm long and 2-3 mm wide, yellowish-brown to dark brown, with few *Lejeunea*-type branches. Stem in cross-section with 24-28 cortical cells surrounding 28-35 similar medullary cells, the ventral merophyte 4-8 cells wide.

Leaf lobes subimbricated, ovate-oblong, ca. 1,3 × 0,9 mm, the apex narrowed obtuse, the margins entire, plane, the ventral margin almost straight; cells subisodiametric, 24-28 × 18-25 μm, with rather coarse, bluntly triradiate trigones and few (0-1) intermediate thickenings. Lobule large, flattened, ca. 1/3-½ × lobe length, subrectangular with the free margin straight and parallel to the keel, the apex sharply or obtusely triangular without teeth, obliquely truncate, meeting the ventral margin of the lobe at an angle less than 90°; hyaline papilla cylindrical, marginal.

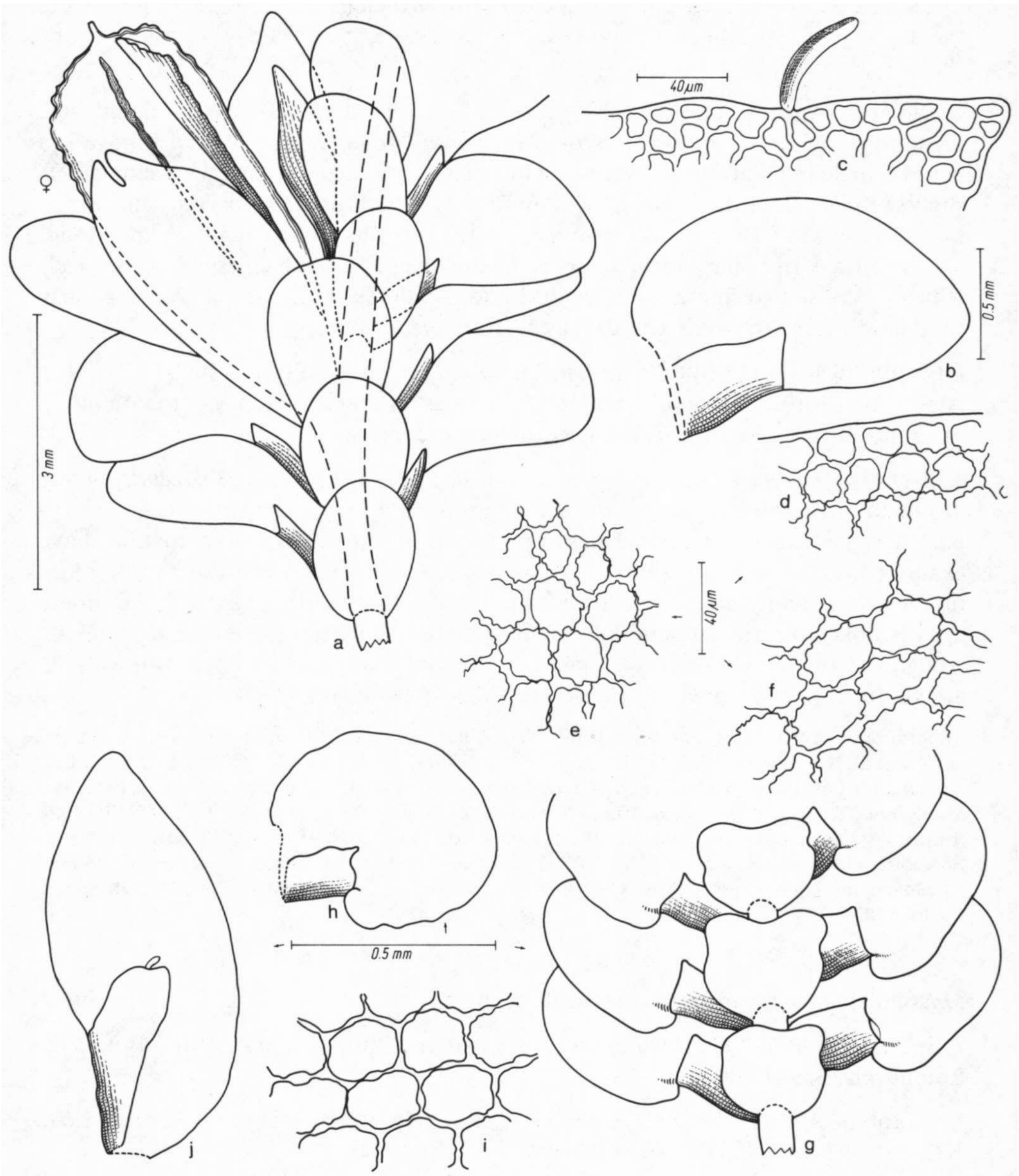


Fig. 2. *Archilejeunea porelloides* (Spruce) Schiffn. and *A. crispistipula* (Spruce) Steph.

a-f. *A. porelloides* (all from Griffin 418). a habitus. b leaf. c lobule apex with hyaline papilla. d-f leafs cells. d leaf margins cells. e median leaf cells. f leaf base cells.

g-j. *A. crispistipula* (all from Griffin 618). g. habitus h. leaf. i. median leaf cells. j. female bract, with hyaline papilla.

Underleaves imbricated, 3,5-4 × stem width, orbicular to 1,5 × as long as wide, the apex rounded, plane or slightly recurved, bases ± cuneate, the insertion line shallowly curved.

Dioicous. Androecium terminal or intercalary, the bracts in 6-14 series, diandrous. Gynoecium with 1-2 innovations of the *Radula-Jubula* type, a paired innovation below, single innovations above, often in seriate, monotropous arrangement; bracts slightly longer than the leaves, the apex rounded to obtuse, the margins entire, the lobule somewhat shorter, acuminate; bracteole ovate-oblong, ca. 1,5 mm long, always bifid with a sharp incision up to 0,3 mm deep; perianth emerged, cylindrical, with 4-5 keels, two lateral, two ventral and 0-1 dorsal keels, the keels irregularly subdentate. Sporophyte: see under subg. *Archilejeunea*.

DISTRIBUTION AND ECOLOGY: Brazil, Venezuela, Ecuador, Peru; 0-1000 m. In inner Amazonian forests on small truncs and on twigs. Apparently fairly common along the upper Rio Negro towards the Venezuelan border (leg. Spruce).

Archilejeunea porelloides is the most robust species of neotropical *Archilejeunea*, although well-grown *A. juliformis* may approach it in size. The two species are apparently very close but nevertheless remain distinct in the material that we have examined. *A. porelloides* shares a robust size, leaves over 1 mm long and ovate-oblong, with underleaves that are usually longer than wide; moreover the lobule apex is obliquely truncate and lacks a discrete tooth. Fertile *A. porelloides* may be recognised by the presence of forked innovations below and single innovations above. In *A. juliformis* we have observed single innovations only.

Specimens examined (*A. porelloides*): BRAZIL: *Amazonas*, Manaus-Caracarai km 130, Rio Lages, Griffin et al. 418, VII.1974 (FLAS, U); Rio Negro, Panuré, Spruce s.n. (MANCH). VENEZUELA: Cassiquiare, Capiguara, Mägdefrau 207, I.1958 (hb. Mägdefrau, U); Rio Guarnia, Caño Pimichin, Mägdefrau 277, II.1958 (hb. Mägdefrau, U); San Carlos de Rio Negro, Delascio et al. 9453, III.1981 (FLAS, U); ibid., Spruce s.n., several colls. including lectotype (MANCH, YU). ECUADOR: Oriente, Bomboiza, Gualayuir, Allioni 600, IX.1910 (U); Mt. Guayrapurina, Spruce s.n., lectotype of *Lejeunea porelloides* var. *andina* Spruce (MANCH). PERU: Moyabamba, Campana Mts., Mt. Pingullu, Spruce s.n. (MANCH, YU).

3. **Archilejeunea crispistipula** (Spruce) Steph. Fig. 2

Spec. Hep. 4: 712 (1911). *Lejeunea crispistipula* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 93 (1884).

Lectotype (nov): Brazil, Amazonas, Rio Negro, Uanauaca, Spruce L60, XII. 1851-52 (MANCH 15083 female; ibid. 15081 male).

Plants creeping, rather small, up to 3 cm long and 1,2 mm wide, glossy yellowish to golden brown, with few *Lejeunea*-type branches. Stem in cross-section with ca. 12 cortical cells surrounding ca. 15 similar medullary cells; ventral merophyte 4 cells wide.

Leaf lobes subimbricated, ovate-orbicular, 0,6-0,8 × 0,5-0,6 mm, the apex rounded, the margins sometimes undulated, especially ventrally, the ventral margin auriculate at the junction with the keel, the auricle often touching or covering part of the distal portion of the lobule; cells ca. 28 × 20 μm, with rather thin, radiate trigones and ca. 2 intermediate thickenings; oil bodies 2-5 per cell, coarsely segmented, *Calypogeia*-type. Lobule inflated, narrow rectangular, up to 2/5× lobe length, the apex truncate with one distinct, 2-3 cells long tooth, the hyaline papilla on the inner surface of the lobule below the tooth.

Underleaves imbricated, 4-5× stem width, suborbicular to reniform, the apex and margins undulate-crispate.

Dioicous. Androecium terminal or intercalary, the bracts in 5-12 series, diandrous? Gynoecium with one innovation of the *Radula-Jubula* type; bracts oblong, up to 1 mm long, the apex narrowed obtuse, the lobule shorter, acuminate-lanceolate; bracteole ovate-oblong, up to 0,9 mm long, short bifid, the incision up to 75 μm deep; perianth emerged, with 5 keels as in *A. porelloides*, the keels irregularly subdentate.

DISTRIBUTION AND ECOLOGY: Brazil, Venezuela, Colombia, Ecuador, Peru; 0-500 m. Restricted to moist or mesic lowland forests of inner Amazonia, on truncs of living trees. Mainly collected along the Rio Negro and near the roots of the Andes.

Archilejeunea crispistipula is the tiniest species of the subgenus *Archilejeunea* and usually more yellowish and fragile than *A. juliformis*. Dry stems easily break into small fragments. Underleaf margins are undulate, while leaf margins may be undulate or plane. The species is much more restricted in its occurrence than *A. juliformis* and apparently less drought-tolerant.

Specimens examined (*A. crispistipula*): BRAZIL: *Pará*, Rio Trombetas, Prance et al. 22187, V.1974 (NY), U); *Amazonas*, Manaus, Ponta Negra, Prance et al. 11700 & 11712 (NY, U); Manaus-Itacoatiara, Ducke forest reserve, Griffin et al. 328 & 349, VII.1974 (FLAS, U); Manaus-Caracarai km 60, Campina forest, Griffin et al. 584 & 971, VIII.1974 (FLAS, U); ibid. km 115, Rio Urubu, Griffin et al. 843, 848, 854 & 901, VII. 1974 (FLAS, U); ibid. km 125, Berg et al. P19483, XI. 1973 (NY, U); ibid. km 130, Rio Lages, Griffin et al. 451, VII.1974 (FLAS, U); Rio Negro, Tapuraquara, road to airport, Prance et al. 15292 (NY, U); Uanauaca, Spruce s.n., type (MANCH); Rio Negro, Panuré, Spruce s.n., several colls. (MANCH); *Acre*, Cruzeiro do Sul, Astrada Alemanha, Prance et al. 11860, IV.1971 (NY,U). VENEZUELA: Upper Orinoco, Punta Pato, Isla Temblador, Mägdefrau 154a, I.1958 (hb. Mägdefrau, U); San Carlos de Rio Negro, Spruce s.n., several colls. (MANCH). COLOMBIA: Rio Apoporis, Cachivera de Jirijirimo, Schultes & Cabrera 42046, III.1951 (FLAS, U). ECUADOR: Mt. Guayrapurina, Spruce s.n. (MANCH). PERU: Yurimaguas-Tarapoto km 56, Frahm et al. 1332 & 1984 (BRYOTROP), IX.1982 (B, U); ibid. km 95, Frahm et al. 1466, IX. 1982 (B, U).

ARCHILEJEUNEA subgenus **Dibrachiella** (Spruce) Schiffn.

Engler & Prantl, Nat. Pfl.-fam. 1,3: 130 (1893).

Lejeunea subg. *Archilejeunea* Spruce sect. *Dibrachiella* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 90 (1884).

Lectotype (nov): *Lejeunea florentissima* Spruce (= *Archilejeunea parviflora* (Nees) Gradst. var. *florentissima* (Spruce) Gradst. & Buskes). This species is chosen as the lectotype because it is the one described by Spruce in greatest detail.

Heterotypic synonym:

Mastigolejeunea sect. Paradoxae Verd., Ann. Bryol. Beih. 4: 118 (1934) syn. nov.

Type: *Mastigolejeunea paradoxa* Verd., Nova Hedwigia XVIII, Bot. I: 5, 1934 (New Guinea, West Irian, "Prauwenbivak, 90 m, auf *Uvaria*", Lam 1182a, FH holotype) = *Archilejeunea mariana* (Gott.) Steph.

The subgenus *Dibrachiella* as delimited here is represented in tropical America by one single variable species, *Archilejeunea parviflora* (Nees) Gradst., with *A. cruegeri, A. viridissima, A. leprieurii, A. florentissima* and *A. auberiana* as synonyms; the latter two constitute the var. *florentissima*. These species were already placed in this subgenus by Spruce (1884) and Evans (1908), but our definition of the subgenus (and of its species) is different from that of previous authors.

According to Spruce the subgenus *Dibrachiella* was essentially characterised by the presence of two instead of one innovation and the smooth instead of rough perianth. None of these characters appear constant, however, as for instance paired innovations are also found in *A. porelloides* and smooth or rough perianths may be found both in *A. juliformis* and *A. parviflora*. However, we found that the presence of *Radula-Lejeunea* type innovations (instead of *Radula-Jubula* type), the pronounced tendency for the lobule to become reduced, and the lack of glossy brownish pigmentation as well as the autoicous inflorescence are excellent characters by which *A. parviflora* (and the subgenus *Dibrachiella, A. olivacea* excepted) is readily distinguished from the other neotropical members of the genus. The sporophyte in *A. parviflora*, however, is similar to that in the subg. *Archilejeunea* (Fig. 4).

Thus delimited, it appears that palaeotropic species of *Archilejeunea*, including the common Asiatic *A. mariana* (Gott.) Steph. placed by some authors in *Spruceanthus**, belong in the subgenus *Dibrachiella*. In fact, judging from their descriptions (Vanden Berghen 1951, Udar & Awashti 1981, 1982) the African and Asiatic species seem very similar or identical to *A. parviflora* s.l. and a detailed taxonomic study into their status should be rewarding. The only palaeotropic species known to us that remains very distinct is *Archilejeunea olivacea* (Hook. & Tayl.) Steph. from the North Island of New Zealand. Through the courtesy of Dr. John Braggins, University of Auckland, we have been able to examine fresh material of *A. olivacea* from the surroundings of Auckland (Waitakere Range, Spraggs bush, Braggins s.n., three colls., 3.VIII.1983), and a slide taken by Dr. Braggins from fresh oil bodies. The oil bodies appear to be ca. 10-20 per cell, subglobose, coarsely segmented, of the *Calypogeia*-type, upon degeneration becoming ± homogeneous before falling apart. The plants have *Radula-Lejeunea* type innovations as is typical for the sub-

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*Udar & Awashti (1981, 1982) and Crandall-Stotler & Geissler (1983) have shown that material identified as *A. mariana* has segmented oil bodies; the species should therefore remain in *Archilejeunea* and not be placed in *Spruceanthus*. *A. mariana* is close to *A. parviflora*, but differs by the tendency of the leaves and bracts to become acute and denticulate-crispate. *Spruceanthus polymorphus* (Sande Lac.) Verd. may be a synonym of *A. mariana*.

genus and a large, suborbicular lobule which, when well-developed, has two spinose teeth, but shows a strong tendency for reduction. The leaf apex in *A. olivacea* is rounded or acuminate, often within one single specimen; plants with acuminate leaves have sometimes been named *Archilejeunea scutellata* (Hook. & Tayl.) Steph. which is a synonym of *A. olivacea**. *Archilejeunea olivacea* is the only genuine dioicous species of the subg. *Dibrachiella* known to us; its lobule characteristics and its dull green colour (when fresh) would also help to distinguish it readily from other species of the genus.

4. **Archilejeunea parviflora** (Nees) Schiffn. Fig. 3

A polymorphic species represented in tropical America by two distinct varieties, which in the past have usually been taken as separate species.

4a. **A. parviflora** (Nees) Schiffn. var. **parviflora**

Hedwigia 33: 181 (1894); *Jungermannia parviflora* Nees, in Martius, Fl. Bras. 1, 1: 353 (1833).

Type: Brazil, "Fl. Amaz.", Maritus s.n. (STR holo, W hb. Lindenberg 6156, G20381).

Heterotypic synonyms:

Archilejeunea cruegeri (Lindenb.) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1,3: 130 (1893) syn. nov. *Lejeunea cruegeri* Lindenb., Syn. Hep.: 319 (1845).

Type: Trinidad, Crüger s.n. (W hb. Lindenberg 6157 holo, G 20378).

Archilejeunea leprieurii (Mont.) Schiffn., in Engler & Prantl. Nat. Pfl.-fam. 1,3: 130 (1893) syn. nov. *Lejeunea leprieurii* Mont., Ann. Sci. Nat. Paris sér. 2,3: 213 (1835).

Type: French Guiana, Leprieur s.n. (PC-Mont. holo).

**Archilejeunea olivacea* (Hook. f. & Tayl.) Steph., Bot. Jahrb. Syst. 23: 314 (1886). *Jungermannia olivacea* Hook. f. & Tayl., London J. Bot. 3: 568 (1844). Type: New Zealand, Colenso s.n., (FH-Tayl. holo; isotype (?) ex hb. Taylor in MANCH).

Archilejeunea scutellata (Tayl.) Steph., Spec. Hep. 4: 735 (1911). syn. nov. *Thysananthus scutellatus* Tayl., London J. Bot. 5: 383 (1846). Type: New Zealand, A. Cunningham s.n., ex hb. Hewitt Watson, II.1844 (FH-Tayl. holo; isotype (?) ex hb. Carrington in MANCH).

The lobule in the holotype specimen of *A. scutellata* is somewhat smaller than in the type of *A. olivacea*, with shorter teeth, but otherwise the two species are quite identical. A second specimen of *A. scutellata* in FH, glued on the holotype sheeth ("Bay of Islands, Dr. Sinclair"), also belongs in *A. olivacea*. However, a specimen in BM labelled "A. Cunningham, New Zealand, hb. Stephani" belongs to *Thysananthus anguiformis*. We have also examined other material in BM identified as *A. scutellata* and found that it belonged to at least four different genera: *Thysananthus anguiformis*, *Mastigolejeunea* sp., *Archilejeunea* (probably *A. mariana*) and even *Strepsilejeunea* sp. (collections made by Hodgson and by Allison).

Archilejeunea parviloba Steph., Spec. Hep. 4: 717 (1911) syn. nov.

Type: French Guiana, Leprieur s.n., ex hb. Jack (G 20792 holo).

Archilejeunea viridissima (Lindenb.) Evans, Bull. Torrey Bot. Club 35: 169 (1908) syn. nov. *Lejeunea viridissima* Lindenb., Syn. Hep.: 320 (1844).

Type: Venezuela, Caracas, ex hb. Hampe (W hb. Lindenberg 6164 holo).

Plants creeping, more rarely (fertile plants) ascending to subpendulous, small to medium-sized, 1,5-4 cm long and 1-2 mm wide, pale yellowish green to brownish green, the older parts turning darker, sometimes blackish but never golden or reddish brown as in subg. *Archilejeunea,* irregularly pinnate with *Lejeunea*-type branches. Stem in cross-section with 12-18 cortical cells surrounding 14-22 ± similar medullary cells; ventral merophyte 4-6 cells wide.

Leaf lobes ovate-suborbicular, 0,7-1 × 0,5-0,7 mm, at opposite sides of the stem sometimes of different sizes (as in *Symbiezidium*), the apex rounded to obtuse, the margins entire, plane or occasionally somewhat incurved, the ventral margin ± straight; cells ca. 15-25 µm in diam., with triradiate, often subconfluent trigones and 0-3 intermediate thickenings (at most 1 per cell wall); oil bodies ± finely segmented, *Calypogeia* or *Jungermannia* type (?), 3-8 per cell mid-leaf, more numerous towards leaf base (up to 12), bluntly ellipsoid, 4-10 × 4-5 µm, with 10-20 segments of about 1 µm in diam., the segments coalescing upon aging of the oil body and the oil body becoming almost homogeneous before desintegration.

Lobule variable in size, often reduced, when well developed ovate, up to 1/3× lobe length, the apex oblique, gradually continuing into the ventral margin of the lobe, without or with a short tooth, 1-2 cells long; hyaline papilla marginal.

Underleaves spatiated to barely overlapping, when spatiated subsquarrose and small, up to 2× stem width, orbicular, when overlapping larger, wider than long, up to 3,5× stem with, the apex and margins rounded, entire, plane, the line of insertion almost straight.

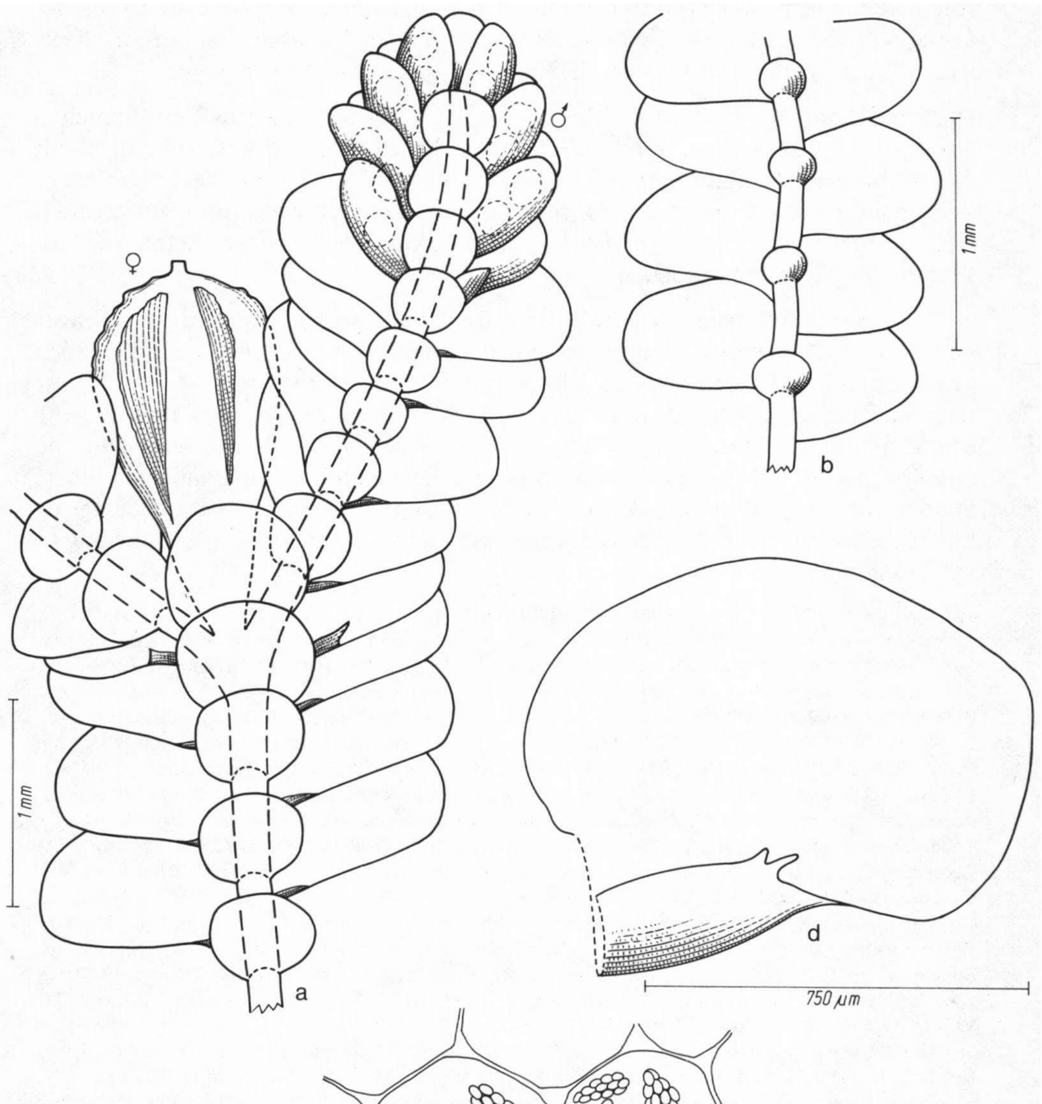
Monoicous, usually fertile; androecia usually terminal on branches close to the gynoecium, the male bracts smaller than the vegetative leaves, in 3-10 series, the lobules becoming as large as the lobe, hypostatic, diandrous.

Gynoecium often in seriate arrangement with paired innovations below (or lacking) and repeatedly fertile single innovations above, the innovations always of the *Radula-Lejeunea* type; bracts about as large as leaves, rounded at apex, the lobule variable, up to 2/3× lobe length but often reduced, ovate-lanceolate with

Fig. 3. *Archilejeunea parviflora* (Nees) Schiffn. var. *parviflora* and var. *florentissima* (Spruce) Gradst. & Buskes.

a-c. var. *parviflora*. a. habitus, lobule present. b. ibid., lobule reduced. c. median leaf cells, with oil bodies. d. leaf of var. *florentissima*, with well-developed lobule.

a from Vital 6688. b. from the type of *A. cruegeri* Lindenb. c from Bekker 1671. d from the lectotype.


♀
♂
a
b
c
d
1 mm
1 mm
750 µm
40 µm

obtuse to acuminate apex; bracteole ovate-oblong to suborbicular, the apex rounded or very short bifid; perianth hardly emerged, obovate-cylindrical, 4-5 keeled with 2 lateral, 2 ventral (always) and sometimes 1 weak dorsal keel, the keels smooth to irregularly denticulate. Sporophyte: as in subg. *Archilejeunea.*

DISTRIBUTION AND ECOLOGY: Mexico, Cuba, Bahamas, Puerto Rico, Jamaica, Trinidad, French Guiana, Suriname, Guyana, Brazil, Venezuela, Colombia, Peru; 0-1500 m. Scattered throughout tropical America but almost lacking in inner Amazonia. In moist lowland rainforests and riparian woodlands on trunks, rotten logs and rocks, rarely on twigs (there replaced by var. *florentissima*), in the Andes in submontane forest up to 1500 m.

Plants without lobules and with tiny, orbicular, widely spatiated underleaves belong here. They may be found creeping over rock or bark in very humid, shaded localities and probably represent a hygromorphic form of the species, which may turn blackish when dry. In other localities lobules may develop, reaching 1/3 the length of the lobe and being ovate in outline, with a very oblique apex and one obscure tooth. Underleaves become somewhat larger and may overlap each other. Shoots with and without lobules may be found on the same plant but the degree of lobule reduction varies. Plants with large, rectangular lobules with 2 teeth belong to var. *florentissima.*

Specimens examined (var. *parviflora*): MEXICO: Veracruz, near biological station 33 km NE of Catemaco, den Held & van Rijn HH17, IV.1973 (U); Cerro de San Gabriel, Santos 3902, XII.1944 (hb. Fulford). CUBA: Guantanamo, La Prenda, Hioram 5113, XII.1921 (HAC, YU); Rangel, Taco-Taco, Pinar del Rio, Acuña 66 & 99, I.1935 (HAC, YU); Sierra del Rosario, NE del Est. For. Las Terrazas, Pócs & Reyes 9042 AT, X.1978 (HAC, U). BAHAMAS: Eight Mile Rocks, Britton & Millspauch 2605, II.1905 (YU). PUERTO RICO: El Yunque, Evans 140, VII.1902 (YU). JAMAICA: Union Hill, E.G. Britton 824, III-IV.1908 (YU). TRINIDAD: Crüger s.n., type of *Lejeunea cruegeri* Lindenb. (W, G). FRENCH GUIANA: Leprieur s.n., type of *Lejeunea leprieurii* Mont. (PC-Mont., G); ibid., type of *A. parviloba* Steph. (G). SURINAME: sine loc., Curie s.n., 1835, sub *Phragmicoma curiaei* (PC-Mont.); Kabalebo area km 212, Bekker 1583, 1621b, 1644, 1671 & 1680, IX.1981 (BBS, U). GUYANA: Georgetown, Quelch s.n., hb. Levier 247 (U); Bartica, First Falls, Richards 366b (YU); Cuyuni River, Camaria Falls, Richards 846 (YU). BRAZIL: "Fl. Amaz.", Martius s.n., type (STR, G, W); *Pará*, Obidos, Spruce s.n. (MANCH, YU); Casiquiare, Spruce s.n. (MANCH, YU); *Amazonas*, Manaus, Rio Negro, Spruce s.n. (YU); *Roraima*, Manaus-Venezuela highway km 517, S. of Igarapé Dias, Buck et al. 1915, XI.1977 (NY, U); *Sao Paulo State*, Conceiçao de Itanhaëm, Rio Mambu, Schiffner s.n., 1901 (W); Cananeia, Casca I., Vital 6688 & 6689, XI.1976 (SP, U); Cardoso I., Yano 451, VIII.1976 (SP, U); Barro do Turvo, Vital 2790a, xii.1973 (SP, U). VENEZUELA: Caracas, type of *Archilejeunea viridissima* (Lindenb.) Evans (W); Upper Orinoco, Isla Cangrejo, Mägdefrau 161, I.1958 (hb. Mägdefrau, U). COLOMBIA: Risaralda, Marsella, Gradstein 3607, VIII.1980, as *Archilejeunea viridissima* (COL, U). PERU: Loreto, Pucallpa to Lima 80 km., Spichiger s.n., V.1980 (G); San Martin, Yurimaguas to Tarapoto 112 km., Frahm et al. (Bryotrop exp.) 1791, IX.1982 (B, U).

4b. **A. parviflora** var. **florentissima** (Spruce) comb. nov.

Lejeunea florentissima Spruce var. *monotropa* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 95 (1884) = var. *florentissima* ICBN art. 26. *Archilejeunea florentissima* (Spruce) Herz., Rev. Bryol. Lichénol. 20: 130 (1951).

Lectotype: Peru, Tarapoto, "in fruticum ramulis secus rivulum Inarona-yacu c. fr.", Spruce L152 (MANCH 15200).

Heterotypic synonyms:

Lejeunea florentissima Spruce var. *calliandra* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 96 (1884) syn. nov.

Type: Ecuador, "prope Guayaquil", Spruce s.n., III. 1861 (MANCH 15199).

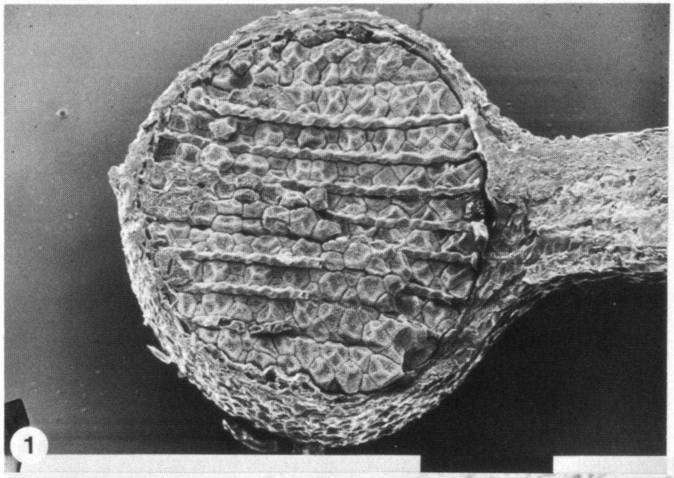
Lejeunea auberiana Mont., in de la Sagra, Hist. Phys. Nat. Cuba Bot. Pl. Cell.: 483 (1842). *Archilejeunea auberiana* (Mont.) Evans, Bull. Torrey Bot. Club 35: 168 (1908).

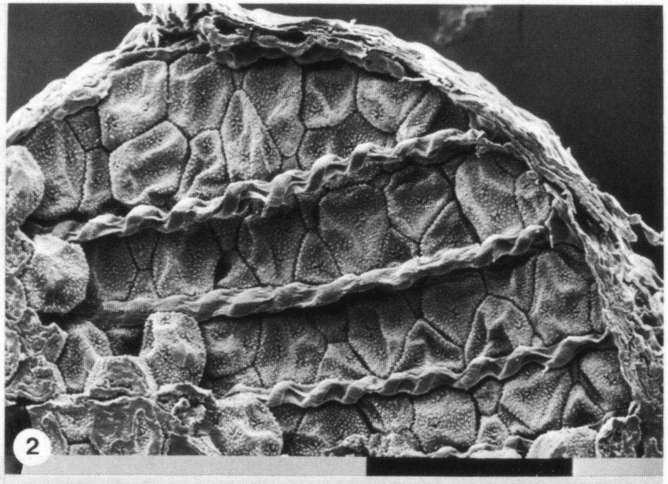
Type: Cuba, "ad ramos ramulosque dejectos...", Auber s.n. (PC-Mont., YU).

Plants usually copiously fertile, ascending to subpendulous, glossy green to greenish brown. Leaves with curved ventral margin and lobules well-developed or, in part, reduced to a small fold; well-developed lobules ca. 1/3-1/2 × lobe length, rectangular, the free margin ± incurved, the apex oblique to subtruncate, with 2 teeth separated by a narrow sinus, the first tooth 2-5 cells long and 2 cells wide at base, the second tooth usually shorter (in the type of *L. auberiana* as large as the first tooth), the teeth erect or curved outwards; hyaline papilla marginal, situated in the sinus between the two teeth. Some shoots with lobules smaller or reduced as in var. *parviflora*. Underleaves spatiated or imbricated, orbicular to reniform, 3-4,5 × stem width, plane. Otherwise as var. *parviflora*.

DISTRIBUTION AND ECOLOGY: Nicaragua, Cuba, Trinidad, Brazil, Colombia, Ecuador, Peru, Bolivia; 0-1000 m. Also reported from Honduras (Herzog 1951). *A. parviflora* var. *florentissima* has the same general distribution in tropical America as *A. parviflora* but has been collected less often. It is usually ramicolous but may also occur on larger branches or truncs; it has furthermore been recorded from living leaves. Records are from moist lowland and submontane forests and from along rivers.

The ramicolous, subpendulous habit and the large, rectangular lobule with 2 teeth are characteristic for this variety, but these features are not constant and creeping forms with smaller lobules may be found which become almost inseparable from var. *parviflora*. Lobule reduction is less extreme in var. *florentissima* than in var. *parviflora*, though. Although var. *florentissima* grows with the typical variety in moist forests and near rivers, we believe that this plant is probably less hygrophytic than the typical variety, which would account for the better development of watersacs (lobules) in var. *florentissima*. Watersac reduction has often been interpreted as a morphological adaptation to hygric environments, but in *Archilejeunea* this reduction is at least in part genotypic as it occurs to varying degrees in subg. *Dibrachiella* but lacks in the species of the other subgenus. The lack of lobule reduction in subg. *Archilejeunea* can so far not be ascribed to a difference in ecology since species of subg. *Archilejeunea* (*A. juliformis* from Suriname and *A. crispistipula* from Peru) have been collected in the same locality as *A. parviflora*,


1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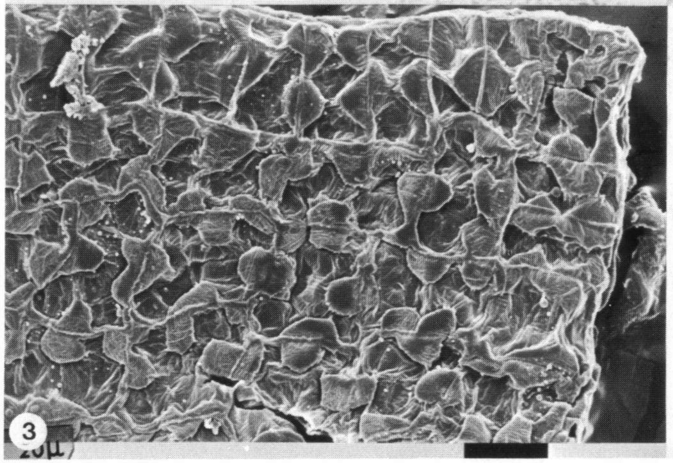
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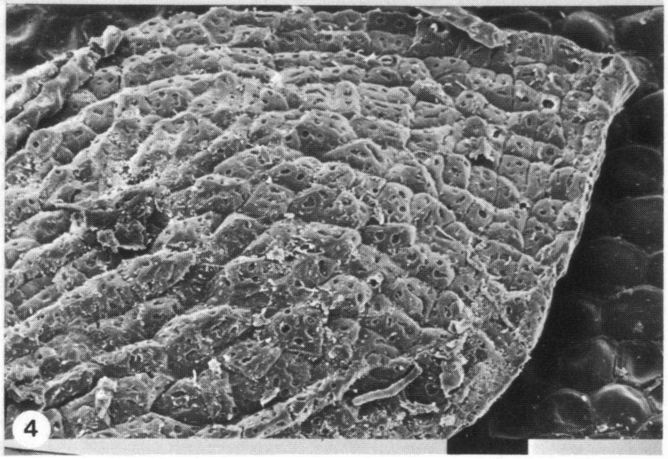
4

yet, admittedly, never mixed. It would be tempting to test the capacity for watersac reduction by transplantation or cultivation experiments; such information is as yet entirely lacking.

Note: The syntype materials of *A. florentissima* in the Spruce herbarium have bidentate lobules as in *A. auberiana*, but the teeth in *A. florentissima* are less pronounced, especially in the var. *calliandra* Spruce, which approaches *A. parviflora* in this respect. Stephani (1911) and Schuster (1980) treated *A. florentissima* as a synonym of *Leucolejeunea unciloba* (Lindenb.). Evans, but we found no material of the latter species among the syntypes of *A. florentissima.*

Specimens examined (var. *florentissima*): NICARAGUA: Escondido river, unknown collector, X.1982 (YU); CUBA: de la Sagra s.n. (PC-Mont.); Auber s.n., type of *Lejeunea auberiana* Mont. (PC-Mont., YU); Matanzas, hills of El Grillo, Britton et al. 793, III.1903 (YU); Retiro, Wright s.n. (YU); El Yunque, Underwood & Earle 1484, XI.1903 (YU); Guantanamo, Baracoa, Pócs & Reyes 9063/AJ (HAC, U). TRINIDAD: Thaxter s.n. (hb. Fulford). BRAZIL: *Pará*, Caripi, "in arborum ramulis", Spruce s.n., paratype of *Lejeunea florentissima* Spruce (MANCH, W, YU); highway Altamira-Itaituba, branch road N off km 20, Prance et al. 24718a, X.1977 (NY, U); *Sao Paulo State*, Barro do Turvo, Vital 2791e, XII.1973 (SP, U); *Rio Grande do Sul*, Parque Flor. do Turvo, Lindeman 6593, XI.1971 (ICN, U). COLOMBIA: Chocó, road Quibdo-Tutunendo, Bischler 177, IV.1957 (COL, PC, U). ECUADOR: Guayaquil, Daule, Spruce s.n., III.1861, type of *Lejeunea florentissima* var. *calliandra* Spruce (MANCH). PERU: San Martin, Tarapoto, Spruce L152, lectotype of *Lejeunea florentissima* Spruce (MANCH); road Yurimaguas-Tarapoto km 112, Frahm et al. 2133 (BRYOTROP), IX.1982 (B, U). BOLIVIA: Beni, Rio Mamore, N. of Guayaramerin, Reese 13115, II.1978 (NY, U).

Excludenda

1. *Archilejeunea clypeata* (Schwein.) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1, 3: 130 (1893).

=*Leucolejeunea clypeata* (Schwein.) Evans, Torreya 7: 227 (1907); Schuster (1980: 820).

2. *Archilejeunea cognata* (Nees) Steph., Spec. Hep. 4: 711 (1911). *Jungermannia cognata* Nees, in Martius, Fl. Bras. 1, 1: 353 (1833). Type: Brazil, Prov. Bahia, Martius s.n. (STR holo) syn. nov.

=*Anoplolejeunea conferta* (Meissn.) Evans, Bull. Torrey Bot. Club 35: 175 (1908).

Fig. 4. SEM analysis of the sporophyte of *Archilejeunea* (Spruce) Schiffn.

1. Capsule length section, showing spore storage *in situ* (bar = 200 μm). 2. Capsule length section, showing elater arrangement and spore storage (bar = 100 μm). 3. Capsule valve outer surface, showing nodular thickenings (bar = 20 μm). 4. Capsule valve inner surface, showing plurifenestrate thickenings (bar = 40 μm). 1 from Child 2202, N. Zealand. 2 from Vital 6688, Brazil. 3-4 from Griffin et al. 418, Brazil.

1 = *A. olivacea* (Hook. & Tayl.) Steph. 2 = *A. parviflora* (Nees) Steph. 3-4 = *A. porelloides* (Spruce) Schiffn.

The original material of *Jungermannia cognata* Nees (STR) consists of two different elements: *Leucolejeunea unciloba* (Lindenb.) Evans (three sterile fragments) and *Anoplolejeunea conferta* (one sterile fragment). Duplicate material in G (hb. Stephani) contains only *Leucolejeunea unciloba*; this plant is depicted by Stephani in his Icones Ined. According to Stephani (1890) there should be another fragment of the *Leucolejeunea unciloba* element in the Lindenberg herbarium (W) which we did not see.

Later descriptions of *Archilejeunea cognata* are evidently based on either the *Anoplolejeunea* element (cf. Nees & Montagne 1836) or the *Leucolejeunea* element (cf. Syn. Hep.; Spec. Hep.). Since the original description was short and vague and, moreover, based on *fertile* specimens with ciliate-dentate perianths ("calycibus... ciliato-dentatis") — while perianths in *Leucolejeunea unciloba* and *Anoplolejeunea conferta* are quite smooth — a satisfactory choice, which agrees with the protologue, cannot be made among the available (sterile) elements. Until an authentic *fertile* specimen is discovered the name might best be interpreted as a synonym of *Anoplolejeunea conferta,* following the earliest interpretation (by Nees & Montagne 1836).

3. *Archilejeunea conduplicata* Steph., Spec. Hep. 4: 712 (1911). Type: Suriname, hb. Flotow 112 (G holo) syn. nov.
=*Dicranolejeunea phyllorhiza* (Nees) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1,3: 128 (1893).

4. *Archilejeunea conchifolia* Evans, Mem. Torrey Bot. Club 8: 128 (1902).
Leucolejeunea conchifolia (Evans) Evans, Torreya 7: 229 (1907); Schuster (1980: 837).

5. *Archilejeunea conferta* (Meissn.) Schiffn., Consp. Hep. Arch. Ind.: 315 (1898).
=*Anoplolejeunea conferta* (Meissn.) Evans, Bull. Torrey Bot. Club 35: 175 (1908).

6. *Archilejeunea cyclostipa* (Tayl.) Steph. ex Bonner, Index Hep. 2: 261 (1962). *Phragmicoma cyclostipa* Tayl., London J. Bot. 3: 387 (1846). Type: Brazil, Pará, "Cincinnati, Hook 1443, Para, on trunc", ex hb. Taylor (MANCH iso); ibid., ex hb. Austin (MANCH iso); ibid., ex hb. Carrington (MANCH iso) syn. nov.
=*Lopholejeunea subfusca* (Nees) Schiffn., Bot. Jahrb. Syst. 23: 593 (1897).

Phragmicoma cyclostipa Tayl. was reduced under *Archilejeunea auberiana* (Mont.) Steph. by Stephani (1890: 15; 1911: 710) but the copious, fertile isotype materials in MANCH belong to *Lopholejeunea subfusca.* Furthermore, the original description points at *Lopholejeunea* rather than *Archilejeunea.*

7. *Archilejeunea fuegiana* (Besch. et Mass.) Steph., Spec. Hep. 4: 714 (1911). *Lejeunea fuegiana* Besch. et Mass., Bull. Mens. Soc. Linn. Paris 79: 638 (1886). Syntype: Tierra del Fuego, Cape Horn, "in cort. cum *Frullaniis*", J.D. Hooker s.n. (MANCH iso)
=*Blepharolejeunea fuegiana* (Besch. et Mass.) Gradst. comb. nov.

The disjunct occurrence of the neotropical-montane genus *Blepharolejeunea* (van Slageren & Kruijt, this volume) in Tierra del Fuego is remarkable, yet fits the distribution pattern of some other montane neotropical bryophytes (Griffin et al. 1981).

8. *Archilejeunea germana* Steph., Spec. Hep. 4: 714 (1911). Type: Brazil, St. Catharina, "inter Ule 71" (G holo)
= *Leucolejeunea* cf. *unciloba* (Lindenb.) Evans.

The type specimen consists of a mere stem fragment of ca. 15 leaf pairs, which may represent a young plantlet of *Leucolejeunea unciloba*. The lobules are remarkably large, about 2/3 × leaf length, with a bluntish apex. The ventral margin of the lobe is concave, yet not incurved as in *L. xanthocarpa*.

9. *Archilejeunea herminieri* Steph., Spec. Hep. 4: 714 (1911). Type: Guadeloupe, Herminier s.n. (G 20789 holo)
= *Amblyolejeunea* ?

The type specimen examined consists of sterile, partly etiolated stem fragments. The ventral merophyte is 2 cells wide and the underleaves are undivided. The lobule shape and the moderately robust size of the plant suggest *Amblyolejeunea fulfordiae* Jov.-Ast.

10. *Archilejeunea huanucensis* (Gott.) Steph., Spec. Hep. 4: 715 (1911). *Lejeunea huanucensis* Gott., Syn. Hep.: 235 (1845). Type (?), "In cort. chinae, Gottsche dedit 1885" (G)
= *Omphalanthus huanucensis* (Gott.) Gradst. comb. nov.

Close to *Omphalanthus filiformis*, but differing in the widely recurved leaf and underleaf apices and the free margin of the lobule, which is inrolled near the base. The trigones are relatively small and the leaf cells are somewhat elongated.

11. *Archilejeunea involuta* Steph., Biblioth. Bot. 87: 248 (1916). Type: Bolivia, Comarapa, Herzog 4289 (G holo) syn. nov.
= *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans, Torreya 7: 229 (1907); Schuster (1980: 841).

12. *Archilejeunea magellanica* Steph., Spec. Hep. 4: 716 (1911). Type: Tierra del Fuego, Borje Bay, Vanadis Exped., ex hb. Uppsala 333 (G 20790 holo) syn. nov.
= *Blepharolejeunea fuegiana* (Besch. et Mass.) Gradst. (see sub *Archilej. fuegiana*).

The leaves and lobule teeth are slightly sharper pointed in this specimen and the leaf cells somewhat larger and the trigones smaller as compared with the type specimen of *B. fuegiana*. Otherwise the two plants are identical.

13. *Archilejeunea negrensis* Steph., Spec. Hep. 4: 716 (1911). Type: Brazil, Manaos, Rio Negro, Spruce s.n. (G 20791 holo)
= ?

Probably not *Archilejeunea* but the specimen is too poor to permit proper identification.

14. *Archilejeunea pabstii* Steph., Hedwigia 34: 61 (1895). Type: St. Catharina, Pabst s.n. (G holo)
= *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans, Torrey 7: 229 (1907).

The synonymy was demonstrated also by Thiers, Brittonia 34: 294. 1982, based on isotype material.

15. *Archilejeunea polyphylla* (Tayl.) Steph., Spec. Hep. 4: 717 (1911)
= *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. I, 3: 128 (1893); Gradstein (1975: 63).

16. *Archilejeunea praetermissa* Steph., Spec. Hep. 4: 718 (1911). Type: Peru, ex hb. Meissner (G 20794) syn. nov.
= *Omphalanthus* cf. *filiformis* (Sw.) Nees

The plants are sterile.

17. *Archilejeunea pseudocucullata* Steph., Hedwigia 34: 61 (1895)
= *Cyrtolejeunea holostipa* (Spruce) Evans, Bull. Torrey Bot. Club 30: 553 (1903).

18. *Archilejeunea saccatiloba* Steph., Hedwigia 34: 61 (1895). Type: Brazil, sine loc., Beyrich s.n. (G 20795 holo)
= *Cyrtolejeunea saccatiloba* (Steph.) Gradst. comb. nov.

Similar to *Cyrtolejeunea antillana* Schust. (Schuster 1970), but lobule more rounded at apex, without distinct apical tooth (with one bluntish, projecting cell only).

19. *Archilejeunea sellowiana* Steph., Hedwigia 34: 62 (1895). *Leucolejeunea sellowiana* (Steph.) Steph., Spec. Hep. 4: 737 (1912)
= *Leucolejeunea unciloba* (Lindenb.) Evans, Torreya 7: 228 (1907); Schuster (1980: 828).

20. *Archilejeunea subinermis* Steph., Spec. Hep. 4: 720 (1911). Type: Mexico, "inter Frullaniam" (G holo) syn. nov.
= *Cyrtolejeunea saccatiloba* (Steph.) Gradst. (see sub *Archilejeunea saccatiloba* Steph.).

The type consists of one small, fertile stem fragment.

21. *Archilejeunea tonduzana* Steph., Spec. Hep. 4: 721 (1911). Type: Costa Rica, "Forests du Rio Naranjo, 200-250 m, III.1893, Tonduz s.n." (G holo)
= *Omphalanthus* cf. *platycoleus* Herz.

A beautiful species resembling *O. platycoleus* by its bluntly 4-angled perianth but autoicous (*O. platycoleus* is said to be dioicous). Another relative is *O. wallisii* (Steph.) Gradst. which, however, has a sharply 5-angled perianth with longer rostrum and is also considered dioicous. This group of species needs further study (cf. Gradstein et al. 1981).

22. *Archilejeunea trigona* (Nees & Mont.) Steph., Spec. Hep. 4: 721 (1911). *Lejeunea trigona* Nees & Mont., Ann. Sci. Nat. Paris sér. 2, Bot. 5: 61 (1836). Type: Peru, d'Orbigny s.n. (STR holo)

= *Dicranolejeunea phyllorhiza* (Nees) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1,3: 128 (1893); synonymy *fide* Kruijt (this volume).

23. *Archilejeunea unciloba* (Lindenb.) Schiffn., in Engler & Prantl, Nat. Pfl.-fam. 1,3: 130 (1893). *Lejeunea unciloba* Lindenb., Syn. Hep.: 331 (1845). Type: Brazil, without collector (W hb. Lindenberg 6234 lectotype)

= *Leucolejeunea unciloba* (Lindenb.) Evans, Torreya 7: 228 (1907); Schuster (1980: 828).

24. *Archilejeunea xanthocarpa* (Lehm. & Lindenb.) Steph., in Engler, Die Pflanzenwelt Ostafrikas C: 65 (1895)

= *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans, Torreya 7: 229 (1907); Schuster (1980: 841).

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References

CRANDALL-STOTLER, B. & GEISSLER, P. 1983. Sporophyte development and structure in *Spruceanthus marianus* (Gott.) Mizut. Candollea 38: 105-124.

EVANS, A.W. 1907. *Leucolejeunea,* a new genus of Hepaticae. Torreya 7: 225-229.

EVANS, A.W. 1908. Hepaticae of Puerto Rico IX. *Brachiolejeunea, Ptychocoleus, Archilejeunea, Leucolejeunea* and *Anoplolejeunea.* Bull. Torrey Bot. Club 35: 155-179.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea.* Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. 1978. *Verdoornianthus,* a new genus from Amazonas, Brazil. Bryologist 80: 606-611.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

GRIFFIN, D., GRADSTEIN, S.R. & AGUIRRE, J. 1981. On a new antipodal element in the neotropical páramos - *Dendrocryphaea latifolia* sp. nov. (Musci). Acta Bot. Neerl. 31: 175-184.

GROLLE, R. 1983. Nomina Generica Hepaticarum: references, types and synonymies. Acta Bot. Fenn. 121: 1-62.

HERZOG, T. 1951. Hepaticae Standleyanae Costaricenses et Hondurenses II. Revue Bryol. Lichénol. 20: 126-175.

MIZUTANI, M. 1961. A revision of Japanese Lejeuneaceae. J. Hattori Bot. Lab. 24: 115-302.

NEES VON ESENBECK, C.G. & MONTAGNE, C. 1836. Jungermanniearum herbarii Montagnearum species. Ann. Sci. Nat. ser. 2, 5: 52-72.

SCHIFFNER, V. 1893. Hepaticae. In: A. Engler and K. Prantl (eds.), Natürliche Pflanzenfamilien 1,3: 3-141. Leipzig.

SCHUSTER, R.M. 1970. New Lejeuneaceae from Dominica and Jamaica. Bull. Torrey Bot. Club 97: 336-352.

SCHUSTER, R.M. 1980. The Hepaticae and Anthocerotae of North America Vol. IV. New York.

SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Jubuleae. Trans. Proc. Bot. Soc. Edinburgh 15: i-xi, 1-308.

STEPHANI, F. 1890. Die Gattung *Lejeunea* im Herbarium Lindenberg. Hedwigia 29: 1-23, 68-99, 133-142.

STEPHANI, F. 1911. *Archilejeunea*. Spec. Hep. 4: 703-736. Geneva.

UDAR, R. & AWASTHI, U.S. 1981. The genus *Archilejeunea* (Spruce) Schiffn. in India. Geophytology 11: 72-79.

UDAR, R. & AWASTHI, U.S. 1982. The status of *Spruceanthus marianus* (Gott.) Mizut. in India. J. Bryol. 12: 33-36.

VANDEN BERGHEN, C. 1951. Contribution à l'étude des espèces africaines du genre *Archilejeunea* (Spruce) Schiffn. Revue Bryol. Lichénol. 20: 112-121.

VERDOORN, F. 1934. Studien über Asiatische Jubuleae. Ann. Bryol. Suppl. 4: 40-192.

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5 | A Review of the Genus Blepharolejeunea S. Arn.

by

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ABSTRACT: The neotropical genus *Blepharolejeunea* S. Arn. emend. van Slag. & Kruijt is represented in Latin America by five species, one of which is newly described. The species are recognised by their leaf lobule, which has a rectangular free margin and possesses two dissimilar teeth: a rounded and inflexed apical tooth and a sharp and straight second tooth. In addition, the cells of leaves, underleaves, bracts and perianth vary from isodiametric with trigones simple triangular to elongated with trigones cordate. The species are *Blepharolejeunea chimantaensis* van Slag. & Kruijt sp. nov. from the tepuis of SE Venezuela, *B. fuegiana* (Besch. & Mass.) Gradst. from the cool regions of S. Chili, *B. incongrua* (Lindenb. & Gott.) van Slag. & Kruijt comb. nov. and *B. securifolia* (Steph.) Schust. from the high Andean forests and páramos, and *B. saccata* (Steph.) van Slag. & Kruijt comb. nov. from scattered localities in Central and Andean South America and of the West Indies. A sixth species *B. harlingii* S. Arn. (the generitype), is reduced to synonymy under *B. saccata*. Ecuador is the centre of diversity with three species present. In an evolutionary sense the genus is an advanced member of the subfam. Ptychanthoideae because of its Lejeuneoid, "nodular-type" sporophyte. A key and descriptions of the taxa are provided.

Introduction

The genus *Blepharolejeunea* was founded by S. Arnell in 1962 as a monotypic new genus, based on a small collection of a new species of Lejeuneaceae with strongly dentate-ciliate leaves from Ecuador, *B. harlingii* S. Arn. Schuster (1980a, 1980b) added *Brachiolejeunea securifolia* Steph. to the genus, based mainly on the leaf lobule structure, which differs from the genus *Brachiolejeunea* (subg. *Brachiolejeunea*) by the rectangulate angle between the edentate anterior lobule margin and the truncate sinus (1980b: 762). Schuster (1980a) created a new subgenus *Oreolejeunea* for *Blepharolejeunea securifolia* (Steph.) Schust., which was later that year elevated to generic level (Schuster 1980b), hence *Oreolejeunea securifolia* (Steph.) Schust. *Oreolejeunea* Schust. was based on a) the edentate female bract lobes, b) the suborbicular (?) female bracts that are rotundate in their distal part, c) the large trigones of the leaves and d) the "clear" male bracts (1980a: 424), all of them different from *B. harlingii* S. Arn. where obovate-triangular female bract lobes are present that are dentate in their apical region and where male bracts have not yet been found.

In the present paper, *Blepharolejeunea* is emended, based on the results of monographic studies of the genera *Brachiolejeunea* (van Slageren, in prep.) and *Dicranolejeunea* (Kruijt, this volume and in prep.). The *Brachiolejeunea* study revealed besides *B. securifolia* one further species, *B. nitidiuscula* (Gott.) Schiffn., with a similar lobule structure as in *Blepharolejeunea*. The revision of *Dicranolejeunea* revealed two such species: *D. incongrua* (Lindenb. & Gott.) Steph. (= *Brachiolejeunea nitidiuscula*) and *D. saccata* Steph. (= *Blepharolejeunea harlingii*). In addition, two further species proved to possess a similar leaf lobule: *Archilejeunea fuegiana* (Besch. & Mass.) Steph. (Gradstein & Buskes, this volume) and a newly discovered species from Venezuela, *Blepharolejeunea chimantaensis* van Slag. & Kruijt. *Blepharolejeunea* is related both to *Brachiolejeunea* and *Dicanolejeunea*. Differences are shown in Tab. 1.

The main characteristic features of the genus *Blepharolejeunea* are a) the outline and dentation of the leaf lobule and b) the variation of trigone shapes in the cells of the leaves, underleaves, bracts and perianth. The leaf lobule outline and dentation differs from *Brachiolejeunea* and *Dicranolejeunea* in the rectangular apex of the free margin and in the two dissimilar teeth: the apical tooth is rounded and strongly inflexed; the second tooth is located on the rectangular apex of the lobule and consists of a straight (to weakly curved) and sharp point and is never inflexed (e.g. Figs. 2.4, 6.5). Moreover, areolation in all species of *Blepharolejeunea* varies from cells elongated with cordate trigones to cells isodiametric with simple triangular trigones, a feature that is also observed in *Dicranolejeunea* (Kruijt, in prep.). With the removal of *B. securifolia* and *B. nitidiuscula, Brachiolejeunea* subg. *Brachiolejeunea* possesses now only species with clearly cordate trigones and elongated leaf cells and is thus more accurately delimited.

Other interesting features that may be briefly discussed here are the anatomy of the underleaf base, the branching type and the sporophyte morphology.

The anatomy of the underleaf base in Ptychanthoideae was studied for the first time by means of length sectioning by Winkler (1970), who showed the presence of a bistratose and a tristratose condition in different genera. Winkler (1970) and Gradstein (1979) suggested that the two types could serve as a taxonomic character at the generic level, but van Slageren (1984) showed the bistratose as well as the tristatose condition to be present in *Brachiolejeunea* subg. *Brachiolejeunea* (at that time still comprising *B. nitidiuscula* and *B. securifolia*). In our opinion the anatomy of the underleaf base may very well present generic characters, even in a quantitative way (compare the different tristratose attachments of *Odontolejeunea* and *Symbiezidium,* Winkler 1970).

It breaks down, however, in *Blepharolejeunea,* which has a tristratose type of underleaf attachment in *B. fuegiana* and *B. saccata* (Figs. 6, 10) and bistratose in *B. incongrua* and *B. chimantaensis* (Figs. 4, 7). *B. securifolia* is most remarkable in this respect by its possession of both the bi- and tristratose attachment (Fig. 3); the bistratose attachment may be short, 40-70 μm, as in *B. incongrua,* or elongated, 90-190 μm, with additional cells between the superior central cell and the lowermost underleaf lamina cell. Accordingly, the length of the underleaf attachment in *B.*

Table 1. A comparison of *Blepharolejeunea*, *Brachiolejeunea* subg. *Brachiolejeunea* and *Dicranolejeunea*

genus character	*Brachiolejeunea* subg. *Brachiolejeunea*	*Blepharolejeunea*	*Dicranolejeunea*
stem anatomy	dorsal cortical cells higher than ventral cortical cells	dorsal cortical cells equally high as ventral cortical cells	dorsal cortical cells smaller or equal in heigth to ventral cortical cells
paraphyllia	lamellate on dorsal stem (weak in *B. spruceana*)	lacking	lacking
leaf cells	elongated with cordate trigones	elongated with trigones cordate to isodiametric with trigones simple triangular	elongated with trigones cordate to isodiametric with trigones simple triangular
oil bodies	homogeneous, *Massula*-type	homogeneous, *Massula*-type	segmented, *Jungermannia*-type (or homogeneous *Massula*-type?)
leaf lobule	not reducing	not reducing	reducing
leaf lobule free margin	weakly curved, no sharp angle	rectangular with sharp angle at 2nd tooth (90-130°)	curved with variable angle at 1st tooth (130-150°), except in strongly reduced lobules
leaf lobule teeth	(2-)3(-4) similar, inflexed teeth	dissimilar: first (apical) tooth blunt, inflexed, 2nd tooth straight and sharp	2(-3) similar, inflexed teeth (but 1st tooth sometimes larger)
underleaf	apical margin recurved, lateral margins incurved	plane	margins narrowly recurved or plane
underleaf - base anatomy	tri-stratose	bi- or tri-stratose (in *B. securifolia* bi- *and* tri-stratose	tri-stratose
male bract lobe	not reduced in size when compared with leaves	not reduced in size when compared with leaves	strongly reduced in size
innovation-type	2 *Radula-Jubula*-type	2 *Radula-Jubula*-type	1-2 *Radula-Jubula*-type
perianth plicae	3 smooth and rounded	3-5 smooth-rounded or dentate-ciliate	3-5 dentate-ciliate
sporophyte-type (see text)	nodular-type	nodular-type	nodular-type
spore rosettes	lacking	present and lacking	present
sporeling-type	*Lejeunea*-type	*Lejeunea*-type	*Lejeunea*-type

securifolia varies considerably: 40-190 μm. This variation does not seem to correlate with other characters investigated, although the elongated bistratose attachment seems to be restricted to well developed specimens. Underleaf attachment is apparently complex in *Blepharolejeunea* and does not contribute to the delimitation of the genus. The number of superior central cells, however, is always four, even in the small *B. saccata*, and appears therefore to be a more constant and reliable generic character, as was already suggested by Gradstein (1979).

Several authors recently paid attention to the morphology of the first leaf cycle at the base of a *Frullania*-type branch (Mizutani 1970, Crandall 1969, Gradstein 1979). Mizutani (1970) recognized three different subtypes of the *Frullania* branch, of which the *Frullania-Ptychanthus*-subtype occurs in various genera of Ptychanthoideae, e.g. *Dicranolejeunea, Brachiolejeunea, Trocholejeunea.* In this subtype, the first branch appendage is a bilobed underleaf, the second appendage is an acroscopic leaf that is somewhat smaller in size than the normal leaf but has the lobule well differentiated, the third appendage is a fully grown basiscopic leaf. A further reduction takes places in the first two appendages of the *Frullania-Jubula*-subtype: the first underleaf is reduced and scale-like, the first acroscopic leaf is reduced in size and has no lobule developed. In three of the five species of *Blepharolejeunea* the first two appendages appear to be a mixture of both subtypes described above. The first branch appendage is a bilobed underleaf that varies in outline from suborbicular in *B. chimantaensis* and thus similar to a stem and branch underleaf (Fig. 4), to suborbicular and bilobed in *B. saccata* (Fig. 10) and *B. securifolia* (Fig. 1), to very asymmetrically bilobed and reduced to a scale in *B. incongrua* (Fig. 10). this can be seen as a variation in the first underleaf of a *Frullania-Ptychanthus* branch. The second leafy appendage, however, is also reduced in size but has no lobule developed and is thus similar to the *Frullania-Jubula*-subtype. The outline varies from suborbicular-bilobed in *B. saccata* (Fig. 10) and *B. securifolia* (Fig. 1) to an asymmetrically bilobed scale in *B. incongrua.* We propose the name *Frullania-Blepharolejeunea*-subtype for this new combination of branch appendages. *B. chimantaensis* and *B. fuegiana* have *Frullania-Ptychanthus*-type branching (Figs. 4, 6). Besides *Frullania* branches, all species of *Blepharolejeunea* have *Lejeunea*-type branches which form in *B. saccata* the majority of the branches present (Tab. 2).

Table 2. Branching and innovation in *Blepharolejeunea.*

+ = majority of branches present; - = minority of branches present; ± = branching types in equal amount present.

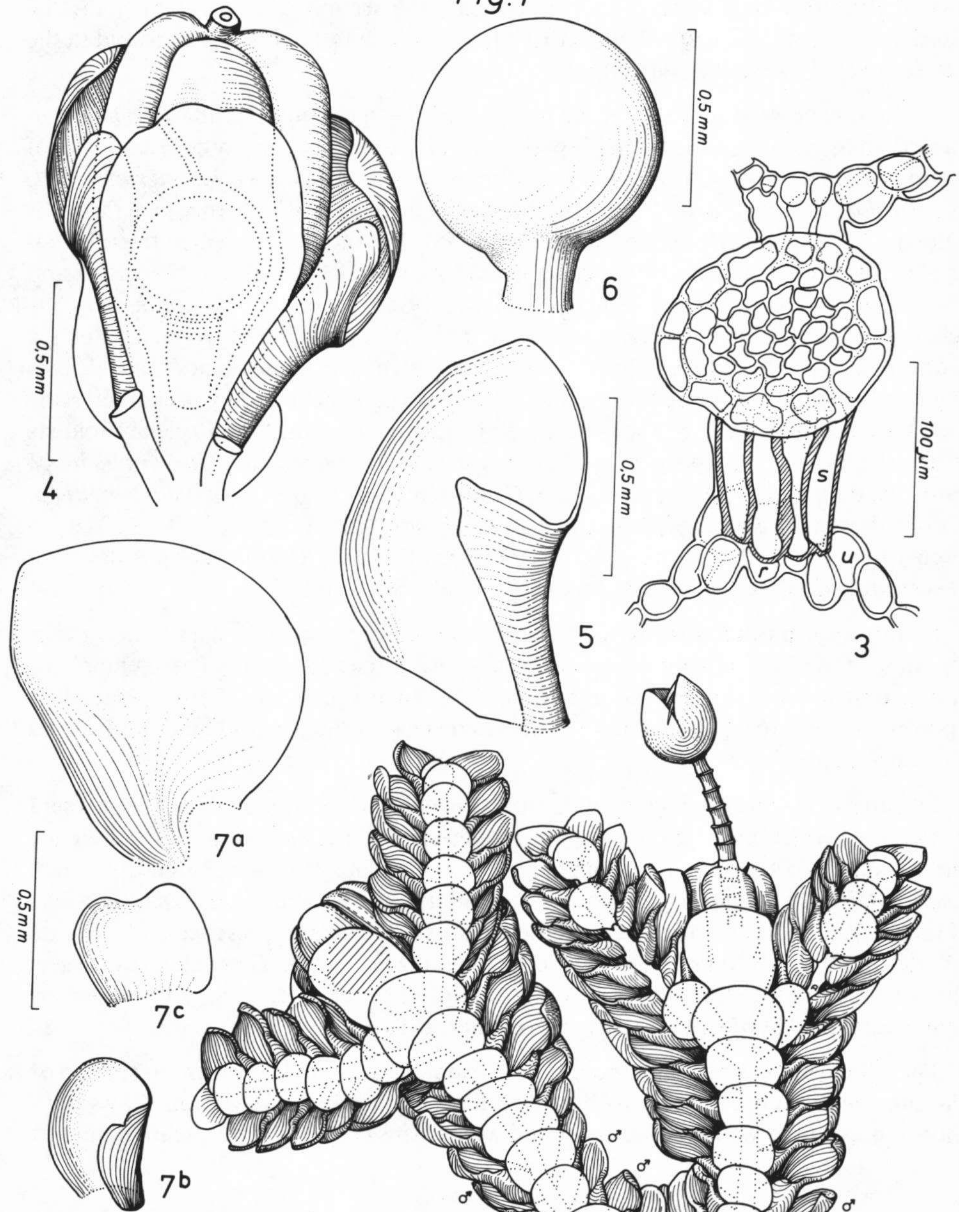
species	*B. chimant.*	*B. fuegiana*	*B. incongrua*	*B.saccata*	*B. securifolia*
branching-type					
Frullania-Ptychanthus	+	±			
Frullania-Blepharolejeunea			+	-	+
Lejeunea	-	±	-	+	-
Radula-Jubula	-	-	-	-	-

Fig. 1. *Blepharolejeunea securifolia* (Steph.) Schust.

1. habitus ventral, with sporophyte. 2-3. stem transverse section with antheridial stalk (2) and with underleaf attachment (3) (r = rhizoid disc initial cell, s = superior central cell, u = underleaf lamina cell). 4. perianth and involucrum. 5. female bract. 6. female bracteole. 7. *Frullania-Blepharolejeunea*-branch appendages: 7a. dorsal stem half-leaf, 7b. first branch underleaf, 7c. first branch acroscopic leaf.

1 from Cleef 1990, Colombia. 2 from Gradstein & Aguirre 3642, Colombia. 3 from Jameson s.n., Ecuador. 4,7 from Cleef 2191, Colombia. 5,6 from Gradstein et al. 3457, Ecuador.

Fig.1



The innovations in *Blepharolejeunea* are always of the *Radula-Jubula*-type, i.e. the first leafy appendage formed is an underleaf, the second is a basiscopic leaf, the third is an acroscopic leaf (Mizutani 1970). This innovation type is also found in the genera related to *Blepharolejeunea.*

In the course of a comprehensive analysis of the sporophyte in the *Ptychanthoideae* (van Slageren & Berendsen, in prep.), scanning electron microscopic analysis of various details of the sporophyte generation was carried out in *B. incongrua* and *B. securifolia,* the only two species of *Blepharolejeunea* of which this generation is known. The sporophyte reflects a type in the Ptychanthoideae in which the thickenings of the inner cell layer of the capsule valves consist of nodules in the angles and on the intermediate, radial cell walls located *inside* the cells. Consequently they are only visible with the light microscope and *not* with the SEM, which shows a smooth inner valve surface (Fig. 11). The outer valve layer presents nodular thickenings on the angles of the cells only (Fig. 11). This valve morphology is characteristic for the sporophyte type of the subfam. Lejeuneoideae; within the Ptychanthoideae it has also been found in the related genera *Brachiolejeunea* (subg. *Brachiolejeunea* only!) and *Dicranolejeunea* (Geissler & Gradstein 1982) as well as in *Neurolejeunea, Odontolejeunea, Stictolejeunea* and *Symbiezidium* (van Slageren & Berendsen, in prep.). The majority of the genera of Ptychanthoideae elaborates capsules with fenestrate, sheetlike thickenings on the inner valve surface.

It thus appears that *Blepharolejeunea* is part of a group of genera which by its "nodular-type" of sporophyte stands apart within the subfamily. The members of this group are considered more advanced in an evolutionary sense, since their sporophyte apparently links the Ptychanthoideae with the generally more advanced Lejeuneoideae.

In transverse section of a closed capsule (Fig. 11), the marginal elaters are present as two axes which meet at right angles in the centre of the capsule and which divide the capsule into four equal sectors (Fig. 11: m.e.). This was already described for *Dicranolejeunea axillaris* (Stotler & Crandall 1969) and *Brachiolejeunea laxifolia* (Fulford 1961). Not mentioned by these authors is the *in situ* presence and location of additional elaters on the inner valve surface (Fig. 11: a.e.). These elaters intersect the four sectors filled with spores at a more or less regular distance, and moreover, remain attached at both ends to the valve inner surface.

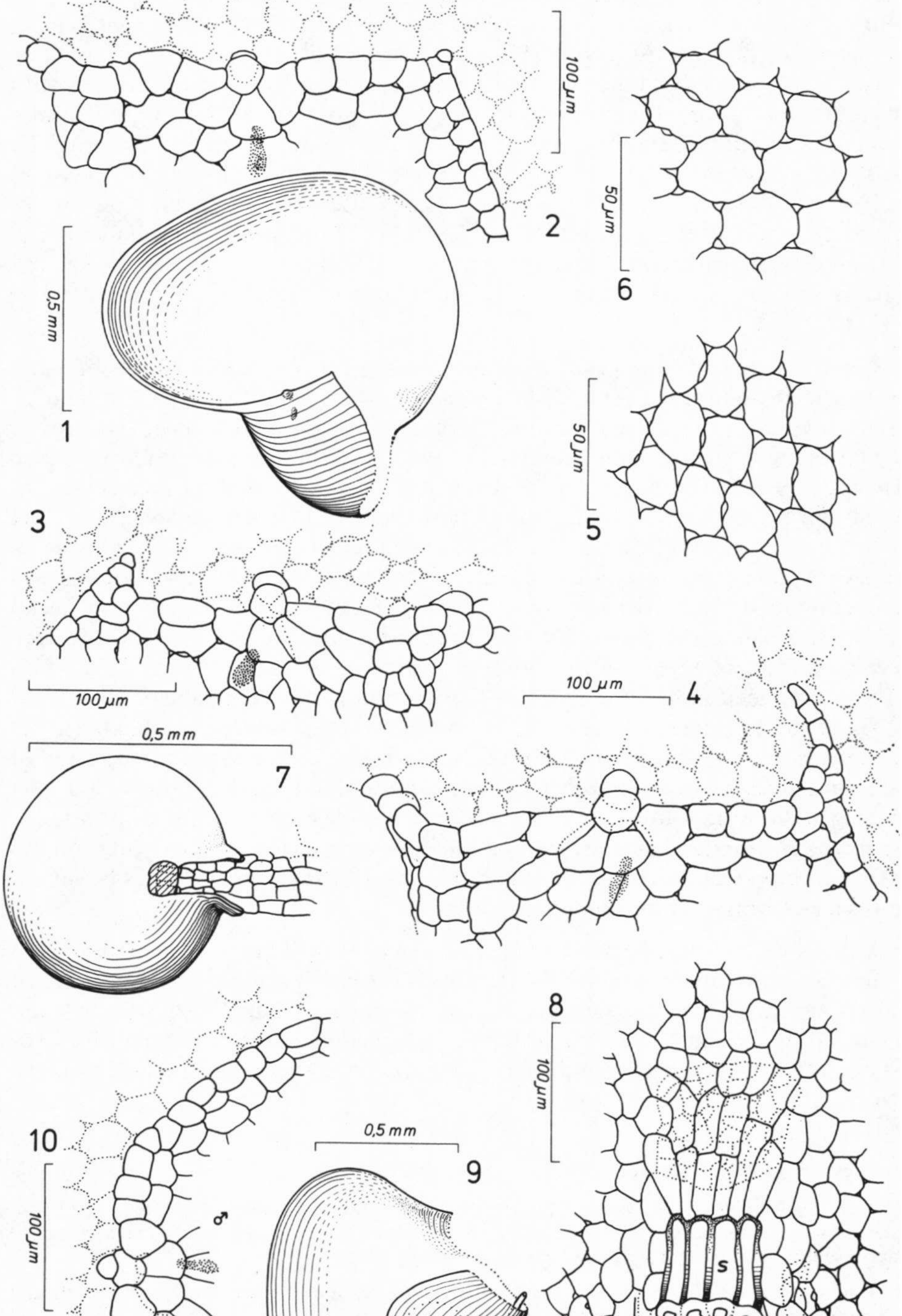
The spore shape is basically more or less rectangular (Fig. 12). In length section of the capsule the spores appear rather brick-like, but a transverse section shows both more elongated as well as more short and wide forms (Fig. 11). The ultrastructure of

Fig. 2. *Blepharolejeunea securifolia* (Steph.) Schust.-continued

1. leaf. 2. leaf lobule margin (detail). 3-4 leaf lobule margin, showing variation in the second tooth. 5-6. mid leaf cells. 7. underleaf. 8. underleaf ventral view, showing four superior central cells (s). 9. male bract. 10. male bract lobule margin (detail), showing reduced second tooth.

1,2,9,10 from Cleef 1990, Colombia 3-5,7 from Gradstein et al. 3457, Ecuador. 6 from Cleef 2291, Colombia. 8 from Gradstein & Aguirre 3642, Colombia.

Fig. 2


100 µm
2
50 µm
6
0,5 mm
1
50 µm
5
3
100 µm
100 µm
4
0,5 mm
7
8
100 µm
10
100 µm
♂
0,5 mm
9
s

the sporoderm presents the following differences at the specific level between *B. securifolia* and *B. incongrua*. In *B. securifolia* the sporoderm is covered with minute, granular verrucae, c. 0,1-0,2 µm in diam. At irregular distance larger verrucae are present, 1,0-1,9(-2,4) µm in diam. These verrucae are in addition covered with small, wratlike processes, appearing as "whitish" punctae on a SEM micrograph (Fig. 12). Rosettes are lacking. The sporoderm of *B. incongrua* is also covered with minute, granular verrucae of c. 0,1 µm in diam. In addition irregular verrucae are present, 0,9-3,0 µm in diam. and covered with small wratlike processes, as well as 6-11 rosettes, consisting of 7-9 radially oriented spinulae and spinae. The diameter of the rosettes is 8,2-10,1 µm; the length of the spines and spinules is 2,3-4,9 µm. The spines become somewhat baculate in well developed rosettes (Fig. 12). The rate of development of the rosettes varies considerably: from ± indistinct to well defined (Fig. 12-4/6).

The five species of the genus *Blepharolejeunea* occur in cool habitats of Latin American regions (Fig. 13). *B. chimantaensis, B. incongrua, B. saccata* and *B. securifolia* are tropical-montane, usually occurring above 1800 m in the páramo region or in the upper cloud forests. *B. fuegiana* is restricted to Patagonia and Tierra del Fuego. The main centre of diversity is Ecuador with three species present. The tropical species occur in the Andes chains from Bolivia to Colombia, with more isolated localities in S.E. Brazil (Sierra Itatiaia, the only location in Brazil where a kind of páramo is present), Costa Rica and Mexico. Presumably *Blepharolejeunea* is continuous through the mountain chains of Central America and insufficient collecting may be the reason for the isolation of the Costa Rican and Mexican localities. More of a relict nature, however, seem to be the occurrences on the tepuis of S.E. Venezuela, where the endemic *B. chimantaensis* is found, and on the islands of Cuba and Dominica (*B. saccata*). The altitude on the Antilles is estimated lower than on the continent (ca. 1000-1800 m), which might be due to the compression of altitudinal zonation on islands. Precise indications of altitude are, however, usually lacking and for the Antilles are only given for one collection on Cuba (1800 m). For *B. fuegiana* altitudinal data are lacking but they are reconstructed as being from 0-500 m. Temperature conditions at the locations of *B. fuegiana* may thus be similar as for the tropical-montane species of the genus.

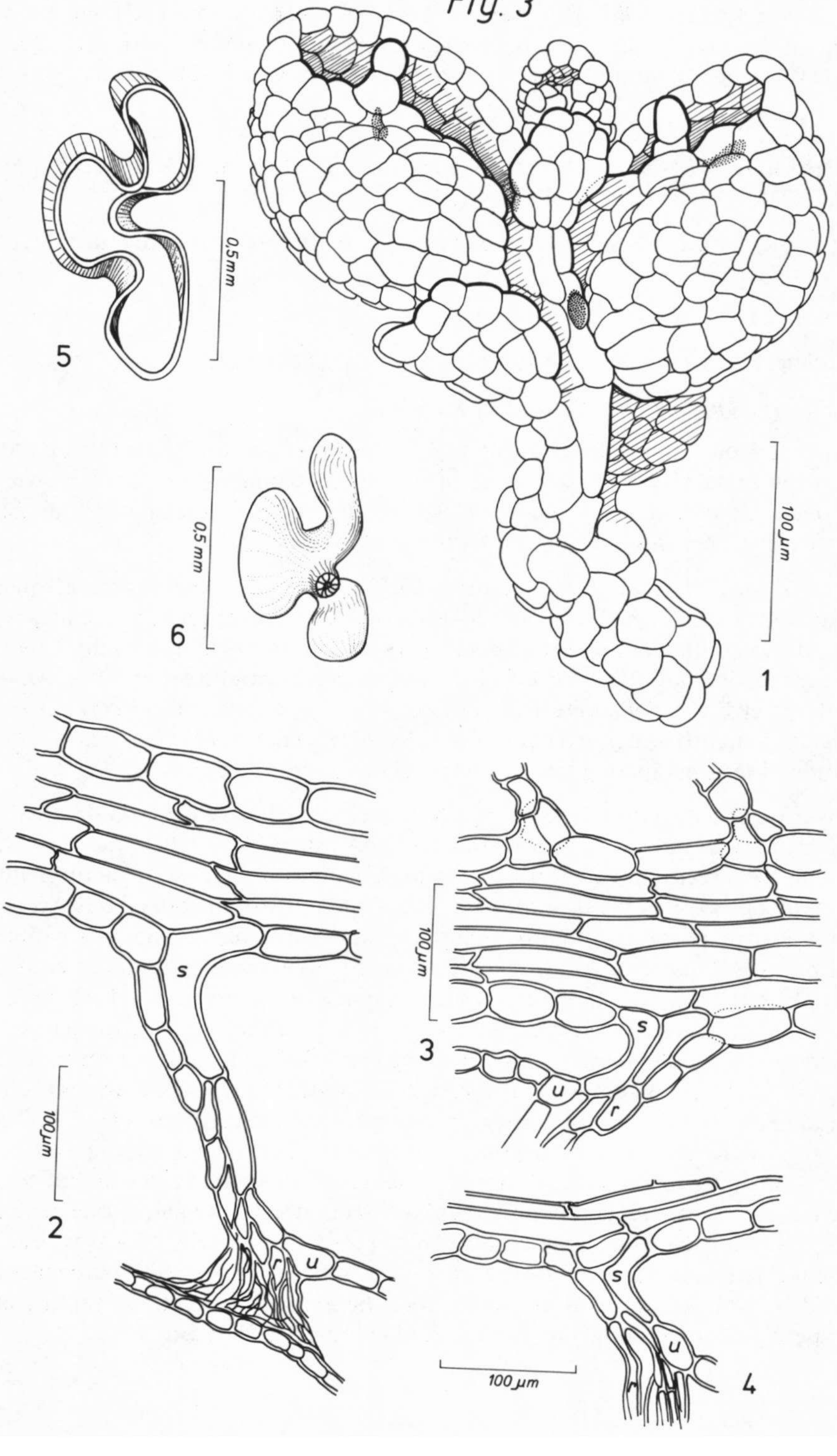
As a whole, *Blepharolejeunea* comprises taxa of limited distribution in the Andes chains with the major gap in distribution corresponding to the arid regions of Northern Chili (Atacama desert). Similar disjunctions have been reported and discussed by Griffin III et al. (1982) and are apparently not uncommon in bryophytes. The disjunction, including the tops of the Venezuelan tepuis, is not so

Fig. 3. *Blepharolejeunea securifolia* (Steph.) Schust.-continued

1. Sporeling, showing primary leaves, primary underleaf and juvenile leaves. 2-4 different underleaf attachments (r = rhizoid disc initial cell, s = superior central cell, u = underleaf lamina cell). 5-6. transverse section of perianth and apical part with beak.

1 from Gradstein et al. 3457, Ecuador. 2 from Cleef 942, Colombia. 3 from Philippi P-253, Peru. 4 from Hans Meyer 4225, Ecuador. 5,6 from Jameson s.n., Ecuador.

Fig. 3



extreme as is present in e.g. *Eopleurozia paradoxa* (Hässel de Menendez & Greene 1980), *Dendrocryphaea* (Griffin III et al. 1982), *Andreaea wilsonii* (Dusén 1903) or *Colura patagonica* (Solari 1976), but represents a pattern, at the generic level, that is apparently frequently found in neotropical-montane mosses and hepatics.

BLEPHAROLEJEUNEA S. Arn., Svensk Bot. Tidskr. 56: 335 (1962); Schuster (1980a: 423), (1980b: 762); Grolle (1983: 7).

Type: *Blepharolejeunea harlingii* S. Arn. (= *Blepharolejeunea saccata* (Steph.) van Slag. & Kruijt).

Heterotypic synonym:

Oreolejeunea Schust., Hep. Anth. N. America 4: 762 (1980).

Type: *Oreolejeunea securifolia* (Steph.) Schust.

Plants dioicous (?) or paroicous, up to 3,5 cm long (*B. securifolia* rarely up to 6,5 cm!), green to darkish green when wet, when dry becoming light to dark brown, in *B. chimantaensis* and *B. incongrua* glossy reddish brown, irregularly branched; vegetative branches short or long, *Frullania*- and *Lejeunea*-type.

Stems flaccid or rigid (*B. chimantaensis*), 0,1-0,2 mm in diam., ventral merophyte outside the underleaf insertion 2-4 cellrows wide; dorsal cortical cells arranged in straight longitudinal rows, the lateral merophytes interlocking dorsally; stem in transverse section with 9-14 thickwalled cortical cells surrounding 15-32 thinwalled medullary cells, *the dorsal cortical cells equally high as the ventral cortical cells, cortical cells slightly wider and equally high as the medullary cells,* medullary cells in longitudinal section tapering towards relatively wide, truncate ends.

Leaves incubous, with a large dorsal lobe and a smaller ventral lobule, laxly to rather densely imbricated, suberect-convoluted when dry, when moist widely spreading and erecto-patent. Lobe (ob)ovate-falcate to broadly so to suborbicular, inserted along ¼-½ of the length of the lateral merophyte, the dorsal base straight and not auriculate, not to slightly arching beyond the stem, the margins entire or with 1-8 teeth (*B. saccata*), the apex widely rounded to minutely apiculate, the apical region plane to incurved, the postical margin plane or upcurved, the keel smooth, rounded or only weakly curved, not or shortly decurrent; cells arranged in ± diverging rows, *isodiametric to slightly elongated* and hexagonal, the median cells (15-)21-47 × (11-)15-36 μm, slightly larger at leaf base, towards the margins becoming gradually smaller, at the margins rectangular to subquadrate, (11-)14-27 μm high; vitta and ocelli absent; trigones and intermediate thickenings present, the trigones small to medium-sized, *simple triangular to cordate,* the intermediate thickenings rarely or frequently present, elliptic-rounded to elongated, one per each (larger) cell wall; cuticula smooth; oil bodies present in all cells of leaves, underleaves and stem cortex, *Massula*-type, in the leaf lobe 10-20 per cell, homogeneous, ellipsoid to globose, up to 8 μm long, upon degeneration becoming septate and subsequently desintegrating into minute granula (obs. S.R. Gradstein).

Lobule 0,4-0,6× the length of the lobe, never reduced, *rotundate-rectangular or short rectangular,* inflated along the keel and with a plane to concave distal part, the free margin plane, truncate, *straight from the keel to the second tooth* with the *blunt, inflexed apical tooth* situated midway, the *second tooth a sharp point, not inflexed,* the free margin straight to weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the ventral margin of the lobe; hyaline papilla inserted on the inner side of the lobule 1-2 cells below the proximal base of the apical tooth; cells of the lobule slightly smaller than the cells of the lobe and arranged irregularly.

Underleaves imbricated to distant, 2-10× the width of the stem, suborbicular, plane, the apex widely rounded, the margins entire, the insertion cuneate or subtransverse, 60-145 μm deep; *underleaf base at the rhizoid disc bi- or tristratose in longitudinal section,* the stalk of attachment 35-190 μm long; the primary rhizoid disc consisting of up to 20 bulging cells, giving rise to short bundles of pale rhizoids.

Androecia located below the gynoecium after 1-4 series of vegetative leaves; bracts and bracteoles in 1-6 series, the bracts very much resembling the leaves but usually slightly smaller in size. The lobule with a more strongly inflated basal part and a concave distal part, epistatic, the free margin similar to the vegetative leaves but the second tooth not always developed, the lobule enveloping one globose antheridium subtended by a curved, uniseriate stalk; bracteoles similar to underleaves, present throughout the male spike.

Gynoecium terminating stems, *Frullania-* or *Lejeunea*-type branches, with two *Radula-Jubula*-type innovations, bracts and bracteole in one series, the bract lobe plane or concave, broadly (ob-)ovate, spathulate or obovate-triangular, the apex rounded, blunt or minutely apiculate, the apical region entire or ciliate, the keel a sharp or wide angle, a wing at the keel usually developed but sometimes reduced to absent, lobule small rectangular or large rectangular-rhomboid, the apex rounded or truncate and then bearing a 1-3 celled tooth; bracteole broadly obovate-oblong or suborbicular, smaller in size than the lobe (except *B. chimantaensis*), weakly to strongly concave, the apex widely rounded to emarginate, plane or recurved, the basal part not inserted on the innovations. Perianth immersed or emergent to 1/5-1/2 of its length, obovoid to obovoid-oblong or cuneiform to pyriform, frequently stalked, ± bilaterally compressed with a broad ventral plica and two sharp lateral plicae or entirely inflated with three rounded or five sharp plicae in the upper 1/5-1/2, the plicae smooth to ciliate on their backs; beak 4-5 cells long, basal cells large and thinwalled with small trigones, apical cells smaller with larger trigones and intermediate thickenings.

Calyptra entirely enveloping the young sporophyte, the upper part (surrounding the capsule) 1(-2) stratose, the lower part (surrounding seta and foot) 3-7 stratose, the two outer cell layers identical to the cells of the upper part, the 1-5 inner layers consisting of much smaller and ± isodiametrical cells, the calyptral stalk very short.

Mature sporophyte exserted up to 1,5 mm above the perianth, the foot consisting of few bulging cells in three layers, the seta articulate, with 16 evenly tiered longitudinal rows of outer cells and four longitudinal rows of inner cells, the capsule globose, dark brown, splitting to 4/5 of its length into four valves; valves suberect, the central part concave, the lateral and apical parts plane and not recurved, two opposite valves bearing five marginal elaters, the other two valves bearing six marginal elaters, the elaters thus forming an interlocking series of six at each connection of two valves before the capsule opens, each valve in addition having three slightly modified elaters that are connected with their apical and basal ends to the inner surface of the valve, the capsule valves bistratose, the outer cells with asymmetrically-nodulose trigones and intermediate thickenings, less developed at the extreme base, the inner cells smooth on their outside surface and bearing irregular nodulose thickenings on their inner cell walls, the capsule base 3-4 stratose, of thinwalled cells; elaters $(2\times5) + (2\times6) + (4\times3) = 34$ per capsule, 140-370 μm long: along the margin of the valves 290-370 μm, the most lateral ones 140-160 μm, on the inner surface of the valve 1(-2) elaters of 145-180 μm and 1(-2) of 195-250 μm, the elaters 14-23 μm wide, with one yellowish-brown, c. 4 μm wide spiral; spores with precocious germination, rectangular, 54-95 μm long, irregular angular when dry, the outer surface covered with numerous irregularly arranged verrucae and (in *B. incongrua* only) with 6-11 rosettes of radially oriented, spinae and spinulae that bear wratlike processes.

Sporelings of the *Lejeunea*-type.

Chromosome number unknown (but $n=9$ in all genera of the subfam. Ptychanthoideae except *Trocholejeunea*, Grolle 1982).

DISTRIBUTION (Fig. 13): C. and S. America, ranging in altitude from sealevel up to 4600 m; the highest records are from Peru (Cordillera Blanca: Pico Cajon Rury, 4600 m) and Colombia (Meta: Cerro Nevada del Sumapaz, 4100 m). The main centre of diversity is Ecuador with three species.

ECOLOGY: mostly epiphytic in moist to wet habitats; preferably growing in loose mats on stems and branches of living trees and shrubs in mountain forests and in páramo regions; often together with other Lejeuneaceae, *Frullania* or, more rarely, with mosses; at higher altitudes (3400-4600 m) also growing epilithic or on soil and then sometimes in rather dense cushions; not epiphyllous.

DIFFERENTIATION: important diagnostic characters are in *italics* in the description.

Key to sterile plants

1. Leaf lobes dentate to ciliate; ventral merophyte 2 cell rows wide.. 4. *B. saccata*
1. Leaf lobes entire; ventral merophyte 2-4 cell rows wide.................... 2
    2. Leaf lobule first tooth consisting of one cell that is part of the lobule margin; stems rigid.. 1. *B. chimantaensis*
    2. Leaf lobule first tooth consisting of one or more cells superimposed on the lobule margin; stems flaccid... 3

3. Leaf lobule keel straight; first tooth made up of 3-5 cells with 1-2 at the base, second tooth made up of (3-)6-10 cells with (1-)2-3 at the base; plants from Patagonia and Tierra del Fuego............................ 2. *B. fuegiana*

3. Leaf lobule keel arched; first tooth 1-3(-4) cells with 1-2 at the base, second tooth 1-3 cells (but sometimes up to 7-8 cells in total with 3-4 at the base in *B. securifolia*); plants from tropical America.. 4

    4. Free margin cells of the leaf lobule 3-5 between keel and apical tooth and 4-7 between apical and second tooth, identical in shape to the other lobule cells.. .... 5. *B. securifolia*

    4. Free margin cells of the leaf lobule 3 (1 short and 2 elongated) between keel and apical tooth and 3 (1 short and 2 elongated) between apical and second tooth, larger than the other lobule cells.................. 3. *B. incongrua*

Key to fertile plants

1. Female bracteole as large as the bracts, strongly concave; female bract lobe entirely concave, strongly so in the apical region; stems rigid with strongly thickened cortical cells............................... 1. *B. chimantaensis*

1. Female bracteole distinctly smaller than the bracts, plane, apical region sometimes concave; female bract lobe plane to (weakly) concave, mainly in the apical region; stems flaccid.. 2

    2. Female bract lobe broadly obovate or ovate-falcate, margins entire....... 3

    2. Female bract lobe spathulate or obovate-triangular, margins entire or ciliate.. 4

3. Perianth cuneiform to pyriform with 2 sharp lateral, smooth to ciliate plicae and 1 broad ventral, smooth plica; female bract broadly obovate, the keel sharp, the lobule small, 0,15-0,30 × the length of the bract lobe......... 3. *B. incongrua*

3. Perianth obovoid to obovoid-oblong with 3 smooth, rounded plicae; female bract ovate-falcate, the keel rounded, the lobule larger, 0,55-0,65 × the length of the bract lobe.. 5. *B. securifolia*

    4. Female bract lobe obovate-triangular, apical margin ciliate; perianth cuneiform to pyriform, 2-plicate, plicae ciliate; leaf lobes dentate-ciliate......... .... 4. *B. saccata*

    4. Female bract lobe spathulate, apical margin entire; perianth obovoid to obovoid-oblong, sharply 5-plicate, the plicae smooth; leaf lobes entire...... .... 2. *B. fuegiana*

1. **Blepharolejeunea chimantaensis** van Slag. & Kruijt spec. nov. Figs 4, 5

Planta dioica (?) ab *B. incongrua*, cui affinis est, differt foliis valde concavis, apice late rotundatis; angulus inter marginem posticam et carinam 135-180°; dens apicalis lobuli unicellularis et inflexus; bracteoli feminae bracteam feminam aequantes, magni, late obovati et valde concavi; perianthia juvenilia tricarinata et pyriformia. Perianthia matura et androecia desunt.

Type: Venezuela, Bolivar, Macizo del Chimantá, sector W del Acopán-Tepui, Steyermark et al. 128593, II. 1983 (U holo, FLAS, VEN).

Plants dioicous (?), medium sized, up to 2,5 cm long, 0,95-1,15 mm wide, darkish green, becoming glossy reddish brown when dry, sparsely and irregularly branched; branches short or long, *Frullania-Ptychanthus*-type, *Lejeunea*-type less frequent.

Stem rigid, 0,1-0,2 mm in diam.; ventral merophyte outside the underleaf insertion 2-4 cellrows wide, the ventral cortical cells rectangular, 85-120 × 35-55 µm, the cell walls unevenly thickened, the dorsal cortical cells rectangular, 45-80 × 35-45 µm; stem in transverse section with 12-13 thickwalled cortical cells surrounding 17-21 thinwalled medullary cells, the dorsal and ventral cortical cells 29-40 µm high, the medullary cells 18-19 µm in diam.

Leaves laxly imbricated. Lobe broadly ovate to suborbicular, strongly concave, 0,70-0,78 mm long, 0,65-0,75 mm wide, inserted along 1/3 of the length of the merophyte, the dorsal base not auriculate, the apex widely rounded, the leaf margin entire, the postical margin upcurved, when spread out forming an angle of 135-180° with the keel; keel smooth, strongly curved, at an angle of 90° with the axis, not decurrent; median leaf cells slightly elongated to isodiametric, 32-47 × 25-36 µm, larger towards the leaf base, at the margins smaller and rectangular-subquadrate, 18-25 µm high; trigones medium-sized, triangular to radiate, intermediate thickenings frequently present, one per each larger cell wall, round to elongated.

Lobule rotundate-rectangular, 0,40-0,45 mm long, 0,35-0,40 mm wide, 0,6× the length of the lobe, inflated along the keel and gradually flattened towards the free margin, the flattened part weakly concave; the free margin plane, truncate, straight from the keel to the second tooth with the apical tooth situated midway, weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the postical margin of the lobe, with two teeth; the apical tooth consisting of only one cell that forms partly the lobule margin and partly expands as a blunt, inflexed tooth, the second tooth a straight, one-celled sharp point, 3-4 cells between keel and apical tooth, (2-)3-4 cells between apical and second tooth, the free margin cells weakly pigmented contrary to the rest of the lobule cells; hyaline papilla one cell below the proximal base of the apical tooth.

Fig. 4. *Blepharolejeunea chimantaensis* van Slag. & Kruijt

1. habitus ventral. 2-3. stem transverse section (3) and with underleaf attachment (2) (r = rhizoid disc initial cell, s = superior central cell, u = underleaf lamina cell). 4. *Frullania-Ptychanthus*-branch appendages: 4a dorsal stem half-leaf, 4b. first branch underleaf, 4c. first branch acroscopic leaf. 5. stem longitudinal section with underleaf attachment. 6. mid leaf cells.

1-6 from Steyermark et al. 128593, Venezuela (type collection).

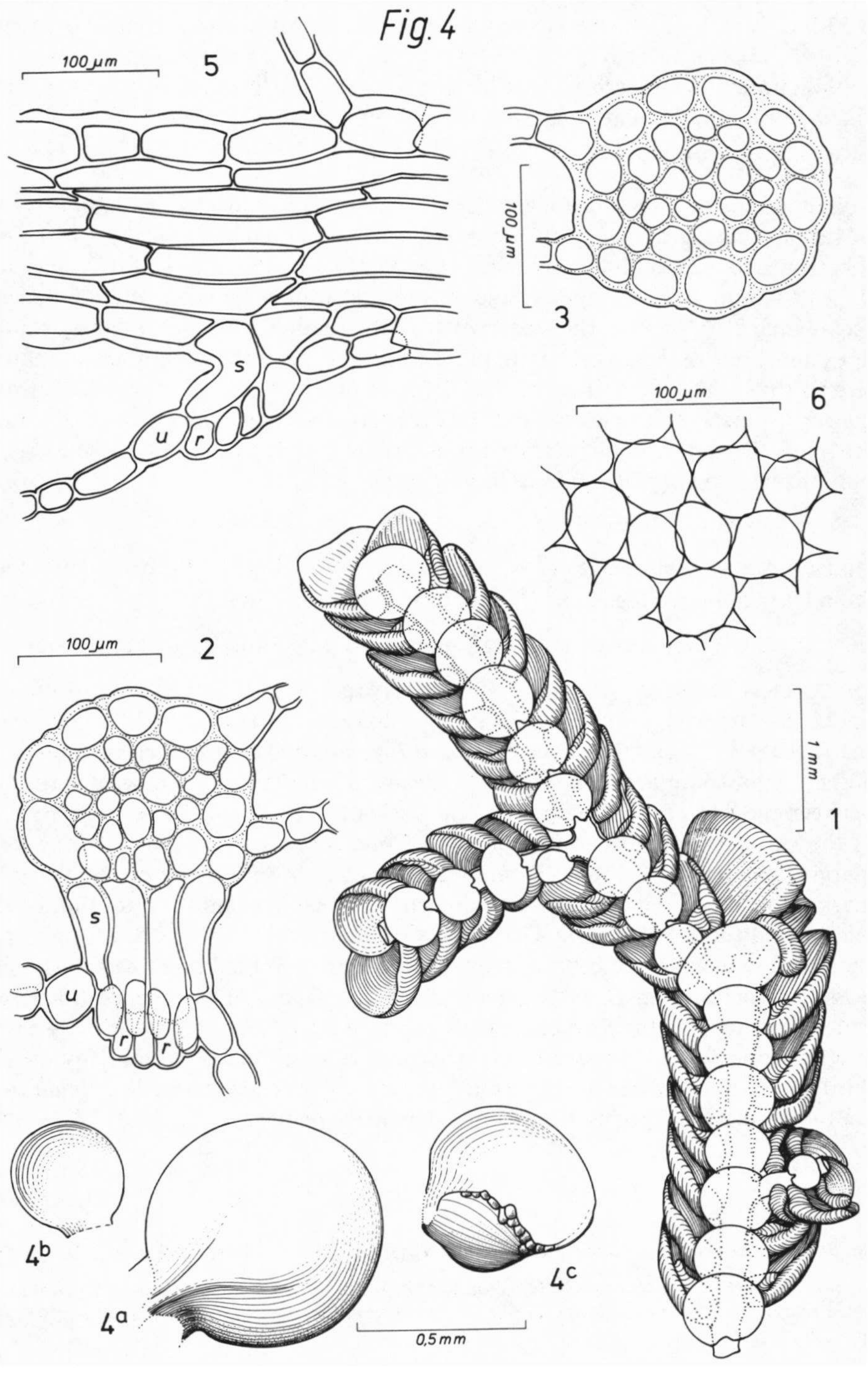


Fig. 4
100 µm
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3
100 µm
6
1 mm
1
100 µm
2
s
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r
r
4b
4a
4c
0,5 mm

Underleaves not to barely imbricated, suborbicular, plane, 0,45-0,55 mm long, 0,53-0,60 mm wide, the bases rounded and shortly decurrent, the cuneate insertion 100-145 μm deep; median cells 32-43 × 21-32 μm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose, 57-90 μm long; rhizoid disc suborbicular, consisting of few small, thinwalled cells.

Androecia not observed.

Gynoecium terminating long or short stems, with two *Radula-Jubula*-type innovations that are not again floriferous; bracts and bracteole in one series, the bract lobe concave, especially in the apical region, broadly obovate, 1,15-1,25 mm long, 0,95-1,05 mm wide, the apex rounded, the keel widely rounded, the lobule small, rectangular, 0,15-0,25 × the length of the lobe, with a truncate to widely rounded apex and a one celled apical tooth; bract without wing at the keel; bracteole equal in size to the bracts, suborbicular, 0,95-1,07 mm long, 1,05-1,25 mm wide, strongly concave, especially the apical and lateral parts, the apex widely rounded and not recurved. Perianth: only juvenile forms present, as far as could be detected, the outline tends to be pyriform as in *B. incongrua*.

Sporophyte not observed.

DISTRIBUTION: Venezuela, the Acopán-Tepui in the State of Bolivar. Only known from District Piar, Macizo del Chimantá at 1850 m altitude.

ECOLOGY: on wet, shaded banks of gullies in a forest on top of table mountains.

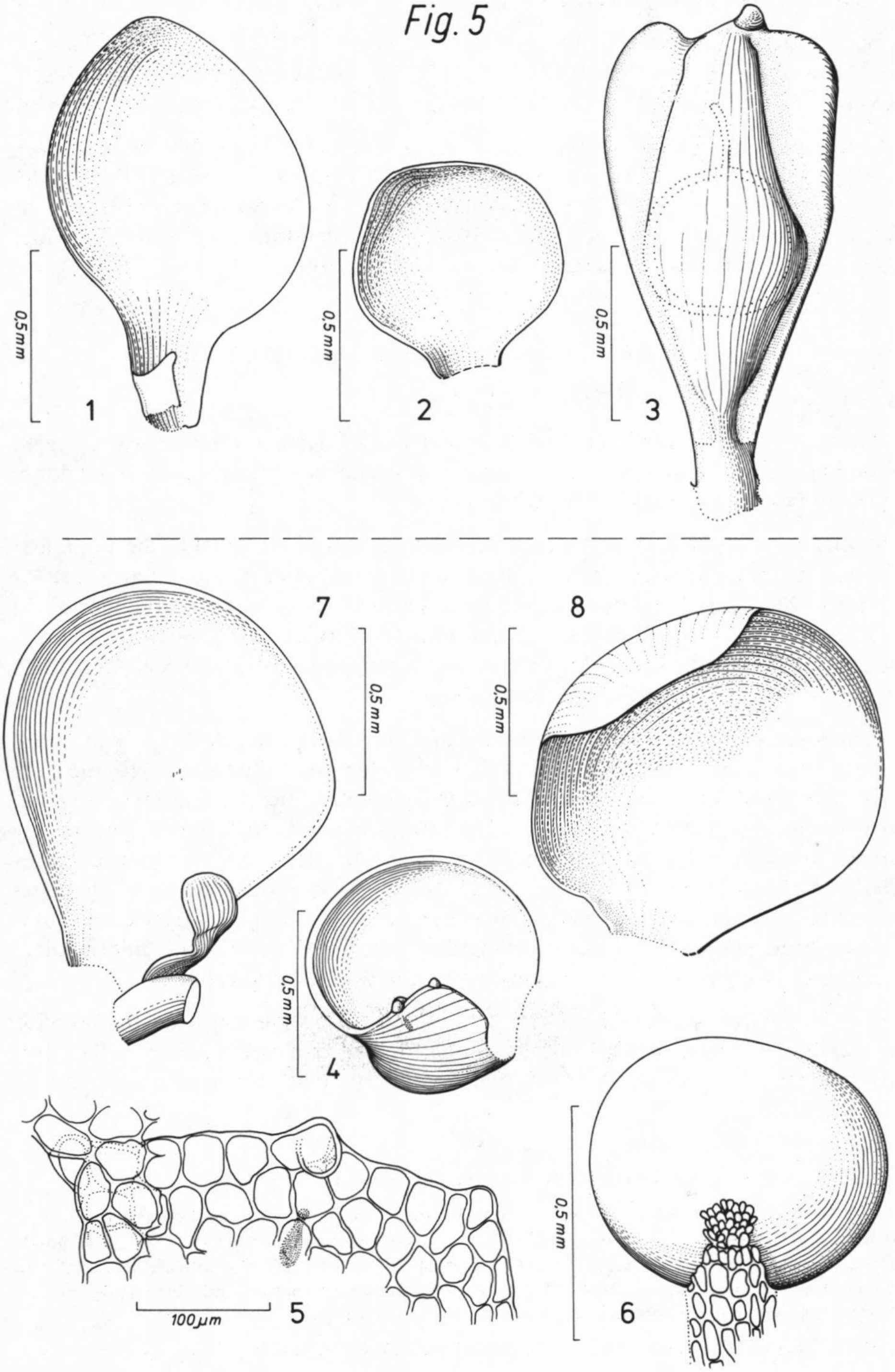
DIFFERENTIATION: *B. chimantaensis* is closely related to *B. incongrua* as is indicated under the latter. *B. chimantaensis* differs, however, in a number of characters: 1) the first leafy appendage of the *Frullania-Ptychanthus*-type branch is suborbicular and not bilobed (in *B. incongrua* scale-like and asymmetrically bilobed); 2) the angle between the leaf postical margin and the keel is 135-180° (in *B. incongrua* 90-120°); 3) the leaf lobule apical tooth consists of one cell, partly in line with the lobule margin and partly inflexed (*B. incongrua*: 1-2 cells superimposed on the lobule margin); 4) the number of free margin cells between keel and first tooth resp. first and second tooth is 3-4 resp. (2-)3-4 cells of identical outline (in *B. incongrua* one short and two elongated cells on the same locations); 5) the keel of the female bract is widely rounded (in *B. incongrua* a sharp angle) and 6) the female bracteole is equal in size to the bracts and strongly concave (in *B. incongrua* distinctly smaller and less concave with a plane to slightly recurved apical part). Notably by the first, third and sixth character mentioned above, and by the rigid stems, *B. chimantaensis* is a rather aberrant species of the genus *Blepharolejeunea*.

Fig. 5. *Blepharolejeunea fuegiana* (Besch. & Mass.) Gradst. and *B. chimantaensis* van Slag. & Kruijt

1-3. *B. fuegiana*. 1. female bract. 2. female bracteole. 3. perianth. 4-8. *B. chimantaensis*. 4. leaf. 5. leaf lobule margin (inner view), showing one-celled apical tooth. 6. underleaf. 7. female bract. 8. female bracteole.

1-3 from Hariot 77, Chili. 4-8 from Steyermark et al. 128593, Venezuela.

Fig. 5



2. Blepharolejeunea fuegiana (Besch. & Mass.) Gradst. Figs. 5, 6

Beih. Nova Hedwigia 80: 108. *Lejeunea fuegiana* Besch. & Mass., Bull. Mens. Soc. Linn. Paris 80: 638 (1896); Bonner (1978: 555). *Archilejeunea fuegiana* (Besch. & Mass.) Steph., Spec. Hep. 4: 714 (1911); Engel (1978: 245;) Solari (1983: 536).

Lectotype: Chile, Cape Horn, J.D. Hooker s.n. (VER holo, MANCH 15092); paratype Chili: Hermite Island, P. Hariot 77, 1.VII.1883 (G 16168, PC). After study of the two syntype collections, we have decided to follow Bonner (1978) in the choice of the lectotype and not Solari (1983), since the Hooker collection provides much better and fruiting material.

Heterotypic synonym:

Archilejeunea magellanica Steph., Spec. Hep. 4: 716 (1911); Solari (1983: 536).

Type: Chile, Borja Bay, s. coll. (G 20790 holo).

Plants paroicous, small, up to 1,0 cm long, 1,05-1,60(-1,75) mm wide, green, becoming light brown when dry, irregularly branched, branches short or long, *Lejeunea*-type and *Frullania-Ptychanthus*-type.

Stem flaccid, 0,11-0,15 mm in diam.; ventral merophyte outside the underleaf insertion 2-4 cellrows wide, the ventral cortical cells subquadrate to rectangular, 30-45(-70) × 27-35 μm, the dorsal cortical cells subquadrate to short rectangular, 32-50 × 20-30 μm; stem in transverse section with 10-12 thickwalled cortical cells surrounding 16 thinwalled medullary cells, the dorsal and ventral cortical cells 20-25 μm high, the medullary cells 15-25 μm in diam.

Leaves laxly imbricated. Lobe obovate and slightly falcate, 0,75-0,95 mm long, 0,60-0,75 mm wide, inserted along 1/4-1/3 of the length of the merophyte, the apex blunt, the apical region incurved, the leaf margin entire, the portical margin plane, when spread out forming an angle of 160-180° with the keel; keel smooth, weakly curved, at an angle of 70-90° with the axis, shortly decurrent; median leaf cells small, shortly elongated to isodiametric 15-21(-32) × 11-15(-20) μm, larger towards the leaf base, at the margins smaller and subquadrate, 11 μm high; trigones medium-sized to large, simple triangular to triangular, occasionally confluent, intermediate thickenings rarely present, one per each larger cell wall, elliptic-rounded.

Lobule ± short rectangular, 0,35-0,45 mm long, 0,25-0,40 mm wide, 0,45-0,55 × the length of the lobe, weakly inflated along the keel and rather abruptly flattened towards the free margin, the large flattened part plane, the free margin plane,

Fig. 6. *Blepharolejeunea fuegiana* (Besch. & Mass.) Gradst.-continued

1. habitus. 2. stem transverse section. 3. stem longitudinal section with underleaf attachment (r = rhizoid disc initial cell, s = superior central cell, u = underleaf lamina cell). 4. leaf. 5-6. leaf lobule margin: 5. outer view, 6. inner view with inflexed apical tooth. 7-8. cells of mid leaf; note confluent trigones (t). 9. underleaf. 10. male bract. 11. *Frullania-Ptychanthus*-branch appendages: 11a. dorsal stem half-leaf, 11b. first branch underleaf, 11c. first branch acroscopic leaf.

1,4-7, 10-11 from Hooker s.n., Chili. 2,3,8,9 from Hariot 77, Chili.

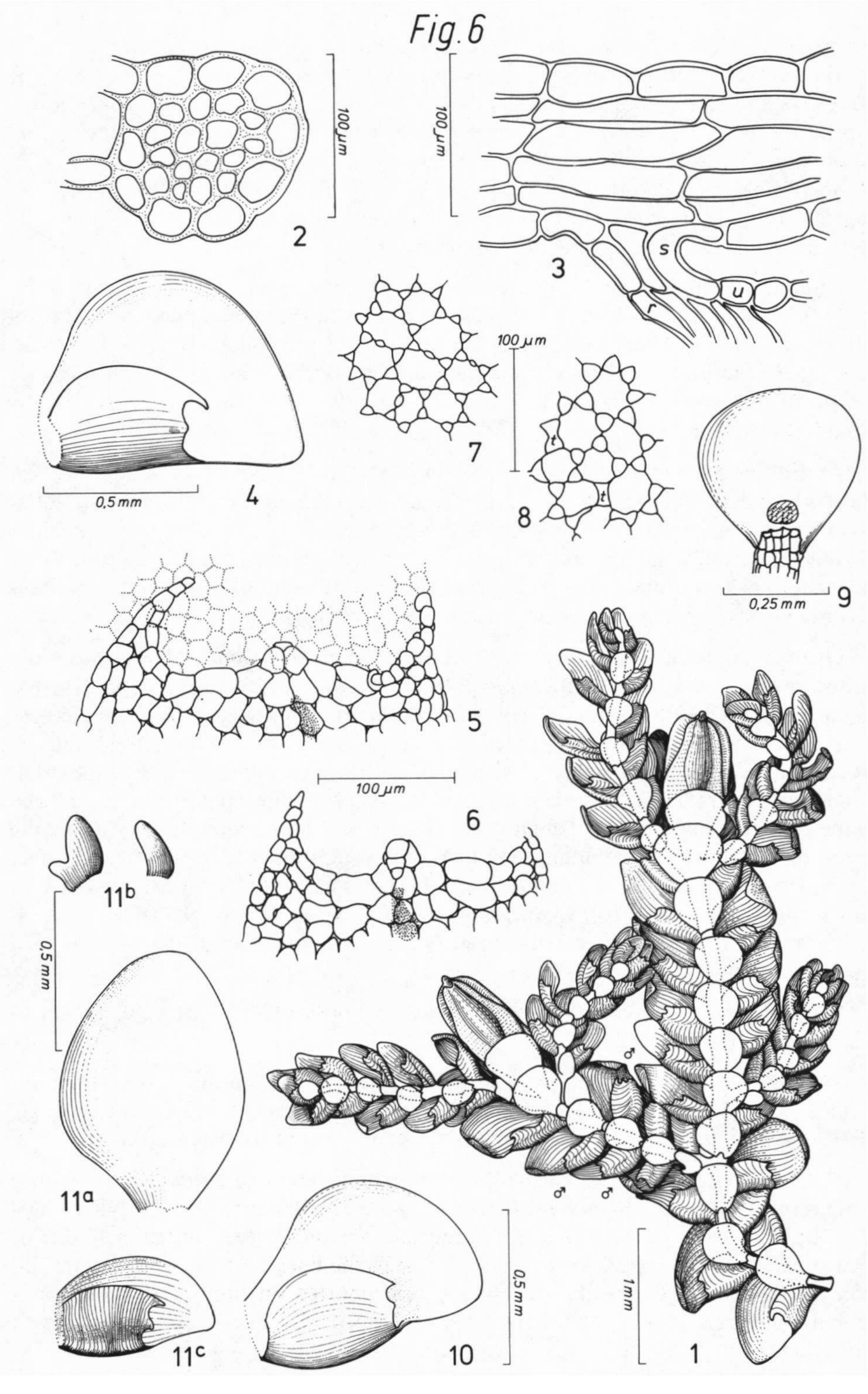


Fig.6

2
100 µm
100 µm
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5
100 µm
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11b
0,5 mm
11a
♂
♂
♂
11c
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1mm
1

truncate, straight from the keel to the second tooth with the apical tooth situated midway, weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the postical margin of the lobe, with two teeth, the apical tooth blunt, inflexed, consisting of 3-5 cells with 1-2 at the base, the second tooth forming a large sharp, straight to curved (not inflexed!) point, consisting of (3-)6-10 cells in total with (1-)2-3 at the base, 4-5 free margin cells between keel and apical tooth, 3-5 free margin cells between apical and second tooth; hyaline papilla one cell below the proximal base of the apical tooth.

Underleaves not to barely imbricated, suborbicular, plane, 0,35-0,50 mm long, 0,32-0,52 mm wide, the apex widely rounded, the bases rounded and shortly decurrent, the widely cuneate insertion 60-115 μm deep; median cells 22-36 × 18-22 μm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc triatratose, 35-54 μm long; rhizoid disc suborbicular, consisting of a few to many small, thinwalled cells.

Androecia located below the gynoecium after 1-2 series of vegetative leaves; bracts and bracteole in 1-3 series, the bracts resembling the leaves but the lobes smaller, ovate, 0,65-0,87 mm long, 0,45-0,60 mm wide, the lobule with a more strongly inflated basal part and a slightly concave distal part, the outline of the free margin as with normal leaves, the bracteoles like the underleaves; bracts monandrous (?, only one degenerated antheridium observed).

Gynoecium terminating stems and long or short *Frullania-Ptychanthus-* and *Lejeunea*-branches, with two *Radula-Jubula*-type innovations, bracts and bracteole in one series; the bract weakly concave, spathulate, 1,07-1,20 mm long, 0,73-0,80 mm wide, the apex blunt to rounded, the keel a sharp angle, the lobule small, ± rectangular, 0,15× the length of the lobe, with a truncate to rounded apex that sometimes bears a blunt, three celled tooth; bract without wing or with a reduced wing that consists only of a small cell row, 108 × 20 μm, running only along the keel; bracteole obovate-oblong, 0,57-0,70 mm long, 0,60-0,63 mm wide, concave, the apex emarginate and slightly recurved. Perianth exserting the bracts for 1/5-1/4, occasionally stalked up to 180 μm, obovoid to obovoid-oblong, 0,90-1,20 × 0,43-0,70 mm, with five sharp, equally sized plicae in the upper half: two ventral, two lateral and one dorsal; beak 4-5 cells long.

Sporophyte not observed; only immature, globose capsules of c. 0,38 mm in diam. present.

DISTRIBUTION: S. Chili (Tierra del Fuego region). Only known from the south temperate region of Tierra del Fuego and the southern Patagonian Channels (Engel 1978). Altitudinal data not available but reconstructed as being from 0-500 m.

ECOLOGY: loosely growing corticolous, often together with *Frullania* spp.; once found together with *Brachiolejeunea spruceana* (Magellan area, s. coll; NY). Engel (1978), in his study of the Brunswick Peninsula, reckons *B. fuegiana* to the group of American temperate species that are restricted to the Fuegian-Brunswick Peninsula. On the Brunswick Peninsula, the species was reported on filmly fern fronds in a climax evergreen *Nothofagus* forest. In the Tierra del Fuego area occurring in moorland.

DIFFERENTIATION: *B. fuegiana* differs from the other species of *Blepharolejeunea* in 1) the obovoid to obovoid-oblong perianth that has five equal and sharp plicae in the upper half, resembling the perianth of the subfam. Lejeuneoideae, 2) the spathulate, weakly concave female bract lobes, 3) the well developed, almost rectangular leaf lobule with its large teeth: 3-5 celled first tooth and 6-10 celled second tooth. 4) the shortly decurrent keel of the leaves, and 5) the small size of the leaf lobe cells: 15-21 × 11-15 μm.

VARIATION: the few specimens examined are morphologically and anatomically very stable. The heterotypic *A. magellanica* is different from the *A. fuegiana* specimens in a) the larger leaf cells, up to 32 × 20 μm, and b) the second leaf lobule tooth which is more reduced and consists of only 3-5(-8) cells with 1-2 at the base. The plants are identical in all other aspects.

3. **Blepharolejeunea incongrua** (Lindenb. & Gott.) van Slag. & Kruijt comb. nov.

Figs. 7, 8, 10

Lejeunea incongrua Lindenb. & Gott., Syn. Hep.: 750 (1847); Gottsche (1863: 281); Stephani (1890: 16, 136). *Dicranolejeunea incongrua* (Lindenb. & Gott.) Steph., Hedwigia 35: 79 (1896), Stephani (1912: 160).

Type: Mexico, Sempoaltepec, Liebmann 170b, VI.1842 (W holo (hb. Lindenberg nr. 6151), C, G 20384, S).

Heterotypic synonym:

Brachiolejeunea nitidiuscula (Gott.) Schiffn., Hedwigia 33: 186 (1894); Stephani (1912: 124); Gradstein et al. (1977: 390) syn. nov. *Phragmicoma nitidiuscula* Gott., Ann. Sci. Nat. Ser. 5(1): 145 (1864); Stephani (1889: 167).

Type: Colombia, Páramo Choachi, 3400 m. Lindig 1739, IX.1860 (G 20220 lecto, BM, MANCH 14083, PC, S).

Plants paroicous, medium-sized, up to 3,5 cm long, 1,1-1,6(-1,75) mm wide, green, light to dark glossy, reddish brown when dry; irregularly branched: part of the plants pseudodichotomous due to floriferous innovations; branches short or long, *Frullania-Blepharolejeunea*-type, *Lejeunea*-type less frequent.

Stem flaccid, 0,10-0,13 mm in diam.; ventral merophyte outside the underleaf insertion 2-4 cellrows wide, the ventral cortical cells subquadrate to short rectangular, 27-55 × 18-32 μm, the dorsal cortical cells subquadrate to short rectangular, 25-40 × 20-27 μm; stem in transverse section with 11-14 thickwalled cortical cells surrounding 15-17 thinwalled medullary cells, the dorsal cortical cells 15-25 μm high, the medullary cells 18-30 μm in diam.

Leaves laxly to densely imbricated. Lobe broadly ovate-falcate to obovate-falcate, 0,75-0,90 mm long, 0,65-0,80 mm wide, inserted along 1/3-1/2 of the length of the merophyte, the dorsal base not auriculate, the apex rounded to minutely apiculate, the apical region incurved, the leaf margin entire, the postical margin plane, when spread out forming an angle of 90-120° with the keel; keel smooth, at an angle of 90-120° with the axis, curved near the base, not decurrent; median leaf cells shortly elongated to isodiametric, 24-30 × 15-25 µm, larger towards the leaf base, at the margins smaller and subquadrate, 13-20 µm high; trigones small to medium-sized, trangular to cordate, intermediate thickenings frequently present, one per each longer cell wall, elliptic-rounded to elongated; oilbodies (Gradstein et al. 1977 sub *Brachiolejeunea nitidiuscula*) homogeneous, *Massula*-type, 10-20 per median leaf cell, ellipsoid to subglobose, 4-6 × 1-2 µm in size.

Lobule rotundate-rectangular, 0,40-0,45 mm long, 0,30-0,45 mm wide, 0,5 × the length of the lobe, inflated along the keel and rather abruptly flattened towards the free margin, the flattened part weakly concave; the free margin plane, truncate, straight from the keel to the second tooth with the apical tooth situated midway, weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the postical margin of the lobe, with two teeth; the apical tooth blunt, inflexed, consisting of 1-2 cells, the second tooth a straight sharp point, consisting of 1-2 cells, one short and two elongated free margin cells between keel and apical tooth as well as between apical and second tooth, the free margin cells usually weakly pigmented contrary to the rest of the lobule cells; hyaline papilla 1-2 cells below the proximal base of the apical tooth.

Underleaves barely imbricated, suborbicular, plane, 0,35-0,50 mm in diam., the apex widely rounded, the bases rounded and shortly decurrent, the cuneate insertion 70-100 µm deep; median cells 18-30 × 13-20 µm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose, 45-70 µm long; rhizoid disc suborbicular, consisting of many small, thinwalled cells.

Androecia located below the gynoecium after 1-2 series of vegetative leaves; bracts and bracteoles in (2-)3-4(-6) series, the bracts resembling the leaves but the lobes smaller, obovate-falcate, 0,65-0,80 mm long, 0,50-0,60 mm wide, the lobule with two *Radula-Jubula*-type innovations; bracts and bracteole in one series, the free margin as with the normal leaves but the second tooth often not developed, the bracteoles like the underleaves; bracts monandrous, antheridium globose, c. 140 µm in diam.

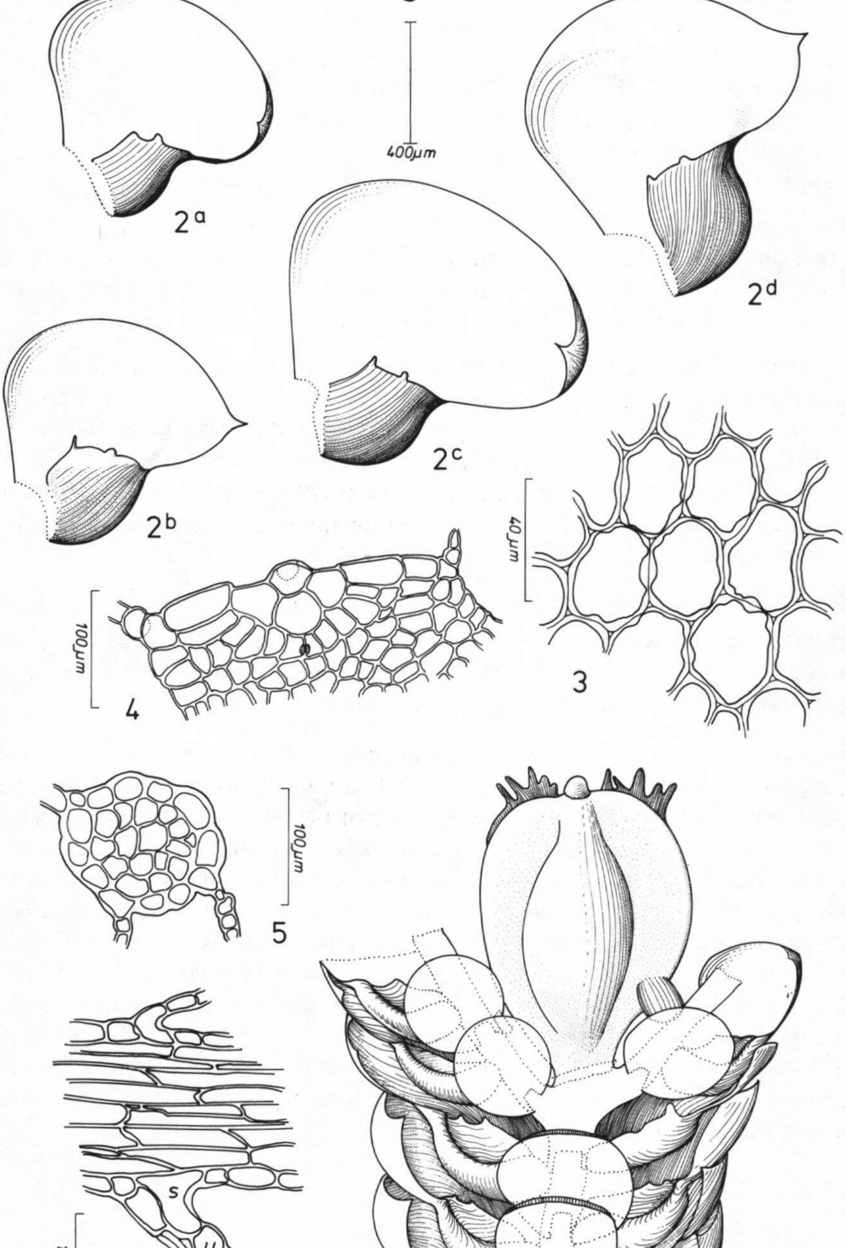
Gynoecium terminating stems and long or short *Frullania* and *Lejeunea* branches, with two *Radula-Jubula*-type innovations; bracts and bracteoles in one series, the bract lobe concave, especially in the apical region, broadly obovate, 0,95-1,20 mm long, 0,70-1,00 mm wide, the apex rounded to minutely apiculate, the keel a sharp

Fig. 7. *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt.

1. habitus ventral. 2. leaves, showing different outline of the lobule (a-d). 3. mid leaf cells. 4. leaf lobule with pigmented marginal cells. 5. stem transverse section. 6. stem longitudinal section with underleaf attachment (r = rhizoid, s = superior central cell, u = underleaf lamina cell).

1 from Gradstein et al. 3570, Ecuador. 2a, 6 from Frahm et al. 808, Peru. 2b, 3-4 from Liebmann 170b, Mexico. 2c from Hegewald 6958, Peru. 2d from Troll 2180a, Colombia. 5 from Aguirre & Gradstein 1326, Colombia.

Fig. 7



angle, the lobule small rectangular, 0,15-0,30× the length of the lobe, with a truncate, occasionally rounded, apex bearing a sharply pointed, 1-3 celled tooth that sometimes expands to 4-10 cells in total with 2-3 cells at the base; bract without wing or with wing at the keel that is a reduced and narrow fold, 180-360 × (15-)35-100 μm, running only along the keel of the bract and not inserted on the innovation; bracteole broadly obovate, 0,60-0,70 mm long, 0,45-0,70 mm wide, concave, the apical part plane to slightly recurved, the apex widely rounded.

Perianth not exserting the bracts when mature but frequently on a 175-350(-520) μm stalk and then exserting the bracts for 1/5-1/3, cuneiform to pyriform, 0,90-1,00 × 0,70-0,80 mm, with one broad ventral plica and two sharp lateral plicae that bear none, or few to many ciliae in the apical region; beak 4-5 cells long.

Sporophyte: seta articulate with a 16 + 4 cell pattern; capsule globose, c. 0,45 mm in diam., splitting to near base into four widely spreading valves, valve inner and outer layer with nodular thickening pattern; spores darkish green, angular when dry, 54-90 μm long, covered with numerous irregular verrucae and 6-11 rosettes of radially oriented spinae and spinulae; elaters (140-)290-360 μm long, 14-18 μm wide, inserted along the margin of the valves and on the inner valve surface, with one, colourless to yellowish-brown, c. 4 μm wide spiral.

Sporeling of the *Lejeunea*-type.

DISTRIBUTION: tropical Andean S. America (Bolivia to Colombia), C. America (Mexico, Costa Rica). Occuring in the high areas of the Andean mountain ranges at (1900-)3100-4100 m altitude. In Costa Rica collected at 2900 m.

ECOLOGY: in loose mats on stems and branches of trees and shrubs, preferably at the edge of wet Andean forests and in wet bamboo páramos as well as in superpáramos. In the páramos, *B. incongrua* is one of the characteristic elements (Gradstein et al. 1977, sub *Brachiolejeunea nitidiuscula*). In Colombia, the species is only recorded from the eastern Cordillera and present in e.g. shrubby communities of *Hypericum laricifolium* and *Aragoa abietina* (Cleef 1981, sub *Brachiolejeunea nitidiuscula*). Occasionally growing terrestric at higher altitudes, (3400-)3700-4100 m, mainly in dense cushions and together with e.g. *Andreaea* spp. (coll. Cleef 1204a, 1889, 7780; coll. Gradstein 4236). *B. incongrua* is also recorded from a trunk in a montane cloud forest in Costa Rica at 2900 m (coll. Griffin 435, 560). Once collected on a palm tree on a town square (coll. Gradstein 3372) at 2500 m. The species apparently tolerates both natural and virtually undisturbed as well as anthropogenous habitats.

Fig. 8. *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt-continued

1. female bracts and bracteole. 2. female bracts. 3. female bract lobule, showing elaborate apex and wing. 4. perianth. 5. perianth dentation.

1,3 from Hegewald 6958, Peru. 2 from Frahm et al. 808, Peru. 4 from Cleef 10047a, Colombia. 5 from Frahm et al. 1145, Peru.

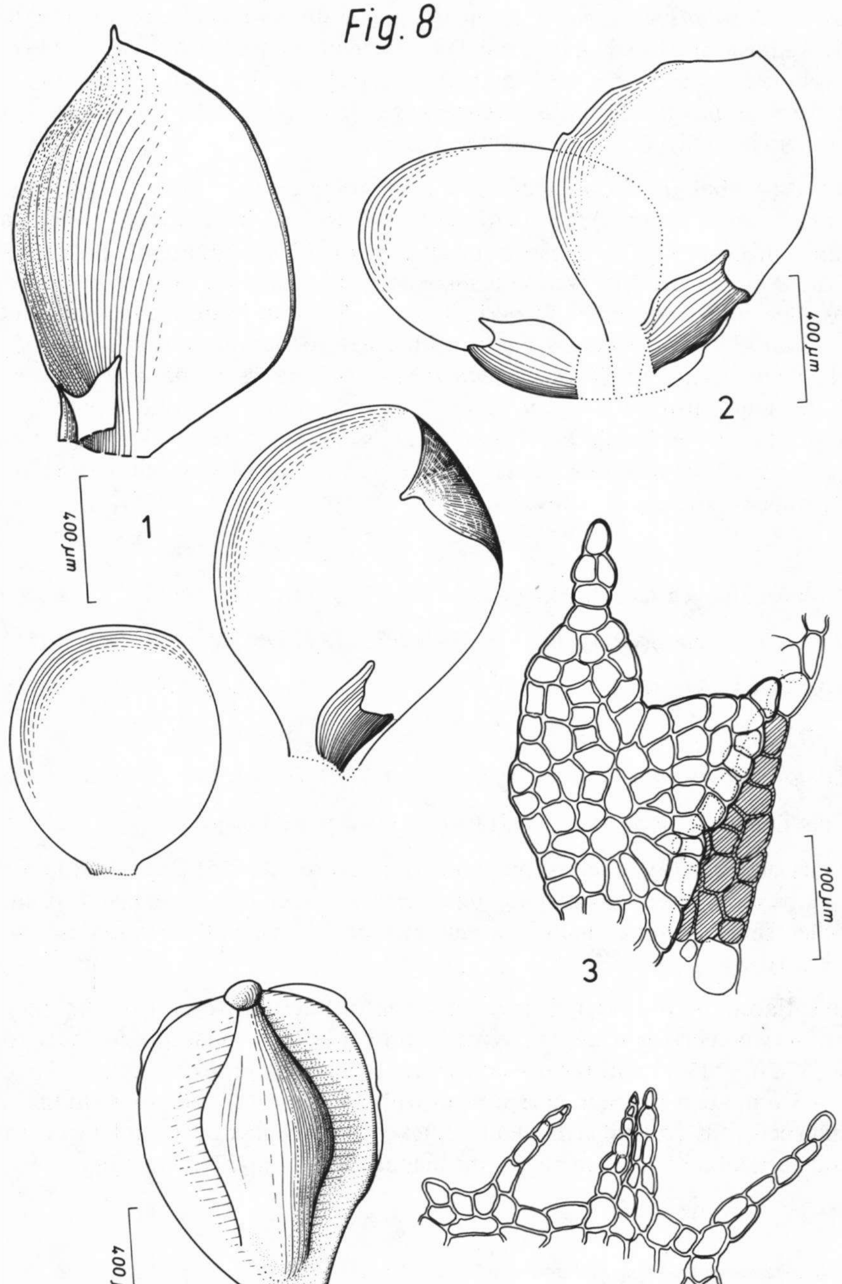


Fig. 8

DIFFERENTIATION: *B. incongrua* and its ally *B. chimantaensis* differ from the other species of *Blepharolejeunea* in 1) their pigmentation of the cells walls, 2) being glossy, reddish brown when dry and 3) by their pigmented free margin cells of the leaf lobule between the keel and the second tooth. Notwithstanding these similarities, *B. incongrua* and *B. chimantensis* differ in a number of characters from each other (see under *B. chimantaensis*).

VARIATION: though *B. incongrua* is morphologically a rather stable species, variation is observed in: 1) the ciliation of the perianth, varying from none to a few to many ciliae (see Fig. 8). Presence or absence of ciliae is apparently not correlated with other characters and even in a single specimen ciliation may vary to a certain extent. Specimens with smooth perianths were previously determined as *Brachiolejeunea nitidiuscula*, whereas plants with ciliate perianths were named *Dicranolejeunea incongrua*. In *Dicranolejeunea* ciliation proves to be a very unreliable character and hardly of use for species circumscription (Kruijt, in prep.); 2) the apical tooth of the female bract lobule varies normally from 1-3 cells, but is occasionally extended to a long and sharp point, consisting of 4-10 cells in total with 3-4 cells at the base (e.g. coll. Hegewald 6958, hb. Hegewald, U; Fig. 8).

4. **Blepharolejeunea saccata** (Steph.) van Slag. & Kruijt comb. nov. Figs. 9, 10

Dicranolejeunea saccata Steph., Hedwigia 35: 78 (1896); Stephani (1912: 168).

Type: Cuba, Wright 1074 (G holo).

Heterotypic synonym:

Blepharolejeunea harlingii S. Arn., Svensk Bot. Tidskr. 56: 335 (1962) syn. nov.

Type: Ecuador, Napo-Pastaza, Harling 3364 p.p. (S holo).

Plants dioicous (?), small to medium-sized, up to 2,0(-2,5) cm long, (0,60-)0,85-1,35 mm wide, green, becoming light brown when dry, irregularly branched, branches short or long, mainly *Lejeunea*-type, occasionally *Frullania-Blepharolejeunea*-type.

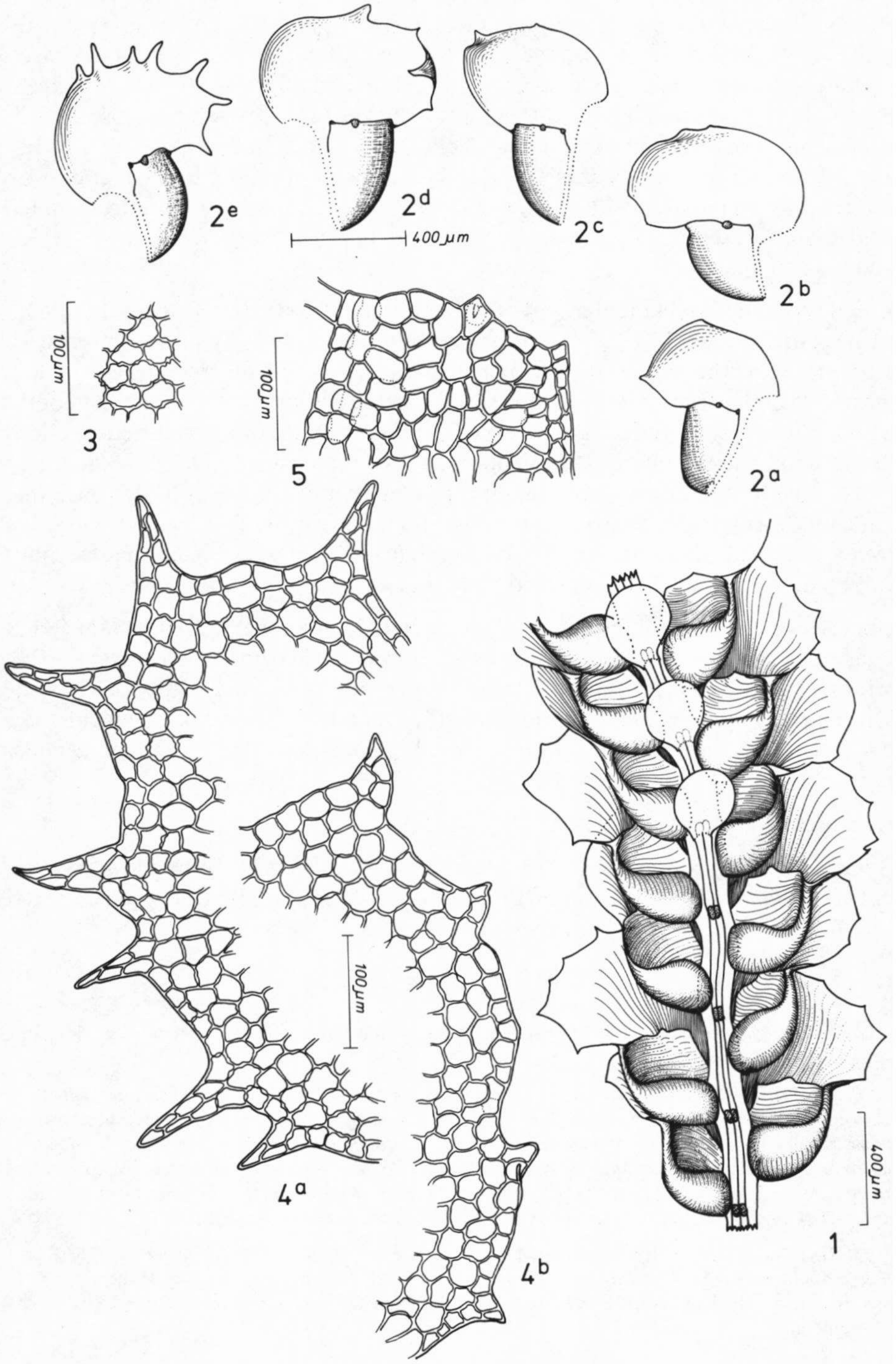
Stem flaccid, 0,10-0,13 mm in diam.; ventral merophyte outside the underleaf insertion two cellrows wide, the ventral cortical cells subquadrate to short rectangular, 35-70 × 35-45 µm, the dorsal cortical cells subquadrate to rectangular, 35-70 × 33-45 µm, stem in transverse section with 9-12 cortical cells surrounding 15-20 medulla cells, the cortical cells slightly thicker than the medulla cells, the dorsal and ventral cortical cells 15-30 µm high, the medullary cells 13-27 µm in diam.

Fig. 9. *Blepharolejeunea saccata* (Steph.) van Slag. & Kruijt

1. habitus ventral. 2a-e. leaves, showing variable dentation. 3. mid-leaf cells. 4a-b. leaf lobe margin, showing variable dentation. 5. leaf lobule.

1,2a,3,4b,5 from Wright 1074, Cuba. 2b from Bisse & Lippold 19065/a2, Cuba. 2c from Standley 57842 p.p., Costa Rica. 2d from Reyes 967, Cuba. 2e,4a from Harling 3364. Ecuador.

Fig. 9



Leaves laxly imbricated. Lobe obovate and strongly falcate, 0,70-1,05 mm long, 0,40-0,60 mm wide, inserted along 1/2 of the length of the merophyte, the apex minutely apiculate, the apical region plane to weakly incurved, the leaf margin with variable dentation: 1-8 teeth, consisting of 1-7 cells in total with 1-3 cells at the base, the postical margin plane, when spread out forming an angle of 90° with the keel, keel smooth, weakly to strongly curved, at an angle of 60-90° with the axis, curved near the base, not decurrent; median leaf cells shortly elongated to isodiametric, 30-45 × 20-27 µm, larger towards the leaf base, at the margins smaller and subquadrate to rectangular, 18-27 µm high; trigones small, cordate to small triangular, intermediate thickenings frequently present, one per each larger cell wall, elliptic-rounded to elongated.

Lobule rotundate-rectangular, 0,43-0,50 mm long, 0,20-0,30 mm wide, 0,5-0,6× the length of the lobe, inflated along the keel and rather abruptly flattened towards the free margin, the flattened part of the lobule concave, the free margin plane, truncate, straight from the keel towards the second tooth with the apical tooth situated midway, straight to weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the postical margin of the lobe, with two teeth; the apical tooth blunt, inflexed, consisting of 1-3(-4) cells, the second tooth a straight, sharp point, consisting of 1-3 cells, five free margin cells between keel and apical tooth, 3-5 free margin cells between apical and second tooth; hyaline papilla 1-2 cells below the proximal base of the apical tooth.

Underleaves distant, suborbicular, plane, 0,20-0,35 mm long, 0,20-0,30 mm wide, the apex widely rounded, the bases rounded and shortly decurrent, the subtransverse to cuneate insertion 72-85 µm deep; median cells 27-33 × 15-27 µm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc tristratose, 48-63 µm long; rhizoid disc suborbicular, consisting of few thinwalled cells.

Androecia not observed.

Gynoecium (only observed in the heterotypic *B. harlingii*!) terminating stems, with two *Radula-Jubula*-type innovations that may be repeatedly floriferous; bracts

Fig. 10. *Blepharolejeunea saccata* (Steph.) van Slag. & Kruijt and *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt.

1-7. *B. saccata*. 1. stem longitudinal section, showing underleaf attachment (r= rhizoid, s= superior central cell, u= underleaf lamina cell). 2. stem transverse section. 3. part of stem ventral, showing underleaf and lobule attachment and ventral merophyte. 4. *Frullania-Blepharolejeunea*-branch, showing dorsal stem half-leaf and first branch leafy appendage (l.a.). 5a-b. first leafy appendage of *Frullania-Blepharolejeunea*-branch. 6. female bracts and bracteole. 7. habitus ventral and female bract and bracteole. 8. *B. incongrua*. 8. first leafy appendage of *Frullania-Blepharolejeunea*-branch.

1 from Reyes 967, Cuba. 2,5b from Wright 1074, Cuba. 3 from Standley 57842, Costa Rica. 4,5a from Bisse & Lippold 19065/a2, Cuba. 6 from Wright 488, Cuba (adapted from Stephani Icones ined.). 7 adapted from Gottsche Icones ined., based probably on Wright 488, Cuba. 8. from Aguirre & Gradstein s.n., Colombia.

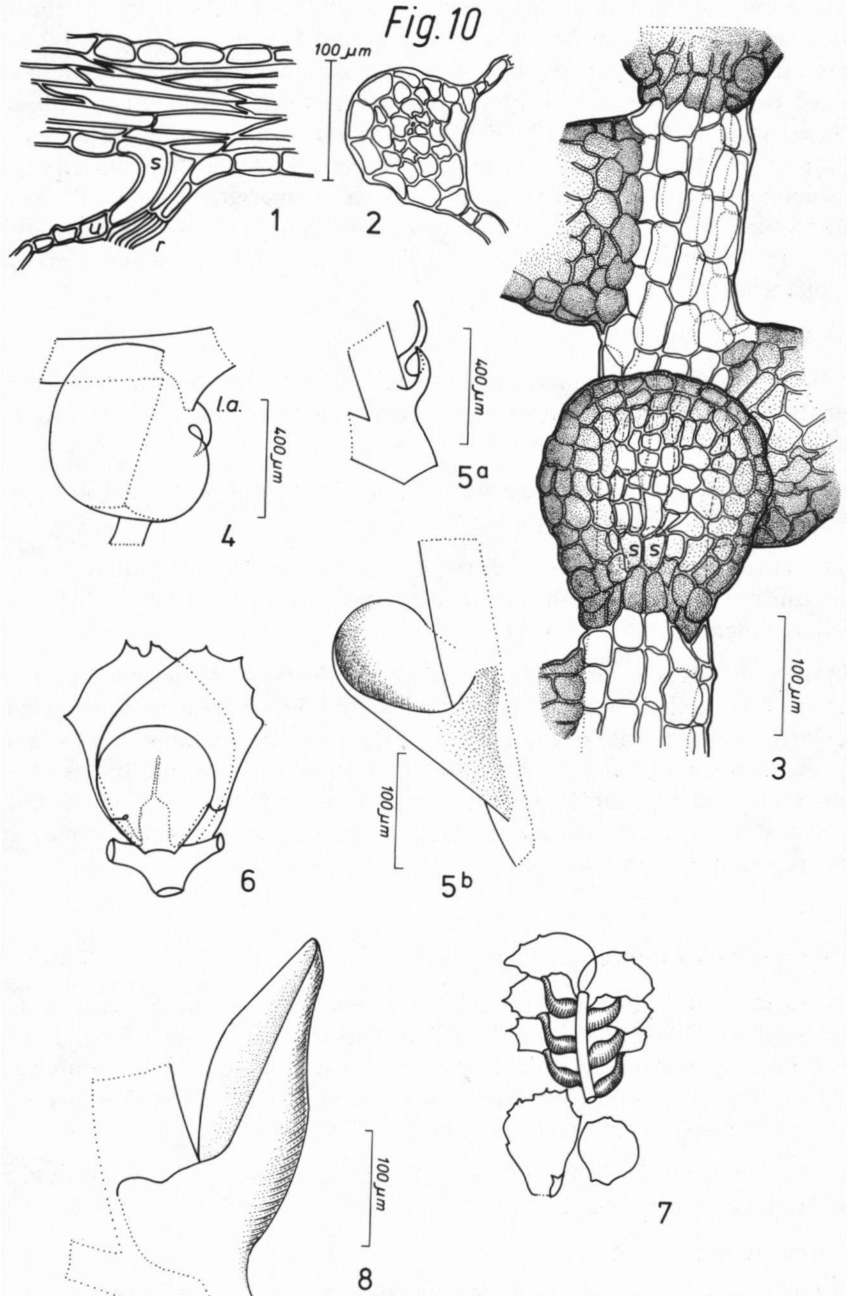


Fig.10

and bracteole in one series, the bract lobe weakly concave, obovate-triangular, 0,70-0,80 mm long, 0,45-0,50 mm wide, the apex broadly rounded to truncate, the apical region irregular ciliate with 7-8 teeth consisting of 4-11 cells in total with 1-3 cells at the base, the keel a sharp angle, the lobule small rectangular, 0,3 × the length of the lobe, the truncate apex with a blunt, one celled apical tooth; bract with a well developed wing at the keel, 180-290 × 50-85 μm, transversally inserted on the innovation; bracteole obovate to obovate-oblong, 0,50-0,60 mm long, 0,30-0,35 mm wide, concave, the apical part plane, the apex emarginate. Perianth exserting the bracts for 1/5, cuneiform 0,70 × 0,52 mm, with one broad ventral plica and two sharp lateral plicae that have a dentate to ciliate wing on the apical and lateral parts; beak four cells long.

Sporophyte not observed.

DISTRIBUTION: Central America, West Indies and Andean South America. Only known from a few, scattered locations on Carribbean islands, Costa Rica and Ecuador, at 1160-1800 m altitude.

ECOLOGY: a small, corticolous species that loosely grows over the substrate, often together with *Ceratolejeunea* spp. and Musci.

DIFFERENTIATION: the species is distinguished by the dentation of the leaf lobe margin, the apical margin of the female bract and of the dorsal stem half-leaf at the *Frullania* branches (Figs. 9.2, 10.6).

VARIATION: the species varies most notably in the dentation of the leaf lobe margin, 1-8 teeth of 1-7 cells in total, (Fig. 9) and of the dorsal stem half-leaf, which is particularly strong dentate in the type of *B. harlingii.* Presumably this variation is also present in the apical region of the perianth and the female bracts, but the extremely toothed type of *B. harlingii* was the only fertile specimen examined. Unpublished icones of *B. saccata* by Stephani show a far less dentate female bract than is present in *B. harlingii.*

5. **Blepharolejeunea securifolia** (Steph.) Schust. Figs. 1, 2, 3

Phytologia 45: 424 (1980). *Brachiolejeunea securifolia* Steph., Spec. Hep. 5: 128 (1912); Schuster (1963: 104), (1980: 762); Gradstein et al. (1981: 239). *Lejeunea* (subg. *Brachiolejeunea*) *securifolia* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 131 (1884) nom. illeg. non Gott. 1882; Stephani (1889): 168. *Oreolejeunea securifolia* (Steph.) Schust., Hep. Anth. N. America 4: 762 (1980).

Type: Ecuador, Quito, Jameson s.n. (NY, YU. The holotype, which should be in MANCH, has not been available).

Heterotypic synonyms:

Brachiolejeunea asplundii Herz., Svensk Bot. Tidskr. 51: 190 (1957); Schuster (1963: 105) syn. nov.

Type: Ecuador, Pichincha, Páramo de Guamaní, Asplund s.n., X.1939 (JE holo).

Brachiolejeunea hans-meyeri Steph., Spec. Hep. 5: 118 (1912); Gradstein et al. (1977: 390) syn. nov.

Lectotype (nov.): Ecuador, Páramo El Altar, Hans Meyer 4220, VII.1903 (G 20133 holo, JE).

Brachiolejeunea schwabei Herz., Rev. Bryol. Lichénol. 23: 60 (1954); Solari (1983: 536) syn. nov.

Type: Chile, Fray Jorge, im Kammwald, 650 m, Schwabe 194 p.p. (The holotype, which should be in JE, has not been available).

?*Oreolejeunea resupinata* (Spruce ex Steph.) Schust., Hep. Anth. N. America 4: 726 (1980) comb. inval.

Plants paroicous, medium-sized, up to 2,5 cm long (rarely pendulous forms up to 6,5 cm!), 1,60-2,20 mm wide, green, becoming light to dark brown when dry, irregularly branched, parts of the plant pseudodichotomous, due to floriferous innovations; branches short or long, *Frullania-Blepharolejeunea*-type, *Lejeunea*-type less frequent.

Stem flaccid 0,10-0,18 mm in diam.; ventral merophyte outside the underleaf insertion 2-4 cellrows wide, the ventral cortical cells subquadrate to short rectangular, 35-63 × 25-35 µm, the dorsal cortical cells subquadrate to rectangular, 30-63 × 27-35 µm; stem in transverse section with 11-14 thickwalled cortical cells surrounding 19-32 thinwalled medullary cells; the dorsal cortical cells 22-45 µm high, the ventral cortical cells 22-35 µm high, the medullary cells (15-)20-27 µm in diam.

Leaves laxly to densely imbricated. Lobe broadly ovate-falcate 0,90-1,40 mm long, 0,70-1,10 mm wide, inserted along 1/3-1/2 of the length of the merophyte, the apex rounded to minutely apiculate, the apical region incurved, the leaf margin entire, the postical margin plane, when spread out forming an angle of 90-120° with the keel; keel smooth, at an angle of 55-90° with the axis, curved near the base, not decurrent; median leaf cells shortly elongated to isodiametric, 27-45 × 15-30 µm, larger towards the leaf base, at the margins smaller and subquadrate, 15-23 µm high; trigones small, cordate to simple triangular, intermediate thickenings frequently present, one per each larger cell wall, elliptic-rounded to elongated; oil bodies (Gradstein et al. 1981 sub *Brachiolejeunea securifolia*) homogeneous, *Massula*-type, 10-15 per median leaf cell, narrow ellipsoid 5-8 × 2-2,5 µm or globose, 2-3 µm, colourless.

Lobule rotundate-rectangular, 0,40-0,60 mm long, 0,35-0,50 mm wide, 0,4-0,5 × the length of the lobe, inflated along the keel and rather abruptly flattened towards the free margin, the flattened part weakly concave; the free margin plane, truncate, straight from the keel to the second tooth with the apical tooth situated midway, almost straight and only weakly curved from the second tooth to the connection with the stem, the free margin not continuing into the postical margin of the lobe, with two teeth; the apical tooth blunt, inflexed, consisting of 1-3 cells, the second tooth forming a straight, sharp point, varying from only one cell to 7-8 cells in total with 3-4 at the base, 3-5 free margin cells between keel and apical tooth, 4-7 free margin cells between apical and second tooth, free margin cells sometimes weakly pigmented; hyaline papilla 1-2 cells below the proximal base of the apical tooth.

Underleaves barely inbricated, suborbicular, plane, 0,50-0,80 mm long, 0,55-0,90 mm wide, the apex widely rounded, the bases rounded and shortly decurrent, the cuneate insertion 90-140 μm deep; median cells 22-42 × 22-25 μm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bi- or tristratose, 40-190 μm long (see introduction); rhizoid disc consisting of few to many (±20) small thinwalled cells.

Androecia located below the gynoecium after 1-4 series of vegetative leaves; bracts and bracteoles in 1-5 series, the bracts resembling the leaves but the lobes smaller, ovate-falcate, 0,60-0,70 mm long, 0,30-0,45 mm wide, the lobule with a more strongly inflated basal part and a concave distal part, the outline of the free margin as with normal leaves but the second tooth often not developed, the bracteoles like the underleaves; bracts monandrous, antheridium globose, c. 140 μm in diam.

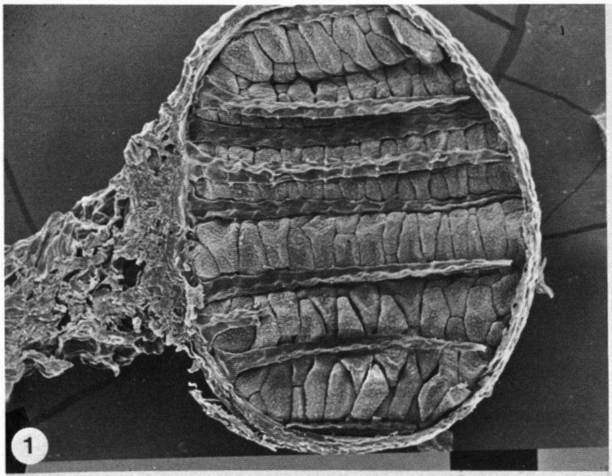
Gynoecium terminating stems or long or short *Frullania* branches, with two *Radula-Jubula*-type innovations; bracts and bracteole in one series, the bract lobe plane, ovate-falcate, 0,95-1,25 mm long, 0,50-0,80 mm wide, the apical region concave, the apex rounded, the keel widely rounded, the lobule rectangular-rhomboid, 0,55-0,65 × the length of the lobe, the apex blunt, no apical tooth developed, bract with wing at the keel that is a small and narrow fold, (160-)220-570 × (30-)75-145 μm, frequently absent, occasionally well developed and up to 610 × 140 μm in size, when present the wing runs along the keel of the bract towards the dorsal-lateral side of the main stem and is not inserted on the innovation; bracteole obovate to broadly so, 0,80-1,00 mm long, 0,45-0,55 wide, the apex widely rounded-truncate, the apical part recurved, the basal part frequently connected with the bract lobules. Perianth exserting the bracts for 1/3-1/2 when mature, frequently on a 350-500(-750!) μm stalk and then sometimes completely exserting the bracts, obovoid to obovoid-oblong, 1,10-1,40 × 0,70-0,80 mm, inflated, with smooth, rounded plicae in the upper 1/3-2/3: two lateral and one broad, frequently sulcate ventral, rarely a small additional plica on the dorsal side; beak 4-5 cells long.

Fig. 11. SEM analysis of the sporophyte of *Blepharolejeunea* S. Arn.

1. Capsule length section, showing marginal elaters and spore storage *in situ* (bar = 100 μm). 2. Capsule transverse section, showing a) marginal elaters (m.e.) in 2 axes meeting at right angles in the centre and b) additional elaters (a.e.) intersecting the four quadrants filled with spores (bar = 100 μm). 3. Valve outer surface, showing thickening pattern (bar = 100 μm). 4. Valve inner surface, showing marginal elaters (m.e.) and additional elaters (a.e.) (bar = 100 μm). 5. Capsule outer surface and articulate seta (bar = 100 μm). 6. Two valves inner surface, showing marginal and additional elaters (bar = 100 μm).

1-2 from Cleef 1990, Colombia. 3 from Cleef 2291, Colombia. 4 from Lukas s.n., Peru. 5 from Griffin et al. 435, Costa Rica. 6 from Gradstein et al. 3372, Ecuador.

1-4 = *B. securifolia* (Steph.) Schust. 5-6 = *B. incongrua* (Lindenb. & Gott.) van Slag. & Kruijt.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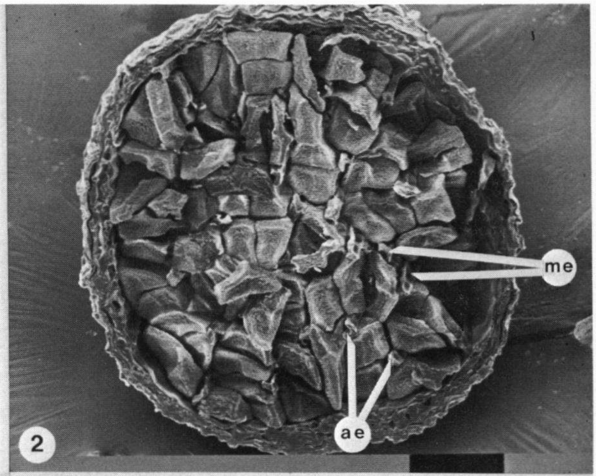
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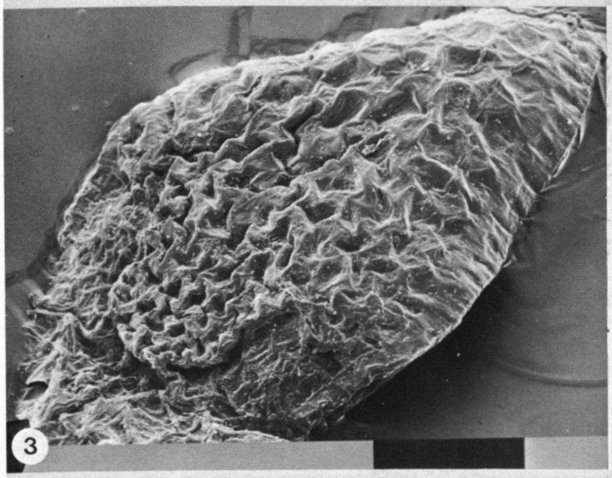
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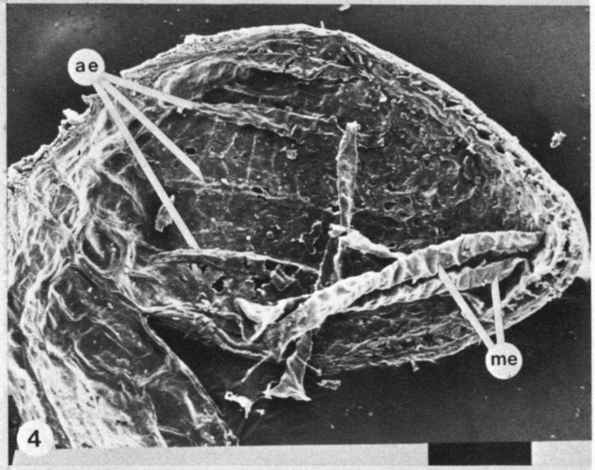
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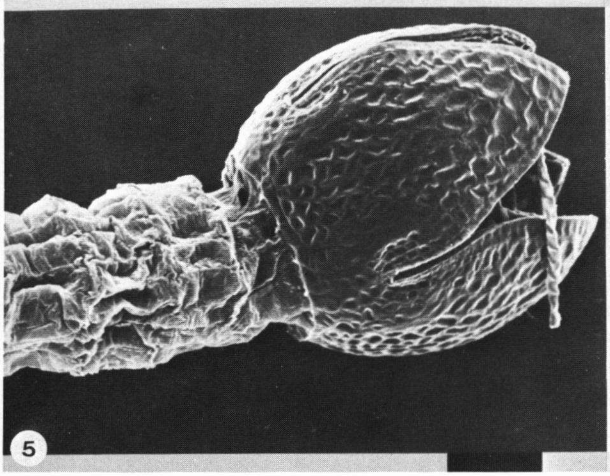
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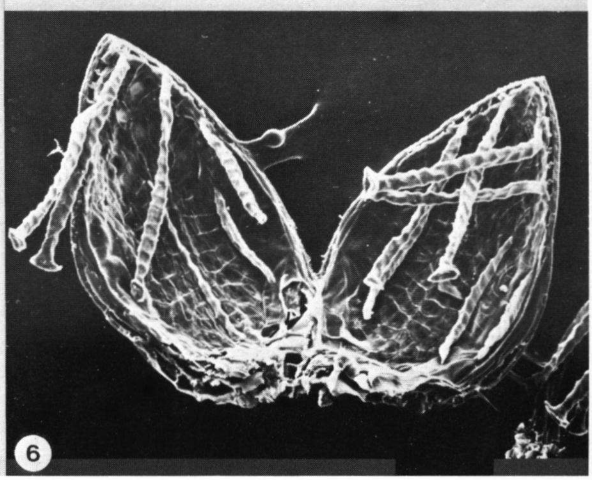
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Sporophyte: seta articulate with 16 + 4 cell pattern; capsule globose, c. 0,60 mm in diam., splitting to near base into four widely spreading valves, valves inner and outer layer with nodular thickening pattern; spores darkish green, angular when dry, 60-95 μm long, covered with numerous short, irregular verrucae; elaters 320-370 μm long, 18-23 μm wide, inserted along the margin and on the inner surface of the valves, with one, colourless, c. 4 μm wide spiral.

Sporeling of the *Lejeunea*-type.

DISTRIBUTION: tropical Andean South America (N. Peru, Ecuador, Colombia), C. America and S.E. Brazil. Occurring in the high areas of the Andean mountain ranges at 3300-4200 m altitude. In Peru collected at 4600 m.

ECOLOGY: in rather loose mats, closely as well as more loosely adnate to stems and branches of trees and shrubs (e.g. *Miconia, Polylepis, Hypericum, Escallonia*) in high Andean forests and páramos (sensu Cleef 1981). At higher altitudes (3800-4200 m) occasionally also growing epilithic. Once reported to grow terrestric in a super-páramo at 4170 m between mosses and *Wernera* sp. (coll. Cleef 8178a). Plants with an unique pendulous (*Omphalanthus*-like!) growth, up to 6,5 cm long, were collected in a Colombian páramo growing on the basis of *Calamagrostis* sp. (coll. Gradstein & Aguirre s.n., 1980). Mats of *B. securifolia* grow often intermingled with other Lejeuneaceae and with *Frullania*.

DIFFERENTIATION: *B. securifolia* is characterized by 1) its obovoid oblong perianth with three rounded plicae in the upper 1/3-2/3; 2) its obovate-falcate female bracts with large rectangular-rhomboid lobules, and 3) by the shape and the number of the free margin cells of the leaf lobule: 3-5 from the keel to apical tooth, 4-7 from apical to second tooth. The margin cells are not pigmented or different in shape from the other lobule cells as in *B. incongrua*, the species most closely related to *B. securifolia*. Besides differences in the characters described above, *B. incongrua* differs from *B. securifolia* by 1) the glossy brown colour when dry and by 2) the small (only 1-2 cells) size of the second tooth of the leaf lobule. The second tooth of the leaf lobule of *B. securifolia* may occasionally become as large as in *B. fuegiana*; differences with that species are discussed under the latter.

VARIATION: *B. securifolia* is morphologically a rather stable species, but some aspects are subject to variation: 1) the wing at the keel of the female bract, usually

Fig. 12. SEM-analysis of the sporophyte of *Blepharolejeunea* S. Arn.-continued.

1. Part of length section, showing marginal elaters and spore storage *in situ* (bar = 40 μm). 2. Spores with elaborate, compound verrucae (bar = 10 μm). 3. Sporoderm, showing verrucate ornamentation with additional wratlike processes (bar = 4 μm). 4. Sporoderm, showing verrucae and a tendency towards rosette formation (bar = 4 μm). 5. Sporoderm, showing verrucae and a distinct rosette (bar = 4 μm). 6. Sporoderm, showing verrucae and a very distinct rosette (bar = 4 μm).

1,4 from Griffin et al. 435, Costa Rica. 2 from Cleef 1990, Colombia. 3 from Lukas s.n., Peru. 5 from Aguirre & Gradstein 1326, Colombia. 6 from Gradstein et al. 3372, Ecuador. 1,4-6 = *B. incongrua* (Lindenb. & Gott.) van Slag. & Kruijt. 2-3 = *B. securifolia* (Steph.) Schust.


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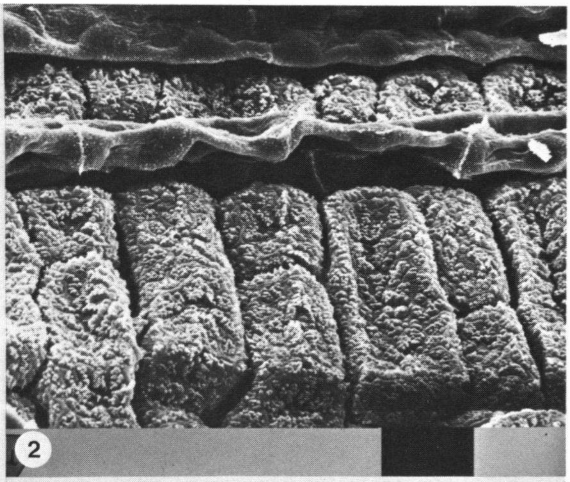
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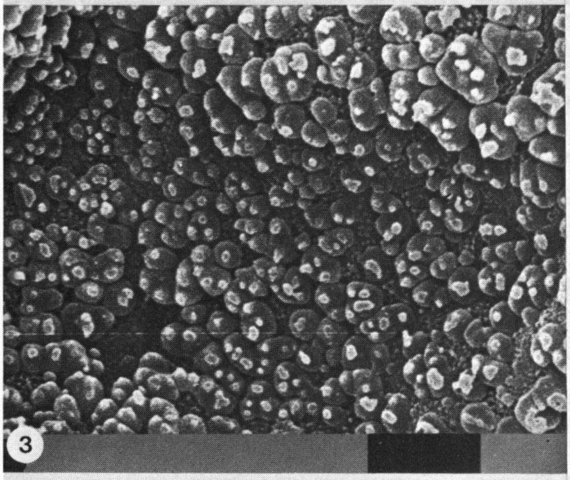
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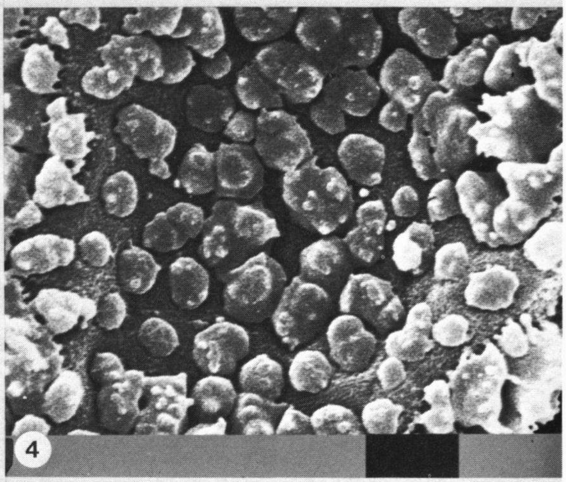
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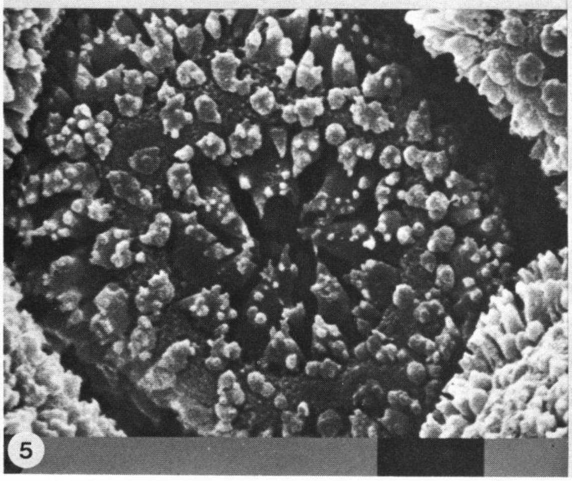
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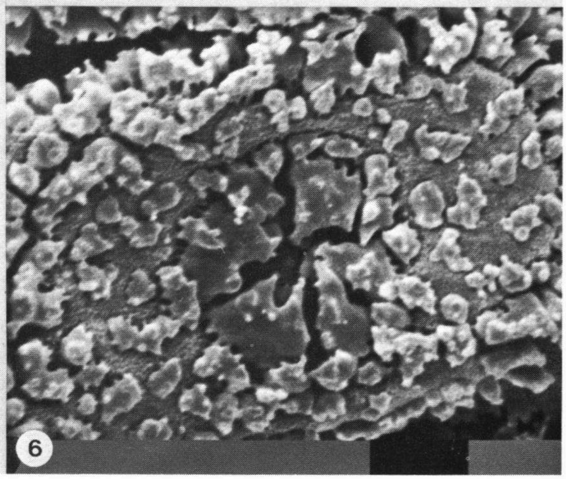
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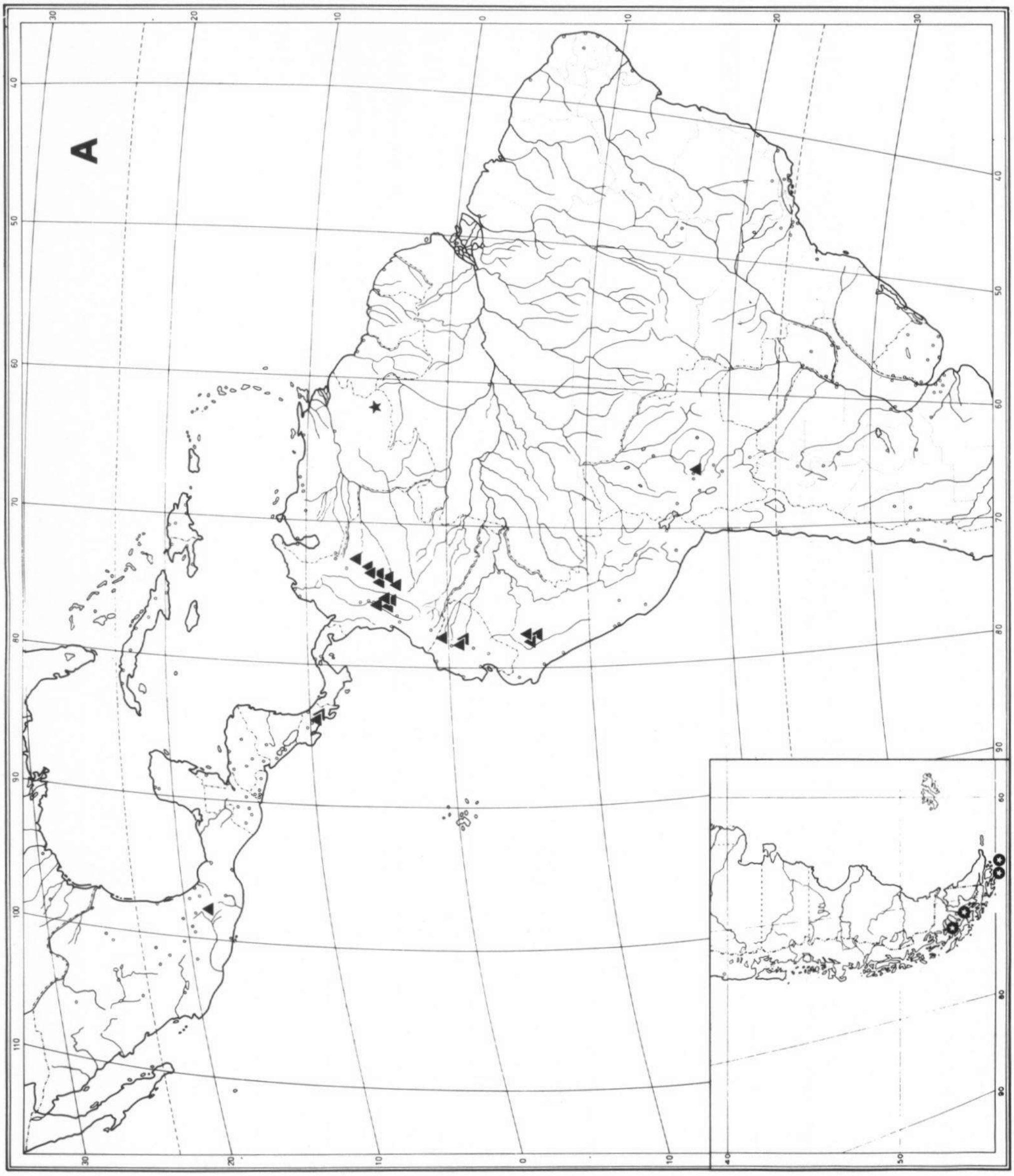
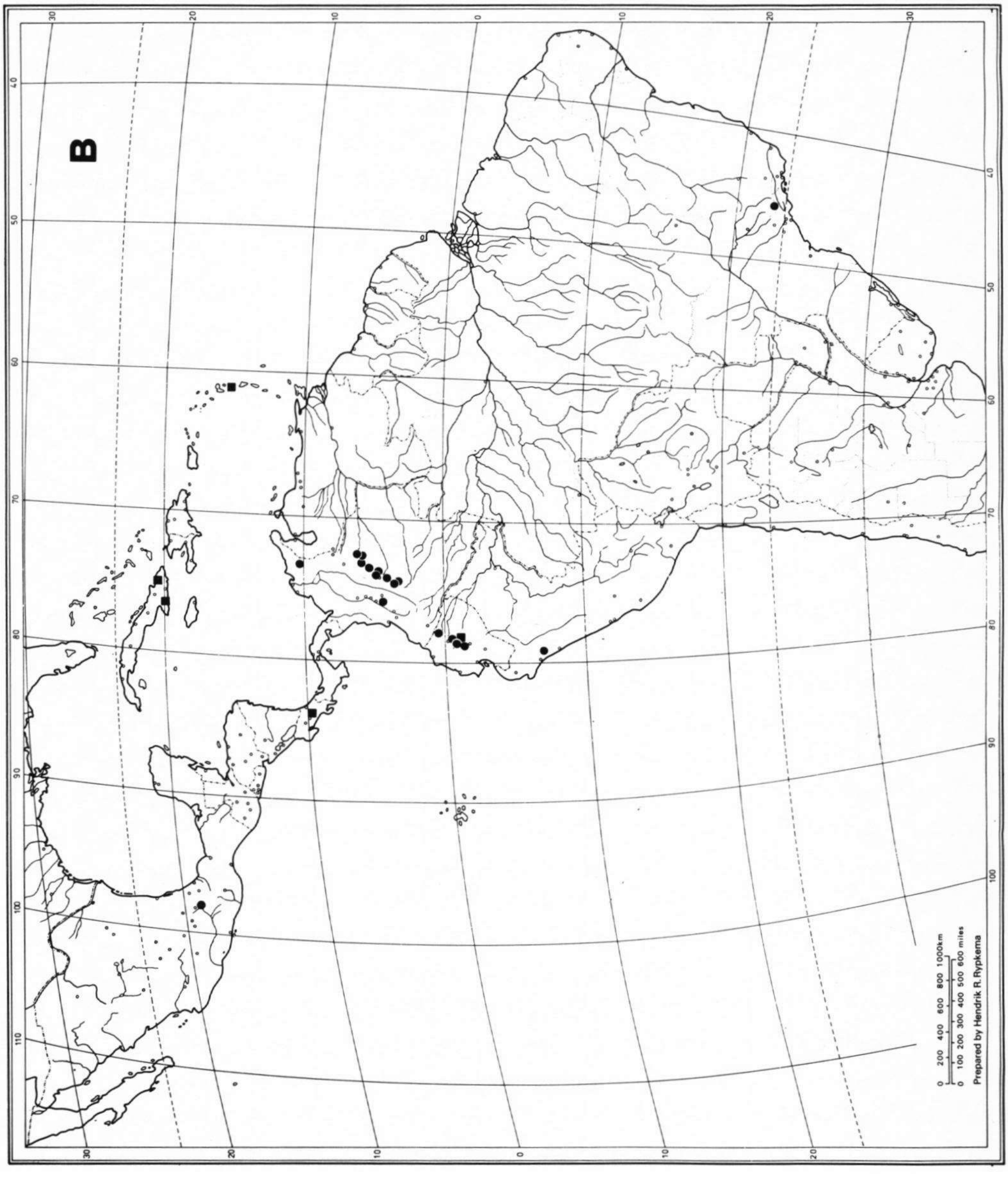


Fig. 13. Distribution of *Blepharolejeunea* S. Arn.

A: ▲ = *B. incongrua* (Lindenb. & Gott.) van Slag. & Kruijt;
★ = *B. chimantaensis* van Slag. & Kruijt;
● = *B. fuegiana* (Besch. & Mass.) Gradst.;



B: ● = *B. securifolia* (Steph.) Schust.;
■ = *B. saccata* (Steph.) van Slag. & Kruijt.

present and averaging 220-470 × 75-120 μm in size, may become much larger, up to 610 × 140 μm, as well as much smaller: only 160 × 30 μm in size. When the wing decreases in size or lacks at all, the bracts become more or less falcate (Fig. 1). 2) The second tooth on the leaf lobule varies from only one cell to 7-8 cells in total with 3-4 cells at the base (see Fig. 2). The length of the perianth stalk varies and may become long (350-750 μm) to such an extent that the perianth emerges completely from the bracts. 4) The underleaf attachment is variable, with two types occurring in this species (see also the introduction). The three-layered *Symbiezidium*-type (Fig. 3) that is 45-90 μm in length and the two-layered *Stictolejeunea*-type (Fig. 3) of which a short form, 40-70 μm long, and an elongated form, 90-190 μm, are present.

Notes:

1) *Brachiolejeunea hans-meyeri* Steph. was made a synonym of *Brachiolejeunea nitidiuscula* (= *Blepharolejeunea incongrua*) by Gradstein et al. (1977), but the involucrum and the free margin of the leaf lobule show that it is clearly conspecific with *Blepharolejeunea securifolia.*

2) type material of *B. schwabei* Herz. was unfortunately not available. Judging from the drawings and description by Herzog (1954), the specimens clearly belong to *Blepharolejeunea securifolia.*

3) *Lejeunea securifolia* Spruce (1884: 131) is illegitimate since it is a later homonym of *Lejeunea securifolia* Gott. (1882: 360 = *Drepanolejeunea securifolia*), as was already noticed by Schuster (1980b). According to the ICBN art. 67.1 note 2 (Voss et al. 1983) the species should therefore be treated as described by Stephani (1912) and consequently cited.

Specimens examined

1. *Blepharolejeunea chimantaensis* van Slag. & Kruijt

See under description.

2. *Blepharolejeunea fuegiana* (Besch. & Mass.) Gradst.

CHILI: Cape Horn, Hooker s.n. (MANCH 15092, VER), the type collection; Hermite Island, Hariot 77, VII.1883 (G 16168, PC); Borja Bay, Vanadis Expedition (G 20790); Cape Horn, s.coll., s.d. (NY).

3. *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt

MEXICO: Sempoaltepec, Liebmann 170b, VI.1842 (W-hb. Lindenberg 6151, C, G 20384, S), the type collection of *Dicranolejeunea incongrua* (Lindenb. & Gott.) Steph. COSTA RICA: Cartago, Cerro Asuncion, macizo Buenavista, Chaverri et al. 1436, 8.VI.1983 (USJ, U); San José, S of Cartago, Griffin et al. 435 & 560, IX.1973 (FLAS, U); COLOMBIA: Antioquía, Llanos de Quivá, Onraedt 83.A.10466, 19.II.1983 (hb. Onraedt); Arauca, Sierra Nevada de Cocuy, Cleef 10047a, VI.1973 (COL, U); Boyacá, Valle de San José, Grubb & Guymer 445a (S), 445b (BM), IX.1957; Boyacá, páramo El Boquerón, Troll 2180a & 2180b, 1929 (NY, S); Boyacá, páramo al NW de Belén, Cleef 1889, II.1972 (COL, U); Boyacá, páramo de la Rusia, Cleef 7253, XII.1972 (COL, U); Boyacá, s.loc. Cleef 9297a, IV.1973 (COL, U); Boyacá, Alto el Paleo above Sácama, Aguirre & Gradstein 2880a & s.n., VIII.1982 (COL, U); Cundinamarca, páramo Choache, Lindig 1739, IX.1860 (BM, G 20220, MANCH 14083, PC, S); the type collection of *Brachiolejeunea nitidiuscula* (Gott.) Schiffn.; ibid., Lindig s.n., IX.1860 (BM, G 20219, G 20221, MANCH 14084, S); Cundinamarca, páramo de Chingaza, Gradstein 4236 (COL, U); Meta, páramo de Sumapaz, Cleef 1204a, I.1972 (COL, U); ibid., Cleef 7780, 7780a & 7881, I.1973 (COL, U); Risaralda, Sta. Rosa de Cabal, Gradstein 3570, VII.1980 (B, BA, BC, BM, COL, COLO, F, FLAS, hb. Fulford, G, hb. Grolle, MEXU, NY, NICH, PC, S, SP, TNS, USJ, VBI; ibid., Aguirre & Gradstein 1282 & 1326, VII.1980 (COL, U); ibid., van Reenen 798, 22.I.1980 (COL, U); Tolima, Sta. Isabel, Aguirre & Gradstein 1503, 1595 & 1650, VII.1980 (COL, U). ECUADOR: Cotopaxi, Gradstein et al. GSV 75 & GSV 100, VI.1976 (U); Imbarura, Otavala, Gradstein et al. 3372, IV. 1976 (U). PERU: Amazonas, Chachapoyas, Hegewald 6958, VIII.1973 (hb. Hegewald, U) & Hegewald 6960b, VIII.1973 (JE, hb. Hegewald); Amazonas, Chachapoyas, road Cajamarca-Chachapoyas, Frahm et al. 1145, IX.1982 (B, BA, C, COL, COLO, DUIS, F, FLAS, G, H, KRA, MEXU, NICH, NY, S, SP, PRC, VBI); ibid., Frahm et al. 1187, IX.1982 (B, U); San Martin, Rioja, road Chachapoyas-Moyabamba, Frahm et al. 808, VIII.1982 (B, U). BOLIVIA: Cochabamba, Herzog s.n., hb. Levier 6083, I.1908 (G 20135, U, YU); s.loc., Wallis s.n., s.d. (BM).

4. *Blepharolejeunea saccata* (Steph.) van Slag. & Kruijt

COSTA RICA: San José, Standley 57842 p.p., 9.III.1926 (JE). CUBA: s.loc., Wright 1074 (G), the type collection; s.loc., Wright 448 (G 22705), Wright s.n. (BM); Holguín, Reyes 967 (HAC, U); Oriente, Sierra Maestra, Bisse & Lippold 19065/a2 (JE). DOMINICA: s.loc., Elliot s.n., s.d. (JE). ECUADOR: Napo-Pastaza, Mera, Harling 3364, XI.1958 (S), the type collection of *B. harlingii* S. Arnell.

5. *Blepharolejeunea securifolia* (Steph.) Schust.

MEXICO: Amecameca, Eggers & Frahm 792219, II.1979 (hb. Eggers, U). COSTA RICA: Macizo Buenavista, Chaverri et al. 1577, 22.VII.1983 (USJ, U). BRAZIL: Itatiaia, Vital s.n., IX.1974 (SP, U). COLOMBIA: Boyacá, Nevado de Cocuy, Bischler 2795 & 2898, VI.1959 (COL, PC, U); ibid. Grubb & Guymer B44A, B44B &B46A, VII.1957 (BM, S), B102e & B416, IX.1957 (BM); Boyacá, Belén, Cleef 1990, 2291 & 2292b, II-III.1972 (COL, U); Boyacá, páramo de Pisva, Cleef & Florschütz 5970a, X.1972 (COL, U); Boyacá, Sácama, Aguirre & Gradstein 2856, VIII.1982 (COL); Boyacá, road Socha-Sácama, Aguirre & Gradstein 2861a, 15.VIII.1982 (COL, U); Cundinamarca páramo de Chisacá, Gradstein & Aguirre 3642, VIII.1980 (COL,U); ibid. Cleef 212a, XII.1971 (COL, U); Cundinamarca, páramo de Cruz Verde, Cleef 2795, IV.1972 (COL,U); ibid., Onraedt 78.A.6019, 78.A.6027, 78.A.6044 & 78.A.6045/b, 7.VIII.1978 (COL, JE, hb. Grolle, hb. Onraedt, U); Cundinamarca, páramo between Cogua and San Cayetano, Cleef 6432a, XI.1972 (COL, U); Cundinamarca, páramo de Palacio, Cleef 6723a, XI.1972 (COL, U); Cundinamarca, alto de Chorreras, Cleef 8350a, I.1973 (COL, U); Cundinamarca, Bogotá, Troll 2181/a (NY) & 2210/a, 1929 (JE); Magadalena, Sierra Nevada de Santa Marta, Winkler C326, I.1967 (hb. Winkler, U); Meta, páramo de Sumapaz, Cleef 942a, I.1972 (COL, U); Meta, Cerro Nevado del Sumapaz, Cleef 7880b & 8178a, I.1973 (COL, U); Risaralda, volcan Isabel, Gradstein & Aguirre s.n., VII.1980 (COL, U); s.loc., Funck & Schlim s.n., s.d. (NY). ECUADOR: Carchi, páramo El Angel, Gradstein et al. 3457, 4.IV.1976 (U); Pichincha, Espinosa s.n., 1933 (JE); Pichincha, páramo de Guamani, Asplund s.n., X.1939, the type of *Brachiolejeunea asplundii* Herz. (JE, S); Quito, Jameson s.n., s.d., the type collection (NY, YU); páramo El Altar, Hans Meyer 4420 (the type of *Brachiolejeunea hans-meyeri* Steph. & 4225, VII.1930 (G 20133 & 20134, JE). PERU: Ancash, Huaraz, Philippi P-253, IX-X.1982 (B, U); Cordillera Blanca, Lukas s.n., V.1932 (JE).

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References

ARNELL, S. 1962. Contribution to the knowledge of the Hepaticae of Ecuador. Svensk Bot. Tidskr. 56: 334-350.

BESCHERELLE, E. & MASSALONGO, C.B. 1886. Hepaticae Novae Americanae Australis (suite). Bull. Mens. Soc. Linn. Paris 80: 637-640.

BONNER, C.E.B. 1978. Index Hepaticarum IX: 405-745. Vaduz.

CLEEF, A.M. 1981. The vegetation of the páramos of the Colombian Cordillera Oriental. Diss. Bot. 61: 1-321. Vaduz.

CRANDALL, B. 1969. Morphology and development of branches in the leafy Hepaticae. Beih. Nova Hedwigia 30: i-vii, 1-261.

DUSÉN, P. 1903. Beiträge zur Bryologie der Magellansländer, von West Patagonien und Südchile. Ark. Bot. 1: 441-465.

ENGEL, J.J. 1978. A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. Fieldiana, Bot. 41: i-viii, 1-319.

FULFORD, M. 1961. The shoot sporophyte relationship in *Brachiolejeunea laxifolia*. Bull. Bot. Univ. Saugar 13: 6-12.

GEISSLER, P. & GRADSTEIN, S.R. 1982. SEM-studies on sporophyte characters in Lejeuneaceae (Ptychanthoideae), a preliminary report (Studies on Lejeuneaceae subfam. Ptychanthoideae VIII). J. Hattori Bot. Lab. 53: 127-131.

GOTTSCHE, C.M., LINDENBERG, J.B.G. & NEES VON ESENBECK, C.G. 1844-1847. Synopsis Hepaticarum. Fasc. 5: 625-834 (1847).

GOTTSCHE, C.M. 1863. De Mexikanske Levermosser. K. Danske Vid. Selsk. Skrifter, Ser. 5, Naturw. og Math. Afd. 6: 97-380.

GOTTSCHE, C.M. 1864. Hepaticae *in* J.J. Trianon & J.E. Planchon: Prodromus Florae Novo-Granatensis. Ann. Sci. Nat. 5: 95-198.

GOTTSCHE, C.M. 1882. Reliquiae Rutenbergianae. Lebermoose. Abh. Naturwiss. Ver. Bremen 7: 338-365.

GRADSTEIN, S.R. 1979. The genera of Lejeuneaceae: past and present. Syst. Ass. Spec. Vol. 14: 83-107.

GRADSTEIN, S.R. & BUSKES, G.M.C. 1984. A revision of neotropical *Archilejeunea*. Beih. Nova Hedwigia 80

GRADSTEIN, S.R., CLEEF, A.M. & FULFORD, M. 1977. Studies on Colombian cryptogams. II. Hepaticae-oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. Proc. Kon. Ned. Acad. Wetensch. Ser. C, vol. 80: 377-420.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Studies on Colombian cryptogams. XIII. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

GRIFFIN III, D., GRADSTEIN, S.R. & AGUIRRE—C., J. 1982. Studies on Colombian cryptogams. XVII. On a new antipodal element in the neotropical páramos - *Dendrocryphaea latifolia* sp. nov. (Musci). Acta Bot. Neerl. 31: 175-184.

GROLLE, R. 1982. *Trocholejeunea* fossil in Europa. J. Hattori Bot. Lab. 51: 175-193.

GROLLE, R. 1983. Nomina Generica Hepaticarum; references, types and synonymies. Acta Bot. Fenn. 121: 1-62.

HÄSSEL DE MENENDEZ, G.G. & GREENE, S.W. 1980. Patagonian bryophytes 1. The occurence of the hepatic *Eopleurozia paradoxa* (Jack) Schust. in Southern Chile. Lindbergia 6: 32-36.

HERZOG, Th. 1954. Zur Bryophytenflora Chiles. Rev. Bryol. Lichénol. 23: 27-99.

HERZOG, Th. 1957. Lebermoose aus Ecuador gesammelt von Dr. E. Asplund. Svensk Bot. Tidskr. 51: 187-196.

MIZUTANI, M. 1970. Branching types of Lejeuneaceae. Misc. Bryol. Lichenol. 5: 81-90.

SCHIFFNER, V. 1894. Revision der Gattungen *Bryopteris, Thysananthus, Ptychanthus* und *Phragmicoma* im Herbarium des Berliner Museums. Hedwigia 33: 170-189.

SCHUSTER, R.M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae. Beih. Nova Hedwigia 9: 1-203.

SCHUSTER, R.M. 1980a. New combinations & taxa of Hepaticae. I. Phytologia 45: 415-437.

SCHUSTER, R.M. 1980b. The Hepaticae and Anthocerotae of North America. IV. i-xviii, 1-1334. New York.

SOLARI, S.S. 1983. Lejeuneaceae catálago de especias Andino-Patagonicas. J. Hattori Bot. Lab. 54: 533-553.

SPRUCE, R. 1884-1885. Hepaticae Amazonicae et Andinae. Trans. & Proc. Bot. Soc. Edinburgh 15: i-xi, 1-590.

STEPHANI, F. 1889. Hepaticae Australiae II. Hedwigia 28: 155-175.

STEPHANI, F. 1890. Die Gattung *Lejeunea* im Herbarium Lindenberg. Hedwigia 29: 1-23, 68-99, 133-142.

STEPHANI, F. 1896. Hepaticae Species Novae IX. Hedwigia 35: 73-140.

STEPHANI, F. 1898-1924. Species Hepaticarum. I-VI. Geneva. (*Archilejeunea* in Vol. IV: 703-735, dated 1911; *Brachiolejeunea* in Vol. V: 110-142, dated 1912; *Dicranolejeunea* in Vol. V: 156-170, dated 1912).

STOTLER, R. & CRANDALL, B.J. 1969. The sporophyte anatomy of *Dicranolejeunea axillaris.* Bryologist 72: 387-397.

VAN SLAGEREN, M.W. 1984. Taxonomic studies on the genus *Brachiolejeunea* (Spruce) Schiffn., a preliminary report. Proceedings of the II Meeting of Central and Eastern European bryologists, Charles University, Prague, 4pp.

VOSS, E.G. et al. 1983. International Code of Botanical Nomenclature. Regn. Veget. III: i-xv, 1-422. Utrecht.

WINKLER, S. 1970. Zur Anatomie der Rhizoidplatten neotropischer holostiper Lejeuneaceen. Rev. Bryol. Lichénol. 37: 47-55.

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NOTE ADDED IN PROOF: Recently Dr. S.R. Gradstein was able to study oil bodies of fresh material of *Blepharolejeunea incongrua* and *B. securifolia.* His observations showed *Jungermannia* rather than *Massula*-type oil bodies in both species. In *B. incongrua* 15-30 oil bodies per median leaf cell were present; each oil body faintly segmented in 3-8 globules. In *B. securifolia* 15-30 oil bodies were present, very small, narrow ellipsoid to subglobose; each oil body made up of 4-10 granules. The presence of *Jungermannia*-type oil bodies shows an affinity of the genus *Blepharolejeunea* rather to *Dicranolejeunea,* where this type of oil bodies has also been found, than to *Brachiolejeunea* which possesses only *Massula*-type oil bodies.

BEIHEFT 80 ZUR NOVA HEDWIGIA

6 | A preliminary Revision of the Genus Dicranolejeunea (Spruce) Schiffn.

by

R. Ch. Kruijt

ABSTRACT: The present paper is preliminary to a monographic treatment of the pantropical genus *Dicranolejeunea* (Spruce) Schiffn. Nine species are recognized: *D. axillaris, D. aberrans* (new to Africa), *D. phyllorhiza* (new to Africa), *D. chrysophylla, D. johnsoniana, D. madagascariensis, D. gilva, D. javanica* and *D. yoshinagana.* The genus *Acanthocoleus* Schust. is reduced to subgeneric rank under *Dicranolejeunea.* Numerous new synonyms are proposed.

Introduction

Spruce erected *Dicranolejeunea* as a subgenus of *Lejeunea* in 1884, containing 4 species of which 3 were new. Schiffner (1893) raised *Dicranolejeunea* to generic rank. Evans (1914) gave the first sharp delimitation of the genus and choose *Dicranolejeunea axillaris* (Nees & Mont.) Schiffn. as the lectotype. Grolle (1966) compared the genus with the allied genera *Lopholejeunea* and *Marchesinia* and Jones (1970) discussed the differences between *Marchesinia* and *Dicranolejeunea.*

Schuster (1970) erected the monotypic genus *Acanthocoleus* Schust., which is reduced here to synonymy under *Dicranolejeunea* as was already suggested by Gradstein (1975). 65 Binomina have been ascribed to *Dicranolejeunea,* most of them from tropical America and fewer from Africa and Southeast Asia. Preliminary to a monographic treatment of the genus (Kruijt, in prep.), this paper presents the main results of the revision of these binomina. Furthermore, a subdivision of *Dicranolejeunea* into two subgenera is presented.

Dicranolejeunea and Acanthocoleus

Schuster (1970) erected the monotypic genus *Acanthocoleus* with the species *A. fulvus* Schust. from the West Indies. "Primarily generic" characters were given in italics. Gradstein (1975) placed *Acanthocoleus* near *Dicranolejeunea* as none of the

Studies on Lejeuneaceae subfam. Ptychanthoideae XI characters given by Schuster (l.c.) seemed sufficient for separating it from that genus. Although the type specimen of *A. fulvus* was unfortunately not received on loan, a comparision between *A. fulvus* and *Dicranolejeunea* can be made based on Schusters excellent description and drawings of *A. fulvus.*

Characters used by Schuster to delimit *Acanthocoleus* are: the 5-keeled perianth, the numerous, segmented oil bodies, the branching type, the stem anatomy, the acute, deflexed leaf apex, the bidentate lobule, the presence of one, sterile innovation and the female bracts with their reduced lobules. I have made drawings of all these characters, except of the branches and innovation (Figs. 1b, c, d, f, g, j, k). The 5-keeled perianth of *Acanthocoleus fulvus* is similar to the perianth of *Dicranolejeunea aberrans* (Lindenb. & Gott.) Steph., a species known from the West Indies, Central and South America and Africa (Figs. 1f, g). This perianth character is not at all stable as 3-, 4- and 5-keeled perianths may occur in this species (collections from Jamaica and Mexico). Oil bodies of *Acanthocoleus fulvus* are also essentially similar to those of *Dicranolejeunea aberrans* (and of *D. axillaris*) described by Gradstein et al. (1977, sub *D. loxensis*). My study has further revealed that the mixed presence of *Frullania* and *Lejeunea*-type branching, considered characteristic for *Acanthocoleus fulvus*, is also found in all species of *Dicranolejeunea,* including *D. aberrans.* The presence of a *Radula-Jubula*-type innovation (Schuster 1970, Fig. 2-10) in *A. fulvus,* is similar to all but one species (*D. javanica*) of *Dicranolejeunea. D. aberrans* has one or two innovations. The underleaves of *Acanthocoleus* are similar to those of *Dicranolejeunea aberrans* (Fig. 1e). The free margin of the leaf lobule of *Acanthocoleus* is ± the same as in *Dicranolejeunea aberrans* (Fig. 1c) and the stem structure is at least resembling that of a Mexican collection of *D. aberrans* (Eggers & Frahm 32), including the thickened ventral medullary cells (Fig. 1d). The cross-section of the perianth of *Acanthocoleus* (Schuster 1980, p. 724, Fig. 645-10) shows two ridges on the keels. These are also found on the ventral keels of the perianths of the above mentioned Mexican specimen of *D. aberrans* (Fig. 1h).

It is concluded that there are no essential characters to separate *Acanthocoleus fulvus* and *Dicranolejeunea aberrans. A. fulvus* is therefore reduced to synonymy under *D. aberrans.* Consequently, *Acanthocoleus* and *Dicranolejeunea* are considered congeneric. Reasons for giving subgeneric status to *Acanthocoleus* are given below.

Subdivision of Dicranolejeunea and conspectus

Dicranolejeunea axillaris (Nees & Mont.) Schiffn., the type species of the genus, differs from the other species of *Dicranolejeunea* is a number of features (characters of the other species in brackets):

a) stem cortex with outwardly bulging cells (without) and the outer medullary layers thickened (unthickened or ventrally slightly thickened), cf. Figs. 1a and d,

b) leaves suberect convoluted when dry (± convoluted leaves but not in the typical suberect position),

c) female bracteole toothed (entire),
d) perianths not stalked (stalked).

In view of the importance of stem anatomy (a) and leaf position (b) in the taxonomy of *Ptychanthoideae* (Gradstein 1975), a subdivision of *Dicranolejeunea* into two subgenera based on these characters is proposed: subg. *Dicranolejeunea* (*D. axillaris* only) and subg. *Acanthocoleus* (Schust.) stat. et comb. nov. (all other species).

DICRANOLEJEUNEA (Spruce) Schiffn.

Engler & Prantl, Nat. Pfl.-fam. I, 3: 128 (1893); Evans (1914: 320). *Lejeunea* subg. *Dicranolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 138 (1884).

Lectotype (Evans 1914): *Dicranolejeunea axillaris* (Nees & Mont.) Schiffn.

DICRANOLEJEUNEA subg. **Dicranolejeunea**

1. **Dicranolejeunea axillaris** (Nees & Mont.) Schiffn.

Engler & Prantl, Nat. Pfl.-fam. I, 3: 128 (1893); Stephani (1912: 163); Evans (1914: 320); Gradstein et al. (1977: 394); Mizutani (1980: 235). Basionym: *Lejeunea axillaris* Nees & Mont., Ann. Sci. Nat. Paris, Bot. 5: 59 (1836); Syn. Hep.: 317 (1845).

Heterotypic synonyms:

Dicranolejeunea ciliatiflora (Spruce) Steph., Spec. Hep. 5: 164 (1912) syn. nov.

Dicranolejeunea dubiosa (Lindenb. & Gott.) Steph., Spec. Hep. 5: 165 (1912) syn. nov.

Dicranolejeunea hypoacantha (Spruce) Steph., Spec. Hep. 5: 166 (1912) syn. nov.

Dicranolejeunea longissima Steph., Spec. Hep. 5: 161 (1912) syn. nov.

Dicranolejeunea pulcherrima Steph., in Herzog, Bibl. Bot. 87: 255 (1916) syn. nov.; Stephani (1923: 384).

?*Dicranolejeunea tridentata* Winkler, Rev. Bryol. Lichénol. 42: 810 (1976) syn. nov.

Lejeunea mexicana Lindenb., Syn. Hep.: 325 (1845) (synonymy fide Stephani 1912 and Gradstein pers. comm.).

DISTRIBUTION: Central and South America.

DICRANOLEJEUNEA subg. **Acanthocoleus** (Schust.) Kruijt stat. et comb. nov.

Acanthocoleus Schust., Bull. Torrey Bot. Club 97: 339 (1970).

Type: *A. fulvus* Schust. (= *Dicranolejeunea aberrans* (Lindenb. & Gott.) Steph.).

2. **Dicranolejeunea aberrans** (Lindenb. & Gott.) Steph.

Spec. Hep. 5: 158 (1912). Basionym: *Lejeunea aberrans* Lindenb. & Gott., Syn. Hep.: 751 (1847); Gottsche (1863: 284).

Heterotypic synonyms:

Dicranolejeunea acuminata (Lindenb. & Gott.) Steph., Spec. Hep. 5: 159 (1912). This synonymy was already recognized by Gottsche (1863: 284).

?*Dicranolejeunea loxensis* (Gott.) Steph., Spec. Hep. 5: 161 (1912) syn. nov.

Dicranolejeunea neesiana Steph., Spec. Hep. 5: 162 (1912) syn. nov.

Dicranolejeunea paulina Gott. ex Steph., Spec. Hep. 5: 167 (1912) syn. nov.

?*Dicranolejeunea sitiensis* Steph. ex Bonner, Index Hepaticarum V: 32 (1965) (nom. nud.) syn. nov.

Acanthocoleus fulvus Schust., Bull. Torrey Bot. Club 97: 339 (1970) syn. nov.

Misapplied name:

Dicranolejeunea mexicana auct. non *Lejeunea mexicana* Lindenb. Collections in NY annotated by Dr. Fulford and probably also those cited in Fulford (1956) belong to *D. aberrans*, but the type of *Lejeunea mexicana* belongs to *D. axillaris* (fide Stephani 1912 and Gradstein pers. comm.).

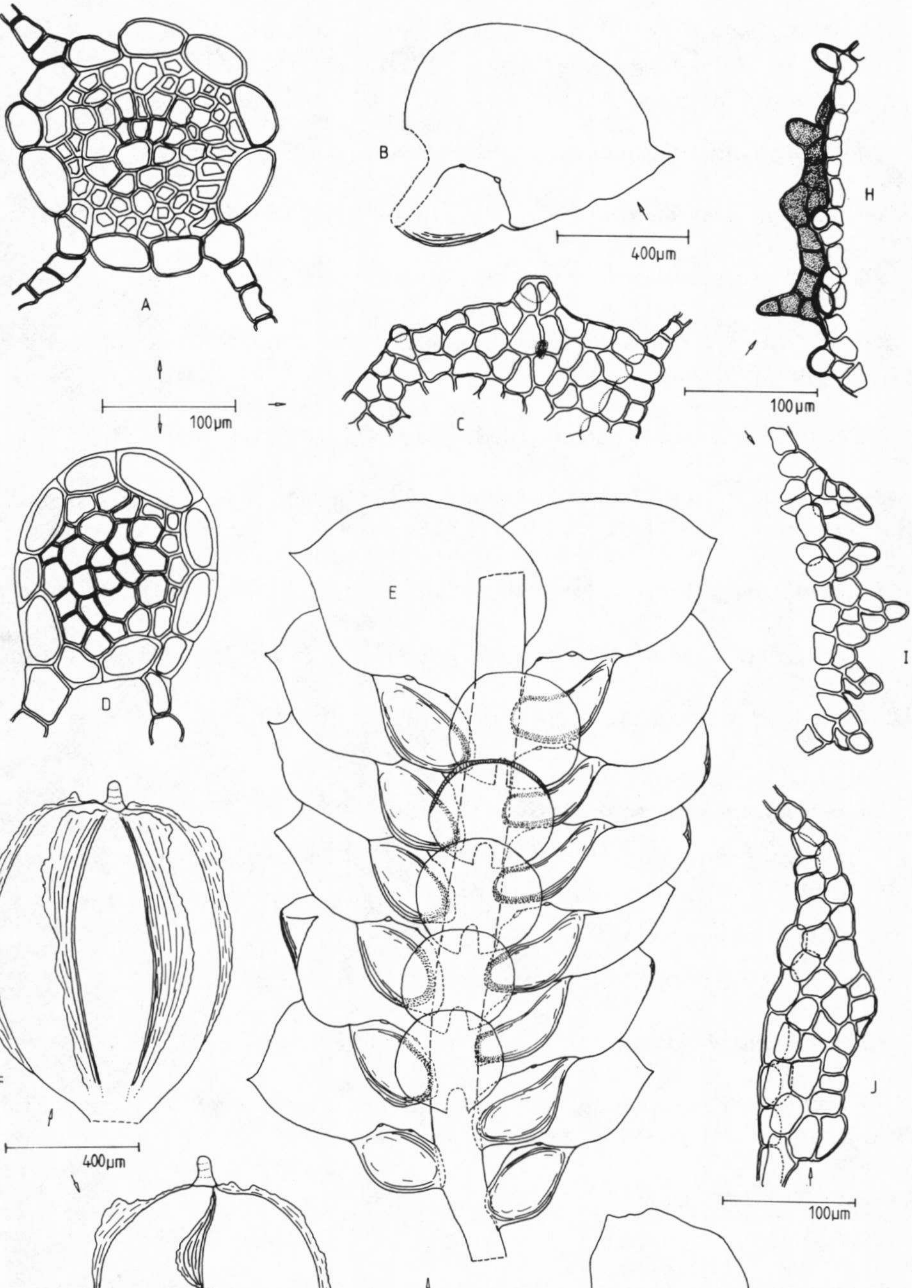
DISTRIBUTION: Central and South America; Africa (new). The species is very closely related to the African *D. chrysophylla* (Lehm.) Grolle.

Fig. 1. *Dicranolejeunea axillaris* (Nees & Mont.) Schiffn. (a) and *Dicranolejeunea aberrans* (Lindenb. & Gott.) Steph. (b-k).

a: stem in cross-section. b: leaf and leaf lobule. c: lobule free margin. d: stem in cross-section. e: portion of the stem in ventral view. f: perianth, ventral view. g: perianth, dorsal view. h: perianth dentation on ventral keel, showing two ridges. i: perianth dentation on lateral keel. j: female bract lobule. k: female bract and bract lobule.

a from Bischler 1769, Colombia. b, c, f, g, j, k from Evans 251, Jamaica. e from Liebman 347, Mexico (type of *D. acuminata* (Lindenb. & Gott.) Steph.) d, h from Eggers & Frahm 32, Mexico. i from Underwood 1126 C, Jamaica.

FIG.1.



3. **Dicranolejeunea phyllorhiza** (Nees) Schiffn.

Engler & Prantl, Nat. Pfl.-fam. I, 3: 128 (1893); Stephani (1912: 162). Basionym: *Jungermannia phyllorhiza* Nees, in Martius, Fl. Bras.: 348 (1833).

Heterotypic synonyms:

Dicranolejeunea lillieana Pears., Ark. Bot. 19: 11 (1924) syn. nov.

Dicranolejeunea pulchella Herz., Rev. Bryol. Lichénol. 20: 139 (1951) syn. nov.

Dicranolejeunea renauldii Steph., Hedwigia 35: 78 (1896) syn. nov.

Dicranolejeunea rotundata Evans, Trans. Connecticut Acad. Arts Sci. 19: 323 (1914) syn. nov.

Dircanolejeunea setacea Steph., Hedwigia 35: 78 (1896) syn. nov.

Lejeunea (subgenus *Odontolejeunea*) *glaziovii* Spruce ex Besch. et Spruce, Bull. Soc. Bot. France 36; 2-11: CXCVII (1889); Spruce (1888: 33 nom. nud.).

Phragmicoma subcristata Lindenb. & Gott., Syn. Hep.: 744 (1847).

Archilejeunea trigona (Nees & Mont.) Steph., Hedwigia 35: 79 (1896) syn. nov.

DISTRIBUTION: Central and South America; Africa (new).

4. **Dicranolejeunea chrysophylla** (Lehm.) Grolle

Trans. Brit. Bryol. Soc. 5: 95 (1966); Jones (1970: 77). Basionym: *Jungermannia chrysophylla* Lehm., Linnaea 9: 423 (1835).

Heterotypic synonyms:

Dicranolejeunea atra (Mitt.) Vand. Bergh., Svensk Bot. Tidskr. 47: 275 (1953).

Dicranolejeunea natalensis (Sim) S. Arnell, Hep. S. Africa: 227 (1963) syn. nov.

Dicranolejeunea madagascariensis Steph. var. *obtusifolia* E.W. Jones, Trans. Brit. Bryol. Soc. 6: 75 (1970) syn. nov.

DISTRIBUTION: Africa.

5. **Dicranolejeunea johnsoniana** (Mitt.) Grolle

Trans Brit. Bryol. Soc. 5: 97 (1966); Jones (1970: 76). Basionym: *Lejeunea johnsoniana* Mitt., J. Proc. Linn. Soc., Bot. (London) 8: 9 (1865).

DISTRIBUTION: Madeira and Canary Islands.

6. **Dicranolejeunea madagascariensis** Steph.

Spec. Hep. 5: 158 (1912); Jones (1970: 73).

[*Lejeunea madagascariensis* Gott. 1882 nom. illeg. non Nees & Mont. 1836.]

Heterotypic synonym:

Dicranolejeunea usambarensis Steph., Spec. Hep. 5: 157 (1912) (synonymy fide Jones 1970).

DISTRIBUTION: Madagascar, continental Africa.

7. **Dicranolejeunea gilva** (Gott.) Steph.

Hedwigia 35: 77 (1896); Stephani (1912: 170); Mizutani (1980: 236). Basionym: *Lejeunea gilva* Gott., Abh. Naturwiss. Ver. Bremen VII: 353 (1882).

Heterotypic synonym:

Dicranolejeunea sikkimensis Steph., Spec. Hep. 5: 170 (1912) (synonymy fide Mizutani 1980).

DISTRIBUTION: Asia.

8. **Dicranolejeunea javanica** Steph.

Spec. Hep. 5: 169 (1912); Mizutani (1980: 240); Verdoorn (1934: 65).

Heterotypic synonym:

Cyclolejeunea fleischeri Steph., Spec. Hep. 5: 184 (1913) (synonymy fide Verdoorn 1934).

DISTRIBUTION: Malesia.

9. **Dicranolejeunea yoshinagana** (Hatt.) Mizut.

J. Hattori Bot. Lab. 24: 174 (1961); Mizutani (1980: 238); Udar & Awasthi (1982: 122). Basionym: *Lopholejeunea subfusca* (Nees) Steph., var. *yoshinagana* Hatt., Bot. Mag. Tokyo 58: 38 (1944).

Heterotypic synonym:

Lopholejeunea javanica Yoshin., Bot. Mag. Tokyo 14: 39 (1900) (nom. illeg.); Horikawa (1929: 423), quod plant. Japon (nec *L. javanica* (Nees) Schiffn.) (synonymy fide Hattori 1952).

DISTRIBUTION: Asia.

Acknowledgements

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I wish to thank Mw. G. Zijlstra and Dr. R. Grolle for nomenclatural advice and Mr. M.W. van Slageren for reviewing the manuscript.

References

EVANS, A.W. 1914. The Yale Peruvian expedition of 1911. Trans. Connecticut Acad. Arts Sci. 18: 295-345.

FULFORD, M. 1956. The young stages of the leafy Hepaticae: a resumé. Phytomorphology 6: 199-235.

GOTTSCHE, C.M. 1863. De Mexikanske Levermosser. K. Danske Vid. Selsk. Skrifter, Ser, 5, Naturw. og Math. Afd. 6: 97-380.

GOTTSCHE, C.M. 1882. Hepaticae *in* Reliquiae Rutenbergianae V. Abh. Naturwiss. Ver. Bremen VII: 335-365.

GOTTSCHE, C.M., LINDENBERG, J.B.G. & NEES VON ESENBECK, C.G. 1844-1847. Synopsis Hepaticarum. Hamburg.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae) with an Arrangement of the Genera of Ptychanthoideae. Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R., CLEEF, A.M. & FULFORD, M. 1977. *Hepaticae*-Oil body structure and ecological distribution of selected species of tropical Andean *Jundermanniales* (Studies on Colombian Cryptogams II). Proc. Kon. Ned. Akad. Wetensch. ser. C, 80: 377-420.

GROLLE, R. 1966. *Dicranolejeunea* auf den Atlantischen Inseln. Trans. Brit. Bryol. Soc. 5: 95-99.

HATTORI, S. 1952. Hepaticae of Shikoku and Kyushu, southern Japan 2. J. Hattori Bot. Lab. 8: 21-46.

HORIKAWA, Y. 1929. Studies on the Hepaticae of Japan. 2. Sci. Rep. Tohoku Imp. Univ. ser. 4, 4: 395-429.

JONES, E.W. 1970. *Dicranolejeunea* and *Marchesinia* (African Hepatics XXII). Trans. Brit. Bryol. Soc. 6: 72-81.

MIZUTANI, M. 1980. Asiatic species of the Genus *Dicranolejeunea* (Notes on the Lejeuneaceae 4). J. Hattori Bot. Lab. 48: 235-242.

NEES VON ESENBECK, C.G. & MONTAGNE, C. 1836. Jungermanniearum herbarii Montangeani species. Ann. Sci. Nat. Paris, Bot. 5: 59.

SCHIFFNER, V. 1893. Hepaticae. In: Engler & Prantl, Nat. Pfl.-fam. I, 3: 3-141.

SCHUSTER, R.M. 1970. Studies on Hepaticae XLIX-LIII. New Lejeuneaceae from Dominica and Jamaica. Bull. Torrey Bot. Club 97: 336-352.

SCHUSTER, R.M. 1980. The Hepaticae and Anthocerotae of North America IV. 1-1334. New York.

SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Trans. & Proc. Bot. Soc. Edinburgh 15: 1-590.

SPRUCE, R. 1888. Hepaticae in Prov. Rio Janeiro a Glaziou lectae, a R. Spruce determinatae. Rev. Bryol. 15: 33-35.

STEPHANI, F. 1898-1924. Species Hepaticarum I-VI. Geneva. *Dicranolejeunea* in vol. V: 156-170 (1912).

UDAR, R. & AWASTHI, U.S. 1982. *Dicranolejeunea yoshinagana* (Hatt.) Mizut. new to Indian bryoflora. Geophytology 12: 122-124.

VERDOORN, F. 1934. Studien über Asiatische Jubulae (De Frullaniaceis XV). Ann. Bryol. Suppl. 4: 40-192.

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7

A New Genus of Lejeuneaceae from Tropical America: Lindigianthus gen. nov.

by

R. Ch. Kruijt and S.R. Gradstein

ABSTRACT: Revisionary work on the genus *Dicranolejeunea* (Spruce) Schiffn. revealed that *Dicranolejeunea cipaconea* (Gott.) Steph. from the páramos and high montane forests of Costa Rica, Colombia, Ecuador and Peru, should be excluded from that genus because of differences in the gametophyte and should be placed in a new, monotypic genus: *Lindigianthus* gen. nov.

Introduction

In the course of a revision of the genus *Dicranolejeunea* (Spruce) Schiffn. (Kruijt, this volume) we came across a hitherto poorly known species from the high Andes of Colombia, Ecuador and Peru, which evidently does not fit in that genus nor in any of the other described genera of Lejeuneaceae. A full description, with new information or anatomy, gametoecia and sporophyte characteristics, as well as a discussion on its affinities, are provided here.

Description

LINDIGIANTHUS gen. nov.

Dicranolejeunea (Spruce) Schiffn. affinis est sed differt a) guttis olei homogeneis, multis, b) cellulis corticeis latioris, sed non altioris quam cellulas medullaris, c) perianthiis omnino compressis, facie dorsalis ventralisque planis, d) lobulis bractearum foeminearum bene preservatis, carinis alatis, e) trigonis cellularum foliarum triradiatis.

Type: *Lindigianthus cipaconeus* (Gott.) Kruijt & Gradst. The genus is monotypic.

Studies on Lejeuneaceae subfam. Ptychanthoideae XII.

Lindigianthus cipaconeus (Gott.) comb. nov. Fig. 1

Lejeunea cipaconea Gott., Ann. Sci. Nat. Paris ser. 5, Bot. 1: 150 (1864). *Dicranolejeunea cipaconea* (Gott.) Steph., Hedwigia 35: 78 (1896); Stephani (1912: 165); Gradstein, Matsuda and Asakawa (1981: 241).

Lectotype (nov.): "Nova Granata, Lindig s.n., original, Gottsche misit" (G 22661). As the syntypes in the Gottsche Herbarium were destroyed, the isosyntype in G has been chosen as the lectotype.

Heterotypic synonyms:

Dicranolejeunea circinnata (Spruce) Steph., Spec. Hep. 5: 159 (1912). *Lejeunea* (*Dicranolejeunea*) *circinnata* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 141 (1884).

Type: "Andes Quitenses, alt. 2600 m., in M. Tunguragua ad terram umbrosam" (MANCH 17628 holo).

Dicranolejeunea jelskii (Loitl.) Steph., Spec. Hep. 5: 159 (1912) syn. nov. *Lejeunea* (*Dicranolejeunea*) *jelskii* Loitl., Diss. Cl. Math.-Phys. Acad. Litt. Cracow 29: 235 (1894).

Type: "Plantae peruvianae ex coll. C. de Jelskii No. 522. *Plagiochila*-Rasen 521, Leg. Const. de Jelski" (G 22671, KRAM, U).

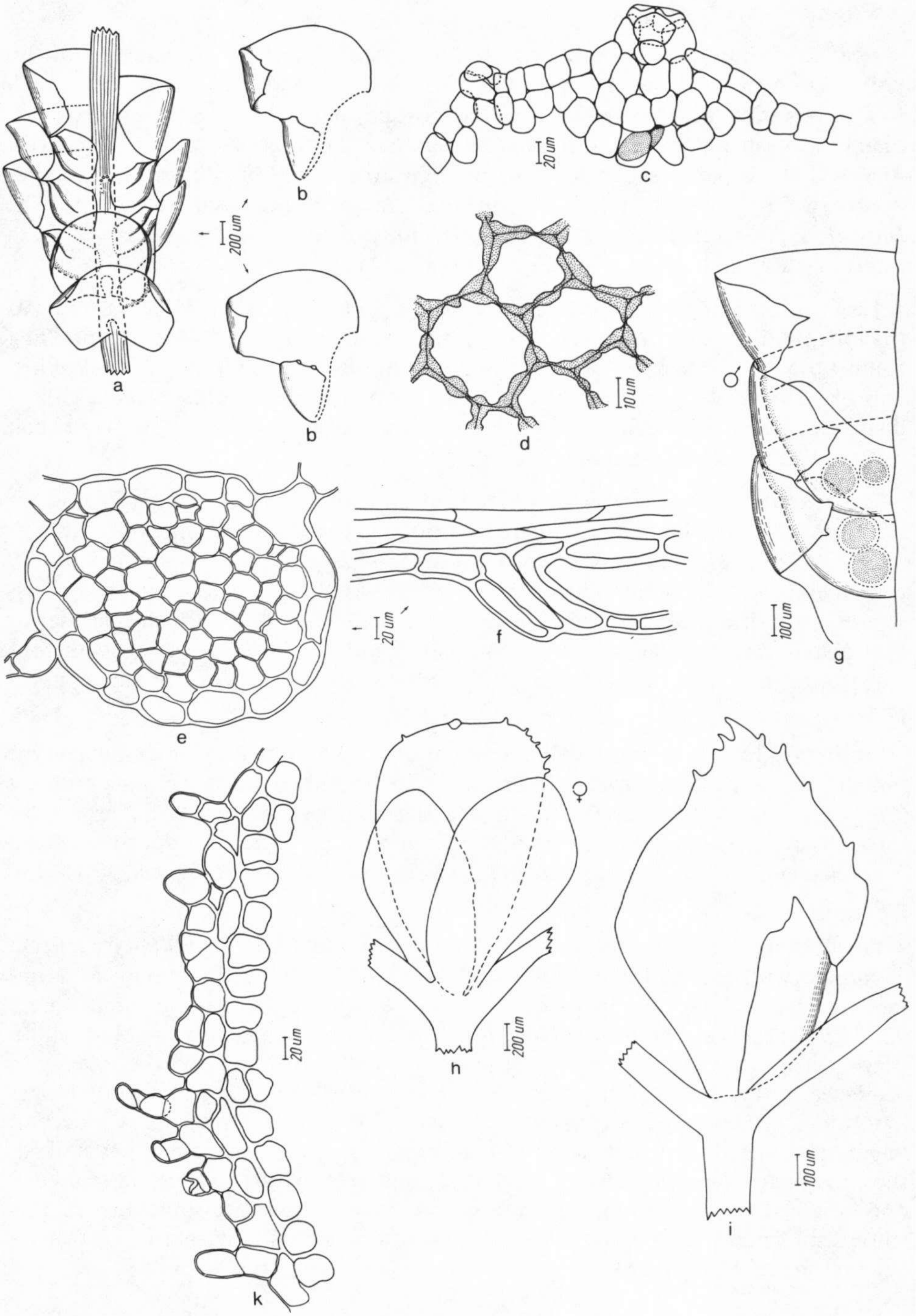
Plants medium-sized to large; stems to 10 cm long, with leaves (1.0-)1,2-2,0(-2,5) mm wide, greenish-brown to glossy-black (after soaking in water and drying again turning dull brown, while leaving a yellowish substance in the water), when wet leaves widely spreading, the leaf-tips pointed downward (Fig. 1a), when dry leaf-tips inrolled, lying against underleaves. Vegetative branches of the *Lejeunea*-type (branch rather thin and short) or *Frullania-Ptychanthus*-type.

Stem in cross-section flattened, 150-370 μm wide and 180-280 μm high. Cortex smooth, the cells not bulging outwards, the radial and tangential walls thickened, sometimes strongly so, in cross-section composed of 10-17 cell-rows, the cells 17-37 μm high and 19-64 μm wide, the ventral cortical cells larger than the dorsal cortical cells. Medulla in cross-section composed of 36-66 cell-rows, the outer medullary layer sometimes thickened, the ventral medullary cells more thickened

Fig. 1. *Lindigianthus cipaconeus* (Gott.) Kruijt & Gradst.

a. Portion of the stem, ventral view. b. leaf. c. lobule margin in detail as seen from the inner side, showing the position of the hyaline papilla. d. Median leaf cells with radiate trigones. e. Stem in cross-section. f. Underleaf attachement in longitudinal section. g. Male bracts with antheridia. h. Gynoecium with mature perianth. i. Female bract, showing enlarged lobule and wing. k. Detail of perianth keel, showing rudimentary dentation.

a, c, e, f from Gradstein and Aguirre 3696 (U); b from Spruce 144 (MANCH); d, h, k from Spruce s.n. (NY); g from Apolliniaire 107 (L); i from Jelski 522 (U).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than dorsal, dorsal cortical cells 1-1,5 times as large as medullary cells. Ventral merophyte (2-)4 cell-rows wide outside the underleaf insertion, within the underleaf insertion 4-5-6 cells wide.

Leaf lobe ovate (Fig. 1b), 1,2-1,5 × 0,9-1,0 mm, imbricate, spreading with tip pointed downward, ± acute, the margin entire or toothed with 1-3(-4) teeth, each tooth consisting of approx. 3 cells, the postical margin plane; apical cells isodiametrical, median cells somewhat elongated, the trigones radiate (Fig. 1d), intermediate thickenings one per (longer) cell wall, ellipsoid to cylindrical, oil bodies homogeneous, small, 10-15 per cell, up to 25 in the larger basal leaf cells, of the *Massula*-type (Gradstein et al. 1981). Plasmodesmata in the cell walls visible in optical view when looking at an angle of approx. 45 °.

Leaf lobule triangular (Fig. 1b), about 0,35-0,45 as wide and 0,25-0,35 as long as the lobe, reduced only in etiolated stems, the basal part inflated; free margin lying against the lobe, with two inwardly curved teeth (Fig. 1c), the first tooth 4-7 celled, approx. 2 times longer than the 2-4 celled second tooth; hyaline papilla entally displaced, inserted 3-4 cell rows below the apical tooth; lobule sinus 160°-180° and apex 180°-220°, the keel strongly arched.

Underleaves strongly imbricate, up to four times as wide as the stem (Fig. 1a), ± reniform with broadly arched-sinuate insertion line; length from upper insertion to apex 420-720 μm (from lower insertion to tip 550-950 μm), greatest width 800-1310 μm; apex rounded, the margins entire, the bases rounded, the base in section tristratose, consisting of three paralell elongated cells (Fig. 1f) of which the inferior central cell may be triangular to cylindrical in outline, in cross-section with four superior central cells; primary rhizoid disc poorly developed; rhizoids almost never produced.

Androecia (only seen once, coll. Apollinaire 107, L) intercalary on *Lejeunea*-type branch, the bracts in approx. 11 pairs of which 4-5 are fertile at the same moment (Fig. 1g); lobule large, approx, half the size of the lobe, epistatic; bracteoles throughout; two antheridia per bract, the antheridial head globose, approx. 190 μm in cross-section, the jacket approx. 15 μm thick, antheridial stalk approx. 30-120 μm long.

Gynoecium terminal, with two innovations of the *Radula-Jubula*-type. Bract rhomboid with rounded angles, entire to toothed (Figs. 1h, 1i), somewhat asymmetrical, with a narrow elongated wing inserted on the innovation; lobule large: 0,5-0,75 × bract length, narrow, sharply rhomboid to elongated rhomboid with a sharply acute tip, the base partly inserted on the innovation: the keel straight, displaced to the middle of the bract (Fig. 1i). Bracteole orbicular to slightly longer than wide, entire to toothed. Perianth exerted to 5,0 × the length of the involucrum, lingulate to broadly lingulate (Fig. 1h), approx. 2,6 × 1,7 mm, sometimes stalked, the apical part somewhat curved to ventral, flattened, with two sharp lateral keels only, the ventral keel lacking, the dorsal and/or ventral surface sometimes ± furrowed, the lateral keels entire or with a few (up to 3 cells long) obtuse teeth on a wing of one cellrow (Fig. 1k).

Sporophyte (Aguirre and Gradstein 6503) with nodular outer and inner capsule wall layers. Spores finely papillose, rosettes rudimentary. Elaters with one spiral thickening. Seta articulate.

DISTRIBUTION AND ECOLOGY: *Lindigianthus cipaconeus* occurs in the upper montane forests and lower páramos of the Andes of Colombia, Ecuador and Peru, and in Costa Rica, at altitudes of approx. 2000-3500 m. Only few collections have been made: in the 19th century by Lindig, Wallis and Apollinaire in Colombia, by Spruce in Ecuador and by Jelski in Peru, and in recent years by the second author et al. in Colombia and Peru, by Van der Hammen and by Onraedt in Colombia, and by Chaverri, Cleef and Madrigal in Costa Rican páramo. The species may grow in great masses as is evident from the large quantities of material collected by Spruce on Mt. Tunguragua and by the second author in the páramo de Guásca, Colombia. At Guásca, the species forms dense, pale-brownish tufts hanging among the rosette leaves of the tree fern *Lomaria* sp. in moist, rather open subpáramo scrub. *Lindigianthus cipaconeus* apparently prefers rather open, yet moist locations on humose soil or on bark of trees of shrubs, growing in pure mats or tufts or creeping loosely among other bryophytes.

Specimens examined: COSTA RICA: Parque Nacional Chirripó, Fila del Cementerio de la Máquina, on truncs of *Quercus costaricensis* in *Quercus* forest, 3000 m., Chaverri, Cleef and Madrigal 1018, 26 March 1983 (CR, U). COLOMBIA: s.l., Lindig s.n., lectotype (G 22661), Wallis s.n., 1874 (G 22663 and 22666), Apollinaire 107 (L male), Apolliniaire 327 (G 22660); Dept. Cundinamarca, Guásca, subpáramo bush, dense tufts among rosette leaves of *Lomaria* sp., 3150 m, Gradstein and Aguirre 3696, 7 Aug. 1980 (ALTA, B, BC, COL, COLO, FLAS, hb. Fulford, G, hb. Grolle, H, MEXU, MICH, NY, PC, PRC, S, TNS, U, USJ, VBI); Dept. Tolima, South slope of Mt. Tolima, high Andean forests, with *Chaetocolea palmata,* 3100 m, Van der Hammen 3383, Aug. 1975 (COL, U); ibid., S. Isabel, trail side near Quebrada de la Damas, Aguirre and Gradstein 1520, Aug. 1980 (BA, BM, COL, F, G, NY, PC, S, TNS, U); Dept. Antioquia, San Pedro, ferme Montanita, 2550 m, Onraedt 83A10307, 2 March 1983 (hb. Onraedt, U); Dept. Huila, La Argentina to Puracé, in bog on tree ferns, 2300 m, Aguirre and Gradstein 6503, X. 1984 (COL, U, with sporophytes!). ECUADOR: Mt. Tunguragua, 2600 m, Spruce 144, type of *Lejeunea circinnata* Spruce (MANCH 17628), Spruce 141 (NY), Spruce s.n. (BM, G 22672, MANCH, NY, U, YU). PERU: s.l., Jelski 522, type of *Lejeunea jelskii* Loitl. (G 22671, KRAM, U); Dept. San Martin, Prov. Rioja, road Chachapoyas-Moyabamba 392 km, "Bergrücken und N.-exponierter Hang in epiphyllenreichem Bergregenwald", 1700 m, Frahm, Geissler, Gradstein, Philippi and Schultze-Motel (Bryotrop expedition) 1267, 11 Sept. 1982 (B, U).

Discussion

Probably because of its resemblance to *Dicranolejeunea axillaris, Lindigianthus cipaconeus* has usually been associated with that genus, e.g. by Spruce (1884, as *Lej. circinnata*), Loitlesberger (1894, as *Lej. jelskii*) and Stephani (1896, 1912, as *Dicranolej. cipaconea*). Besides *Lejeunea circinnata,* Spruce included three further species in his subgenus *Dicranolejeunea,* which all proved to be conspecific with *D. axillaris* (Kruijt, this volume). Loitlesberger apparently had little notion of the circumscription of *Dicranolejeunea,* as one of two species which he placed in *Dicranolejeunea* was a species with divided underleaves (*Lejeunea scabriflora* Loitl.)

Stephani, finally, treated *Dicranolejeunea* in a very uncareful manner and assigned species, now belonging to at least eight (!) different genera (*Dicranolej., Brachiolej., Caudalej., Marchesinia, Lopholej., Cyclolej., Acrolej.* and *Odontolej.*), to this group. It thus appears that for the earliest authors *Dicranolejeunea* was a rather vaguely circumscribed group and their association of *Dicranolej. cipaconea* with that genus is therefore not very significant. Evans (1914) gave the first lucid account of *Dicranolejeunea* and defined the main generic characters. Diagnostic data on stem anatomy (Evans 1935) and oil bodies (Gradstein et al. 1977) were added later. A comparison between *Dicranolejeunea cipaconea* and the genus *Dicranolejeunea* as defined by Evans reveals the following discrepancies:

1. Stem anatomy: while in *Dicranolejeunea* cortical cells in stem cross-section are much wider and higher (1,5-3,5 ×) than medullary cells (cf. Bischler 1965), in *D. cipaconea* cortical cells are wider than medullary cells but ± similar in height (Fig. 1e).

2. Oil bodies: segmented in *Dicranolejeunea* (cf. Gradstein et al 1977) but homogeneous in *D. cipaconea* (Gradstein et al. 1981).

3. Trigones: simple triangular to cordate in *Dicranolejeunea,* but radiate in *D. cipaconea* (Fig. 1d).

4. Female bracts: lobule ± reduced and keel without or with rudimentary wing (by exception winged in *D. phyllorhiza*) in *Dicranolejeunea.* In *D. cipaconea,* however, the lobule is well developed and the keel is broadly winged (Fig. 1i).

5. Perianth: in both taxa perianths are ± compressed, but in *Dicranolejeunea* the ventral perianth surface is always swollen and bears 1-2 keels, whereas in *D. cipaconea* both the ventral and dorsal surface of the perianth are strongly flattened and plane, without keels (Fig. 1h).

So where does *Dicranolejeunea cipaconea* belong? A relationship to consider next is its affinity to *Marchesinia,* with which it shares characters of the oil bodies (both *Massula*-type), trigones (both tri-radiate), gynoecium (both flattened perianth), and several other traits not mentioned above. We have discussed the affinity to *Marchesinia* with Dr. Patricia Geissler, who is preparing a monograph of this genus. It seems that the following characters of *Dicranolejeunea cipaconea* are unusual for *Marchesinia:*

1. the complete lack of pigment formation in the cell walls. Many taxa of Ptychanthoideae turn blackish in the field or when dry, because of decoloration of the cytoplasma, but only a few (*Marchesinia, Lopholejeunea, Neurolejeunea, Symbiezidium, Brachiolejeunea* subg. *Plicolejeunea, Thysananthus*) produce dark pigments in the cell walls. The ability to produce such pigments is apparently constant on the generic (or subgeneric) level.

2. The leaves when moist are somewhat recurved-convoluted in *D. cipaconea* (Figs. 1a, b) whereas in *Marchesinia* they are always widely spreading and ± flattened.

3. An important difference is found in the stem structure of the two taxa. In *D. cipaconea* stems are rather fragile and made up of relatively few, thinwalled cells; the ventral merophyte is only (2-)4 cells wide. In *Marchesinia,* on the other hand, stems are more robust and rigid, made up of more numerous, thickwalled cells; the ventral merophyte is ca. 6-12 cells wide. In stem cross section, it appears that in *Marchesinia* cortical cells are about similar in size and shape to the medullary cells, whereas in *D. cipaconea* the cortical cells are much wider than the (outer) medullary cells (Fig. 1e).

4. Male bracts are epistatic in *D. cipaconea* (Fig. 1g), whereas in *Marchesinia* they are hypostatic. By this character the species would seem to fit better in *Dicranolejeunea,* which has male bracts epistatic as well. Epistatic male bracts are less common than hypostatic bracts and either presence is usually constant on the generic level (Gradstein 1975), although both bract types have been found in *Thysananthus* (unpubl. obs.).

5. The perianth keels of *D. cipaconea* bear a few teeth (Figs. 1h, k), whereas in *Marchesinia* they are quite smooth. This difference should not be overrated, however. Although presence or absence of perianth "ornamentation" has been treated as a generic character in the past (Gradstein 1982), perianths within *Dicranolejeunea, Lopholejeunea* and *Symbiezidium* — all three allies of *Marchesinia* — vary from ciliate-laciniate (the usual condition) to completely smooth in *Dicranolejeunea chrysophylla* (Lehm.) Grolle, *Lopholejeunea erugata* Thiers, *L. gradsteinii* Udar & Awashti and *Symbiezidium madagascariensis* Steph.. It should be noted, that Stephani's illustration of the perianth of *Dicranolejeunea cipaconea* (Icon. Ined. G002348), showing the presence of a ventral keel is erronous.

6. The wing of the female bract, seen in *D. cipaconea,* is a character hitherto not yet recorded for *Marchesinia.*

7. Finally, the sporophyte structure precludes inclusion in *Marchesinia,* which has plurifenestrate thickenings on the inner capsule-valve surface.

Summing up, it appears that *Dicranolejeunea cipaconea* is somewhat intermediate between *Dicranolejeunea* and *Marchesinia,* although the above discussed characters indicate that the species belongs to neither of these genera. We have therefore placed the species in the new genus *Lindigianthus,* named in honour of the important 19th century collector of Andean cryptogams who gathered the type specimen, Alexander Lindig.

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References

BISCHLER, H. 1965. Récherches sur l'anatomie de la tige chez les Lejeuneaceae 2. Les sous-familles Lejeuneoideae tribu Ptychantheae, Nipponolejeuneoideae et Myriocoleoideae. Rev. Bryol. Lichènol. 33: 399-458.

EVANS, A.W. 1914. Hepaticae. Yale Peruvian Expedition of 1911. Trans. Connecticut Acad. Arts. Sci. 18: 291-345.

EVANS, A.W. 1935. The anatomy of the stem in the Lejeuneae. Bull. Torrey Bot. Club. 62: 187-214, 259-280.

GEISSLER, P. & GRADSTEIN, S.R. 1982. SEM-studies on sporophyte characters in Lejeuneaceae (Ptychanthoideae), a preliminary report. J. Hattori Bot. Lab. 53: 127-131.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae). Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. 1982. Generic concepts in Lejeuneaceae. Nova Hedwigia Beih. 71: 201-203.

GRADSTEIN, S.R. CLEEF, A.M. & FULFORD, M.H. 1977. Oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. Proc. Kon. Ned. Akad. Wetensch. ser. C, 80: 377-420.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

LOITLESBERGER, G. 1894. Hepaticae. In: I. Szyszylovics, Diag. plantarum novarum a cl. D. Const. Jelskii in Peruvia lectarum I. Diss. Class. Math.-Phys. Ac. Litt. Cracow 29: 232-239.

SPRUCE, R. 1884. Hepaticae of the Amazon and of the Andes of Peru and Ecuador. Trans. Proc. Bot. Soc. Edinburgh 15: i-xi, 1-590.

STEPHANI, F. 1912. Species Hepaticarum 5. Geneva.

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8

Schiffneriolejeunea sect. *Pappeanae* en Afrique

par

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Abstract: The pantropical genus *Schiffneriolejeunea* Verd. is represented in Africa by eight species, four of which constitute the section *Pappeanae* sect. nov. The species of this section are easily recognized by the smooth, brownish pigmented perianth, which is enveloped in a more or less flower-like involucre. The species are *Schiffneriolejeunea pappeana* (Nees) Gradst., a widespread montane mist-epiphyte, *S. fragilis* Gradst. & E.W. Jones from lowland tropical West Africa and the Congo Basin, *S. madagascariensis* (Steph.) Gradst. from Madagascar and Reunion, and *S. parviloba* (Steph.) Gradst. from the Mascarenes. The largest taxonomic diversity is in Madagascar and the Mascarenes, where *S. pappeana* is represented by several infraspecific taxa: var. *pappeana* (the widespread variety), var. *pappeana* fo. *verrucosa* fo. nov. (Madagascar only), var. *integra* var. nov. (Madagascar only) and var. *bidentata* var. nov. (Madagascar and the Mascarenes). A key and descriptions of the taxa of the sect. *Pappeanae* are provided.

Introduction

Le genre pantropical *Schiffneriolejeunea* Verd. emend. Gradstein (1974) est représenté sur le continent africain par une demi-douzaine d'espèces (Vanden Berghen 1976, Jones 1982): *S. altimontana* Vanden Berghen (Zaïre, Rwanda, Tanzanie), *S. ferruginea* (Steph.) Gradst. (Nigéria, Cameroun), *S. fragilis* Gradst. et E.W. Jones (Afrique occidentale et bassin du Congo), *S. occulta* (Steph.) Gradst. (Afrique occidentale), *S. pappeana* (Nees) Gradst. (répandu) et *S. polycarpa* (Nees) Gradst. (répandu). Parmi ces taxons, *Schiffneriolejeunea pappeana* est facilement reconnaissable par son périanthe enflé et lisse, sauf éventuellement dans la partie tout-à-fait apicale de l'organe où sont parfois esquissées 3 carènes fort obtuses. Ce périanthe est étroitement enveloppé dans de grandes bractées et bractéole involutées, dans leur moitié inférieure, en un tube présentant, le cas échéant, un rétrécissement au-dessus du sommet du périanthe; la partie supérieure des bractées et bractéole est souvent étalée et forme alors une espèce de coupe plus ou moins ouverte. Comme Jones (1954) l'avait noté, ces bractées et bractéole sont variables en ce qui concerne leurs dimensions et leur forme; en particulier, le sommet de la

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bractéole est plus ou moins profondément bidenté ou bilobé. Les fluctuations mises en évidence sont pourtant relativement mineures et il est impossible de leur attribuer une importance taxonomique.

La situation est différente à Madagascar et aux Mascareignes où *Schiffneriolejeunea pappeana* est accompagné de taxons affins dont deux sont suffisamment distincts pour être élevés au rang d'espèce. Deux autres taxons sont considérés comme des variétés. Cet ensemble relève, au sein du genre *Schiffneriolejeunea*, d'une section bien individualisée:

Schiffneriolejeunea sect. **Pappeanae** sect. nov.

Syn: *Phragmilejeunea* Schust., Journ. Hattori Bot. Lab. 11: 27 (1954).

Diagnose latine: Schuster & Hattori (1954) sub *Phragmilejeunea* Schust.

Plantes dioïques à tiges feuillées longues de 1-3(-6) cm et larges de (0,8)1,2-2(-2,8) mm. Amphigastres souvent obtrapézoïdaux. Bractées et bractéole ♀ précédées de quelques feuilles et amphigastres plus grands que les feuilles et amphigastres végétatifs, l'ensemble formant un involucre enveloppant le périanthe. Celui-ci relativement petit, enfoui dans les bractées et bractéole, enflé ou comprimé, lisse, dépourvu de carènes ou présentant des esquisses de 3 carènes dans la partie tout-à-fait apicale de l'organe; cellules du périanthe à parois pigmentées de brun jaune ou de brun rouge, précocement durcies, déjà avant la maturation complète du sporophyte; bec longuement cylindrique, à ouverture longtemps dépassée par l'extrémité du col de l'archégone fécondé. Espèce-type: *Schiffneriolejeunea pappeana* (Nees) Gradst.

Clé des taxons subordonnés à la section Pappeanae

1. Feuilles souvent squarreuses. Amphigastres habituellement obtrapézoïdaux. Périanthe enflé. Involucre à partie inférieure enveloppant étroitement le périanthe et à partie supérieure étalée-squarreuse; lobule des bractées ♀ plus long que la moitié de la longueur du lobe; bractéole ♀ plus ou moins fortement convexe ventralement (Groupe du *Schiffneriolejeunea pappeana*).
   2. Amphigastres plus hauts que larges à plus larges que hauts, plans ou à bord partiellement révoluté, soit au sommet, soit latéralement. Bord ventral des lobes foliaires involuté; le sommet jamais involuté. Dent apicale du lobule foliaire solitaire ou, rarement, accompagnée de 1(2) dents proximales moins apparentes que la dent apicale.
      3. Feuilles longues de 0,9-1,2(-1,4) mm, non fragiles. Mérophyte ventral large de 6-8 cellules corticales. Base des amphigastres habituellement auriculée. .... 1. *S. pappeana*
      4. Dent apicale du lobule foliaire non accompagnée d'une dent supplémentaire.

5. Bractéole ♀ normalement bidentée au sommet. Cellules du périanthe sans verrue au centre de leur face externe (Montagnes de l'Afrique tropicale, Afrique du Sud, Madagascar, La Réunion).... .... a. var. *pappeana*

6. Cellules des bractées ♀ à face externe lisse....... fo. *pappeana*

6. Un certain nombre de cellules de la partie médiane-transversale des bractées ♀ pourvues d'une verrue conique ou subcylindrique au centre de leur face externe (Madagascar)...... fo. *verrucosa*

5. Bractéole tronquée-sinuée à rétuse au sommet. Cellules du périanthe portant fréquemment une verrue au centre de leur face externe (Madagascar)................................ b. var. *integra*

4. Dent apicale du lobule foliaire accompagnée de 1(2) petites dents supplémentaires. Lobe des bractées ♀ habituellement arrondi au sommet (Madagascar et Mascareignes)............ c. var. *bidentata*

3. Feuilles longues de 0,6-0,95 mm, habituellement fragiles et cassantes. Mérophyte ventral large de 4-5 cellules corticales. Base des amphigastres cunéée, rarement pourvue d'esquisses d'oreillettes (Afrique tropicale, à basse altitude)................................... 2. *S. fragilis*

2. Amphigastres plus larges que hauts, à marge étroitement révolutée sur tout le pourtour ou sur la plus grande partie du pourtour. Bord ventral et souvent aussi le sommet des lobes foliaires involutés. Dent apicale du lobule foliaire unicellulaire et obtuse, généralement accompagnée de 1(-3) dents supplémentaires, la première d'entre elles habituellement plus apparente que la dent apicale, proximales par rapport à celle-ci (Madagascar).................. .... 3. *S. madagascariensis*

1. Feuilles jamais squarreuses. Amphigastres obovales-obcunéés, à bords latéraux convexes. Périanthe plus ou moins comprimé. Involucre n'enveloppant pas étroitement le périanthe, à partie distale non squarreuse; lobule des bractées ♀ plus court que la moitié de la longueur du lobe; bractéole plane (Mascareignes).. .... 4. *S. parviloba*

1. **Schiffneriolejeunea pappeana** (Nees) Gradst. Figs. 1-7

Journ. Hattori Bot. Lab. 38: 335 (1974).

Phragmicoma pappeana Nees in Gottsche, Lindenberg et Nees, Syn. Hep.: 296 (1845). *Omphalanthus pappeanus* Hampe et Nees nom. inval. in synon., Syn. Hep.: 296 (1845). *Lejeunea pappeana* (Nees) Mitt., Journ. Linn. Soc. London Bot. 7: 167 (1863). *Marchesinia pappeana* (Nees) O. Kuntze, Revis. Gen. Plant. 2: 837 (1891). *Acrolejeunea pappeana* (Nees) Schiffn., Hedwigia 33: 182 (1894). *Ptychocoleus pappeanus* (Nees) Steph., Spec. Hep. 5: 28 (1912); Arnell (1953: 183, fig. 12, a-i); Jones (1954: 398, fig. 2). *Archilejeunea pappeana* (Nees) Sim, Trans. Roy. Soc. South Afr. 15: 51, fig. (1926). *Phragmilejeunea pappeana* (Nees) Schust., Journ. Hattori Bot. Lab. 11: 27 (1954); Arnell (1963: 233, fig. 171).

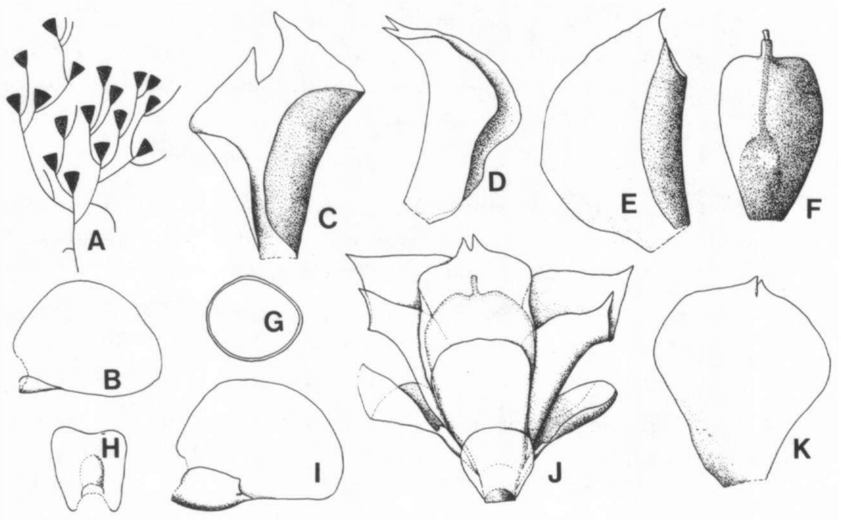

Fig. 1. *Schiffneriolejeunea pappeana* var. *pappeana*.

A: Plante ♀ représentée schématiquement (×2,1). B: Feuille à lobule réduit, détachée de la tige et étalée (×22). C: Bractée ♀ (×22). D: Bractéole ♀ (×22). E: Bractée ♀ (×22). F: Périanthe (×22). G: Coupe transversale dans un périanthe, à hauteur des 3/4 de l'organe (×22). H: Amphigastre (×22). I: Feuille à lobule normal, détachée de la tige et étalée (×22). J: Sommet d'un rameau porteur d'une gynécie, en vue ventrale (×22). K: Bractée ♀ étalée (×22).

A-E: De Sloover 19064. F et G: Onraedt 74 M 2122. H-K: Lisowski s.n. (Guinée).

Lectotype: Afrique du Sud, Province du Cap, "prope Georgetown", Pappe s.n. (STR; isolectotypes: BM, W). Paratype: Afrique du Sud, Province du Cap, "Zwellendam" [actuellement Swellendam], Pappe s.n. (STR, S, W). La plante récoltée à Georgetown fut envoyée par Kunze à Hampe et dénommée provisoirement *Frullania pappeana* Hampe in sched. Lorsque Nees reçut ce spécimen, il lui attribua le nom de *Omphalanthus pappeanus* Hampe et Nees in sched. Par après, il décrivit l'espèce dans le Syn. Hep. sous le nom de *Phragmicoma pappeana* Nees. L'échantillon provenant de Zwellendam fut d'abord déterminé par Lindenberg comme *Lejeunea fertilis.* La plante fut envoyée à Nees avec une annotation sur l'étiquette "ist wohl ihr *Phr. pappeana*". Les deux échantillons, constitués de plantes femelles, répondent à la description originale mais seule la plante récoltée à Georgetown porte sur son étiquette les noms attribués à l'espèce par Nees et Hampe. Ceci nous permet de choisir cette plante comme lectotype de l'espèce.

Synonymes hétérotypiques:

Lejeunea (*Acro-Lejeunea*) *borgenii* Steph., Hedwigia 29: 133, pl. 14, fig. 10 (1890); Pearson (1892: 4, pl. 1, fig. 1-14). *Acrolejeunea borgenii* (Steph.) Steph., Engler Bot. Jahrb. 20: 317 (1895); Steph. in Engler, Die Pflanzenwelt Ostafrikas C: 65 (1895). *Ptychocoleus borgenii* (Steph.) Steph., Spec. Hep. 5: 31 (1912).

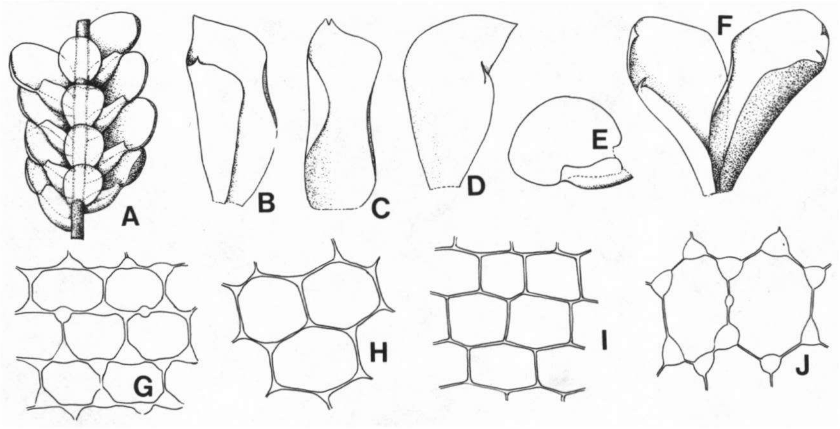

Fig. 2. *Schiffneriolejeunea pappeana* var. *pappeana*.

A: Fragment de tige feuillée, en vue ventrale (×22). B: Bractée ♀ (×22). C: Bractéole ♀ (×22). D: Bractée ♀ (×22). E: Feuille détachée de la tige et étalée (×22). F: Bractées ♀ (×22). G-J: Cellules du périanthe (× 335).

A-G: Cremers 1986, plante remarquablement petite. H: Onraedt 74 M 2122. I: Onraedt 74 M 8152. J: Lisowski s.n. (Guinée). On note l'importance très variable des épaississements des parois cellulaires du périanthe.

Type: Madagascar, Borgen s.n. (G: holotype, BM, F, L, MANCH, O, W). Plusieurs spécimens authentiques ont été déterminés "*Phragmicoma fulva* G." (cf. Gradstein 1975: 130).

Ptychocoleus quintasii Steph., Spec. Hep. 5: 28 (1912).

Type: St. Thomé, Fr. Quintas s.n. (G).

Ptychocoleus dismieri Steph. nom. inval. in Icon. Ined. (=*Acrolejeunea floribunda* Steph. in sched.).

Basé sur: Madagascar, Roteraux s.n. (G).

Plante dioïque formant des feutrages denses, vert olivâtre à brun cuivré ou brun noir; tiges feuillées longues de 1,5-3,5(-6) cm et larges de (0,9-)1,2-2,2(-2,8) mm. Tige irrégulièrement ramifiée, lâchement chez les plantes ♂, souvent densement chez les plantes ♀, avec des stolons microphylles appliqués contre le substrat et des rameaux dressés ou pendants, longs de 0,5-2(-3) cm, la plupart du type '*Lejeunea*', certains du type '*Frullania*' (rameaux végétatifs longs); diamètre: 120-180(-200) µm; en coupe: 18-25 cellules corticales à parois minces ou uniformément épaissies, entourant 20-40 cellules médullaires; cellules corticales, principalement les dorsales, à parois pigmentées de brun plus ou moins foncé, les dorsales hautes de 20-27 µm, les ventrales plus petites, hautes de 15-20 µm; cellules médullaires à parois non

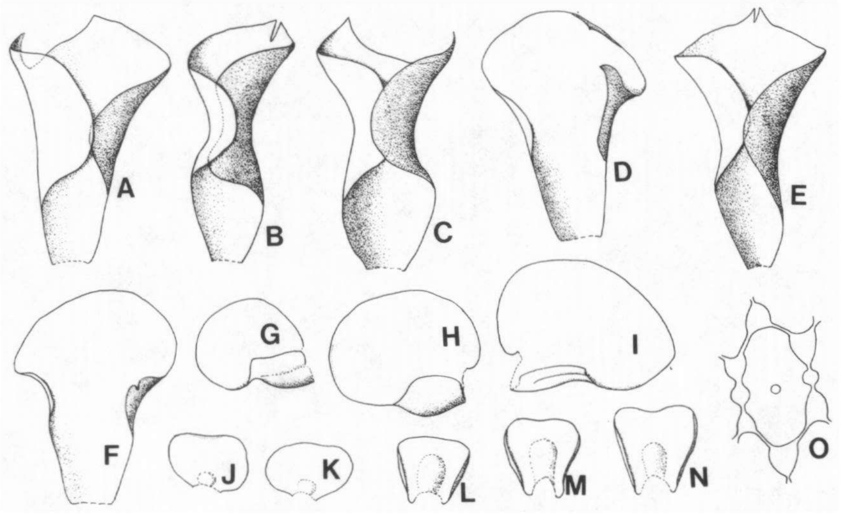

Fig. 3. *Schiffneriolejeunea pappeana* var. *pappeana* fo. *pappeana* et fo. *verrucosa*.

A: Bractée ♀ (×22). B: Bractéole ♀ (×22). C: Bractée ♀ (×22). D: Bractée involucrale ♀ située immédiatement sous une bractée interne (×22). E: Bractéole ♀ (×22). F: Bractée involucrale ♀ (×22). G, H et I: Feuilles détachées de la tige et étalées (×22); on note la variabilité de la longueur relative du lobule. J-N: Amphigastres (×22); on note la variabilité du rapport de la largeur à la hauteur et de sensibles différences dans le développement des oreillettes basilaires. O: Cellule d'une bractée ♀ dont la paroi externe est pourvue, au centre, d'une papille (×400).

A-F: De Sloover 17530 bis. G: Cremers 1896. H, J et K: Onraedt 71 M 5507. I, L, M, N et O: Onraedt 74 M 8079 (type de la fo. *verrucosa*).

pigmentées, d'un diamètre de 15-25 µm; mérophyte ventral large de 6-8(-10) cellules corticales.

Feuilles imbriquées, étalées-squarreuses, à branche dorsale de la ligne d'insertion sur la tige correspondant au 1/2-1/3 de la longueur du mérophyte; lobe concave ventralement, ovale-elliptique, entier, obtusement arrondi au sommet, à bord ventral souvent involuté, à base dorsale arquée ou tronquée, parfois pourvue d'un petit appendice arrondi, ne débordant pas la tige ou la débordant légèrement, (0,55-) 0,7-0,85(-1,2) mm × (0,8-)0,9-1,2(-1,8) mm; lobule plus ou moins rectangulaire, normalement aussi long que les 2/5-1/2 du grand axe du lobe, (0,12-)0,2-0,3(-0,4) mm × (0,26-)0,4-0,6(-0,75) mm, parfois plus petit et fortement réduit, enflé en fuseau le long de la carène et à partie apicale généralement étalée sur le lobe; carène faiblement arquée formant un angle proche de 180° avec le bord ventral du lobe et un angle de 45-60° avec la tige; dent apicale obtuse ou aiguë et incurvée, formée de 1(2) cellules, longue de 12-15(-30) µm, parfois réduite (Onraedt 69 R 92); papille hyaline insérée à la base de la dent apicale, sur la face interne du lobule; bord libre convexe, habituellement entier-sinué, rarement pourvu d'une 2e dent à 1-2 cellules,

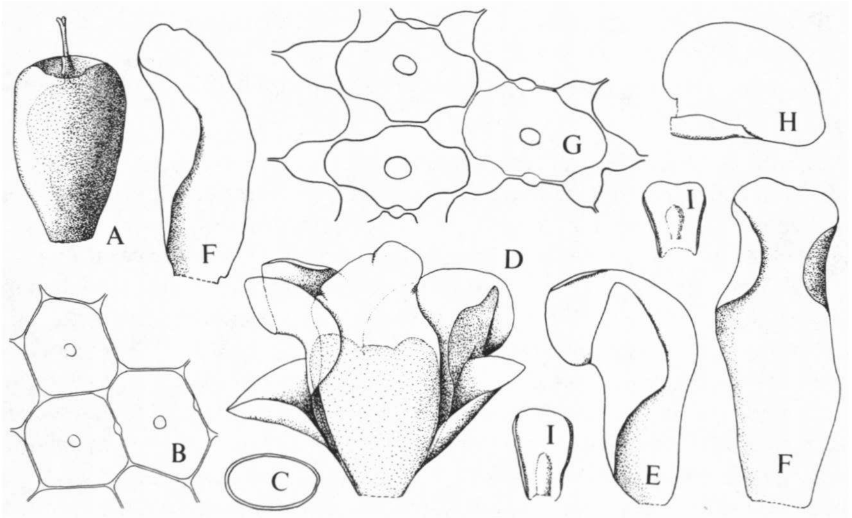

Fig. 4. *Schiffneriolejeunea pappeana* var. *integra.*

A: Périanthe (×22). B: Cellules du périanthe portant une verrue au centre de leur face externe (×500). C: Coupe transversale dans un périanthe (×22). D: Gynécie, en vue ventrale (×22). E: Bractée ♀ (×22). F: Bractéole ♀ (×22). G: Cellules du lobe d'une bractée ♀ portant une verrue au centre de leur face externe (×500). H: Feuille détachée de la tige et étalée (×22). I: Amphigastre, en vue ventrale (×22).

A-I: Tixier 10145 (type).

soit bien marquée, soit obtuse et faiblement proéminente, exceptionnellement accompagnée d'une 3e dent. Cellules foliaires hexagonales-allongées, à parois présentant des trigones, parfois très grands, à 2 côtés convexes et à un côté concave, parfois des épaississements intermédiaires noduleux; cellules au centre du lobe: (13-)15-20(-25) μm × 18-28(-32) μm; cellules apicales: 10-15 μm × 12-15(-20) μm; cellules basilaires: 18-26 μm × 20-33(-36) μm; dans chaque cellule (2)3-6(-8) oléocorps, irrégulièrement globuleux ou fusiformes, granuleux, longs de 4-14 μm.

Amphigastres contigus ou imbriqués, 3-4 fois aussi larges que la tige, obtrapézoïdaux à largement spatulés, habituellement un peu plus hauts que larges, parfois plus larges que hauts, tronqués ou rétus au sommet, souvent concaves ventralement, à côtés latéraux parfois étroitement récurvés, faiblement auriculés à la base, rarement cunéés et brièvement décurrents sur la tige, à ligne d'insertion arquée, pourvus d'une bosse médiane; dimensions: (0,25-)0,4-0,6(-0,75) mm × (0,3-)0,4-0,7(-0,9) mm.

Andrécie au sommet d'un rameau plus ou moins allongé, du type '*Lejeunea*', proliférant et devenant intercalaire, à 4-10(-12) paires de bractées fortement imbriquées, plus petites que les feuilles végétatives, hypostatiques; carène hémicirculaire; partie apicale du lobule non dilatée, à bord libre formant un angle arrondi et obtus avec le bord ventral du lobe, souvent pourvue d'une dent apicale bien développée, parfois longue de 3 cellules; bractéoles tout le long de l'andrécie, plus petites que les amphigastres, squarreuses; (1)2 anthéridies subglobuleuses à l'aisselle de chaque bractée, diamètre: (150-)180-210(-225) µm.

Gynécie au sommet d'un rameau plus ou moins allongé du type '*Lejeunea*'; pas d'innovations du type '*Radula*' mais parfois 1-2(3) innovations du type '*Lejeunea*', habituellement terminées par une gynécie. Bractées grandes, imbriquées avec la bractéole et avec 1-2 paires de feuilles modifiées insérées immédiatement sous elles et plus grandes que les feuilles végétatives, l'ensemble formant une espèce de coupe, à partie basilaire étroite, parfois un peu étranglée à mi-hauteur, à partie apicale dressée à largement ouverte; bractées très concaves, à partie inférieure engainante, à partie supérieure dressée ou étalée, à carène arrondie et peu marquée; lobe obovale-oblancéolé, parfois un peu falciforme, entier-sinué, rarement paucidenticulé dans sa partie apicale, acuminé ou aigu au sommet, éventuellement terminé par un apicule formé d'une file de 2-5 cellules placées bout à bout, plus rarement arrondi, obtus ou subobtus, (0,6-)0,8-1 mm × (1,1-)1,3-1,8(-2,2) mm; lobule lancéolé, généralement libre sur environ le 1/4 de sa hauteur, habituellement aigu-acuminé ou apiculé au sommet, (0,2-)0,4-0,6(-0,8) mm × (0,9-)1,2-1,7(-1,9) mm. Bractéole convexe ventralement, obovale à obovale-spatulée, normalement bidentée au sommet, à dents généralement aiguës et séparées par un sinus aigu ou arrondi atteignant le 1/10-1/4 de la longueur de l'organe, rarement tronquée et sinuée à superficiellement lobée au sommet; bords entiers ou parfois pourvus de 1(-3) dents dans leur partie apicale, fréquemment largement involutés et engainant le périanthe; dimensions: (0,7-)0,9-1,2(-1,3) mm × (1,1-)1,2-1,6(-2,2) mm. Cellules des bractées et de la bractéole, principalement celles de la moitié basilaire de ces organes, à paroi externe parfois pourvue d'une petite verrue conique située approximativement au centre. Périanthe enfoui dans l'involucre, très largement claviforme, enflé et lisse, dépourvu de carènes ou présentant 3 courtes esquisses de carènes très obtuses dans la partie tout-à-fait apicale de l'organe; sommet largement arrondi, tronqué ou ombiliqué; dimensions: 0,55-0,9 mm × (0,85-)1-1,3 mm; cellules du périanthe à face externe rectangulaire-hexagonale, à parois pigmentées de brun jaune ou de brun rouge, minces, pourvues de petits trigones ou de trigones bien développés, parfois fortement noduleux, accompagnés, le cas échéant, d'épaississements intermédiaires et d'une petite verrue conique située au centre de la face externe, 22-32 µm × 27-40 µm; bec cylindrique, long de (70-)100-150(-200) µm, haut de (5)6-8(-12) assises de cellules à face externe subcarrée, 13-15 µm × 14-18 µm, à ouverture entière, longtemps dépassée par le sommet du col de l'archégone.

Pédicelle du sporophyte à 16 rangées de cellules externes et à 4 rangées de cellules internes, articulé. Capsule subglobuleuse, s'ouvrant en valves, à partir du sommet jusqu'aux 4/5 environ de sa longueur; valves largement étalées à 2 strates de cellules, celles de la moitié apicale de l'assise interne à parois colorées en brun orangé et irrégulièrement plurifenestrées; cellules des valves à parois plus ou moins pourvues d'épaississements dans leur moitié basilaire. Spores ovoïdes-anguleuses, 40-45 µm × 50-65 µm, couvertes de nombreuses petites épines et de 15-20 rosettes d'environ 10 µm de diamètre, formées chacune de 5-10 petites épines triangulaires et incurvées. Elatères, au nombre d'environ 9 par valve, longues et étroites, 12-13 (-18) μm × 370-450 μm, avec 1(2?) bandes spiralées brun clair, larges de 5-6 μm.

DISTRIBUTION ET ÉCOLOGIE: *Schiffneriolejeunea pappeana* a été noté en Afrique tropicale à des altitudes comprises entre 1000 et 2500 m, rarement plus bas; en Afrique australe, l'espèce descend jusqu'au niveau de la mer. Elle croît principalement en épiphyte sur les troncs, les branches et les brindilles des arbres et arbustes; plus rarement, elle colonise des rochers ou est observée sur des feuilles. La plante a été récoltée dans des forêts fermées plus ou moins dégradées, dans des forêts claires, ainsi que sur des arbres isolés, toujours dans des stations relativement bien éclairées mais fréquemment noyées dans le brouillard, à degré hygrométrique de l'air constamment élevé.

Observations:

1. Une plante récoltée aux Victoria Falls, Zimbabwe (G) a été déterminée *Ptychocoleus pulopenangensis* (Gott.) Trevis. (= *Schiffneriolejeunea pulopenangensis* (Gott.) Gradst.) par Stephani et a été publiée sous ce nom par Arnell (1963). En réalité, l'échantillon répond à la diagnose de *S. pappeana*. *S. pulopenangensis* est une espèce indomalaisienne inconnue en Afrique (Gradstein & Inoue 1980).

2. Le lobule foliaire de *S. pappeana*, lorsqu'il est bien développé, est étroitement rectangulaire et aussi long que les 2/5-1/2 de la longueur du lobe. Parfois, pourtant, il est réduit. L'ouverture, au niveau du sinus, est fort étroite car la partie apicale du lobule est appliquée sur le lobe.

3. Le bord des pièces de l'involucre ♀ est normalement entier, sauf la bractéole ♀ interne qui est habituellement bidentée au sommet. On observe pourtant parfois des populations de plantes qui possèdent quelques dents supplémentaires, notamment dans la partie apicale de la bractéole interne. Celle-ci est rarement plus ou moins entière, arrondie au sommet. Une variation homologue est observée chez les échantillons de *S. polycarpa* récoltés en Afrique.

4. Des oléocorps ont été décrits par Arnell (1953); Gradstein les a observés chez des plantes récoltées en Tanzanie (Pócs 6068 et 6071), dans l'Ouganda (Wood 1201) et à Madagascar (Aptroot s.n.). Les échantillons originaires de la Tanzanie et de Madagascar avaient 3-6 oléocorps, longs de 6-14 μm, dans chaque cellule foliaire. Les oléocorps des plantes de l'Ouganda avaient les mêmes dimensions mais étaient plus nombreux dans chaque cellule (environ 8).

VARIABILITÉ: L'espèce, telle que nous la concevons, est particulièrement variable, tout spécialement à Madagascar et aux Mascareignes. On observe notamment, chez certaines populations de ces îles de l'Océan Indien, une tendance au développement de dents supplémentaires sur le bord libre des lobules foliaires, à l'apparition de verrues au centre de la face externe des cellules du périanthe et des bractées ♀ et ♂, à la suppression des dents du sommet des bractéoles ♀, à la disparition de l'acumen terminal du lobe des bractées ♀. Trois variétés et une forme ont été reconnues. Leurs caractères distinctifs apparaissent dans la clé des taxons relevant de la section *Pappeanae*.

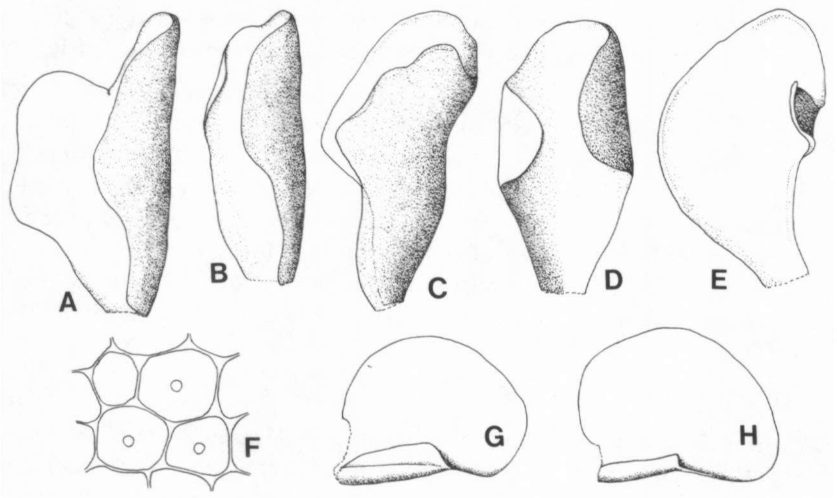

Fig. 5. *Schiffneriolejeunea pappeana* var. *integra.*

A et C: Bractées ♀ (×22). B et D: Bractéoles ♀ (×22). E: Bractée involucrale ♀ située immédiatement sous les bractées internes (×22). F: Cellules d'un périanthe avec une verrue au centre de la face externe (×500). G et H: Feuilles détachées de la tige et étalées (×22).

A-G: Onraedt 71 M 5374. H: Tixier 10145 (type).

a. var. et fo. **pappeana** (Figs. 1, 2, 3A-G) - Lobules foliaires à bord libre entier-sinué, dépourvu de dent supplémentaire entre la dent apicale et la tige. Bractées ♀ à lobe et lobule aigus ou apiculés au sommet. Bractéole ♀ normalement bidentée au sommet. Cellules du périanthe sans verrue au centre de leur face externe. - Distribution: Montagnes de l'Afrique tropicale, Afrique du Sud, Madagascar, La Réunion. Une forme faiblement caractérisée a été reconnue à Madagascar: fo. **verrucosa** fo. nov. (Figs. 3, I, L-O) - A forma *pappeana* differt cellulis centralis bractearum foeminearum verrucosis. - Typus: Madagascar, Onraedt 74 M 8079 (herb. Onraedt). - Distribution: Madagascar.

b. - var. **integra** var. nov. (Figs. 4, 5) - A varietate *pappeana* differt lobulis bractearum foeminearum bracteolisque apice rotundatis integris. - Typus: Madagascar, région orientale de l'île, au pK 300, Tixier 10145 (BR). - Distribution: Madagascar.

c. - var. **bidentata** var. nov. (Figs. 6, 7) - A varietate *pappeana* cui affinis sed differt lobulis bidentatis. - Typus: La Réunion, entre Saint-Pierre et Saint-Benoît, 800 m, Onraedt 71 R 9275, septembre 1971 (U: holotype; herb. Onraedt et herb. Grolle: isotypes). - Distribution: Madagascar et Mascareignes.

Exemplaires examinés(*S. pappeana*): a. var. *pappeana.* GUINÉE: Région de Macenta, massif du Ziama, au sommet d'une montagne, 1250 m, S. Lisowski s.n., mars 1962 (BR). CAMEROUN: Mont Cameroun, Jumbo, Dusén 690 p.p., avec le type de *Schiffneriolejeunea ferruginea* (Steph.) Gradst. (S);

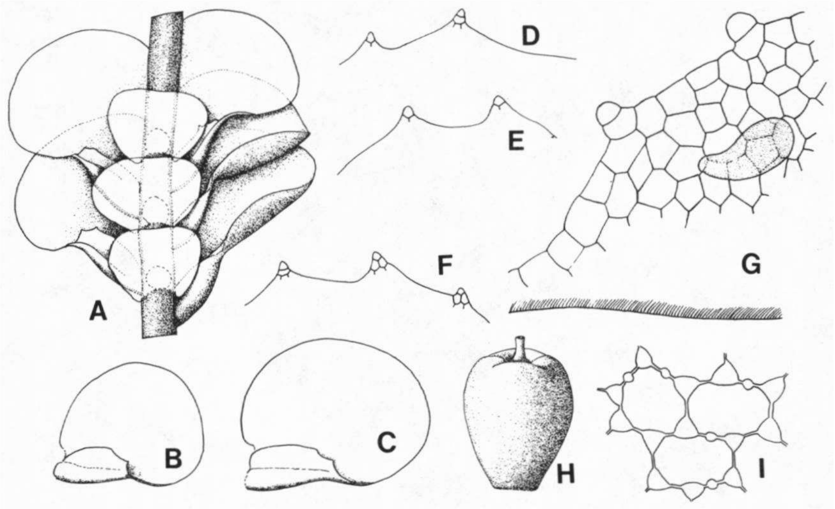

Fig. 6. *Schiffneriolejeunea pappeana* var. *bidentata*.

A: Fragment de tige feuillée, en vue ventrale (×22). B et C: Feuilles détachées de la tige et étalées (×22). D, E et F: Bord libre de lobules foliaires avec la dent apicale (à droite chez D, à gauche chez E et F) et une ou deux dents supplémentaires (×115). G: Partie distale d'un lobule foliaire, avec la dent apicale, une dent supplémentaire et la papille hyaline déplacée sur la face interne du lobule (×300). H: Périanthe (×22). I: Cellules du périanthe (×310).

A et D-F: Onraedt 71 R 9275 (type). B, C, H et I. Cremers 2755, G: Onraedt 74 M 2129.

id., Mimbia, E.W. Jones 305 et 312, mars 1948 (K). ANNOBON: Versant occidental du cratère du N, Byström 271, mai 1953 (UPP). FERNANDO PO: Mann 694 p.p. (NY); Moka, Byström s.n., 1953 (UPP). ST. THOMÉ: Quintas s.n., type de *Ptychocoleus quintasii* Steph. (G). ETHIOPIE: sine loc, Schimper s.n. (BM). KENYA: Mt. Kenia, Zelecoski s.n. (BM). OUGANDA: Lac Victoria, île Bugula, Wood 1200, juin 1950 (K., herb. E.W. Jones); Mubende, distr. Kakumiro, Wood 1201, août 1953 (herb. E.W. Jones); Ruwenzori, Fort Portal, Expéd. Duc des Abruzzes, 1906, avec *Acrolejeunea fuscescens* Gola (TO). RWANDA: Préfecture de Cyangugu, forêt de Rugege, environ 2 km au sud de Gisakua, J.L. De Sloover 19064, août 1974 (NAM, BR); Préfecture de Gisenyi, Gikungu, 2000 m, J.L. De Sloover 18612, juillet 1974 (NAM, BR). ZAIRE: Lesse, forêt vierge aux bord de la Semliki, Bequaert 3131, mars 1914 (BR); Betongwe, J. Louis 4508, juillet 1937 (BR); Yangambi, plateau de la Lusambila, J. Louis 4269, juin 1937 (BR); Haut Zaïre, zone d'Opala, près du village Lifera, entre Kenake et Masua, S. Lisowski 43330, novembre 1976 (BR). ANGOLA: Distr. Golungo alto, Cungulangulo, Welwitsch 285, février 1855 (BM). TANZANIE: Nombreuses récoltes des Southern Highlands, des Mts Uluguru, des Mts Usambara et du Mt. Kilimandjaro, leg. Pócs et al. (U, EGR). ZIMBABWE: Monts Vumba, Schelpe 5416 et 5775a, juin 1955 (BM, UPP); Mimunzi près de Inyanga, Vanden Berghen 240 et 241, décembre 1973 (BR); Mts Chimanimani, Melsetter, Vanden Berghen 805, janvier 1974 (BR); Victoria Falls, leg.?, octobre 1909, sub *Acrolejeunea pulopenangensis* (G); Zomba Plateau, Mlungusi River, Crundwell 253, juillet 1969 (herb. E.W. Jones). PROVINCE DU CAP: Nombreux échantillons, parmi lesquels le type, dans divers herbiers. MADAGASCAR: Sine loc., Likora 56 et 85, 1891 (BM, G); sine loc., Forsyth Major 500, 512, 535, 462, 501 (BM, G 835/ 3, 4, 6, 7 et 8, sub *Acrolejeunea madagascariensis* Steph.); sine loc. J.W. Hildebrandt (G 835/5, sub *Acrolejeunea madagascariensis* Steph.); Mont d'Ambre, Diego Suarez, Chenagon s.n., 1890 (PC); Andapa, Mission catholique, Onraedt 71 M 5032, juillet 1971 (herb. Onraedt, U); in montibus Ankaratra, Borgen s.n. P. 1876 (G 14611, holotype de *Acrolejeunea borgenii* Steph.; isotypes: BM, MANCH, O, U, W); Monts Ankaratra, au lac Alaotra, Humbert et Cours s.n.,

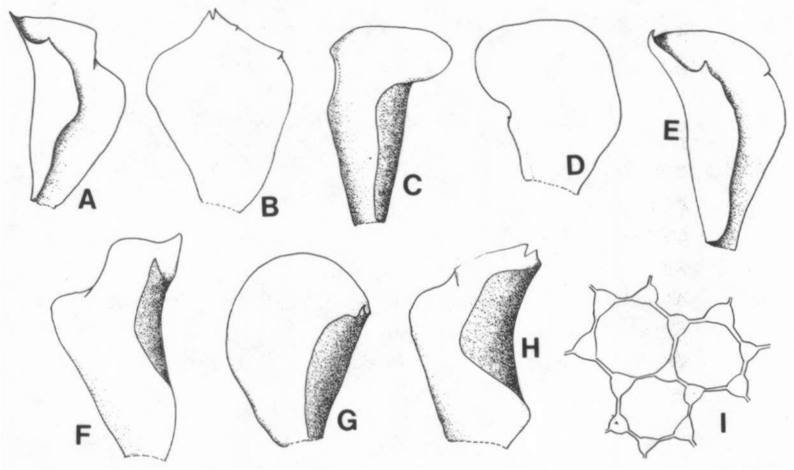

Fig. 7. *Schiffneriolejeunea pappeana* var. *bidentata*.

A et C: Bractées ♀ (×22). B: Bractéole ♀ (×22). D et G: Bractées involucrales ♀ situées immédiatement sous les bractées internes (×22). E et F: Bractées ♀ (×22). H: Bractéole ♀ (×22). I: Cellules du périanthe (×330).

A-I: Cremers 2755.

octobre 1937 (PC); Province de Tananarive, forêt de la Mandraka, 1230 m, Onraedt 74 M 2192, février 1974 (herb. Onraedt, U); id. au lac de Mantasoa, 1400 m, Onraedt 74 M 2122, 74 M 8151 et 74 M 8152, mai 1974 (herb. Onraedt, U); Analabé, près de Ambositra, 1800 m., Onraedt 70 M 387, janvier 1970 (herb. Onraedt, U); Ambatofitorahana, 35 km au S d'Ambositra, 1650 m, Onraedt 71 M 5401, août 1971 (herb. Onraedt, U); Ambohimaha, Onraedt 70 M 560, janvier 1970 (herb. Onraedt, U); 50 km au NE de Anjazorobe, Cremers 1896 et 1897, septembre 1971 (herb. Onraedt, U); Majakatompa, Benoist s.n., 1951 (PC); Préfecture de Mananjary, forêt de Ranomafana, 900 m, Onraedt 74 M 8158, mars 1874 (herb. Onraedt); R.N. de Marojéjy, 1450 m, Guillaumet 4133/15, octobre 1972 (herb. Onraedt); Betsileo, ex herb. Lacouture 127 et 128 (G 14623 et 835/9, sub *Acrolejeunea madagascariensis* Steph.); Monts Betsileo, Villeumier s.n. (F); id., Wittmann s.n. (W); id., Montaut s.n., 1893 (G); Fort-Dauphin, 10 m, Onraedt 71 M 5507, juin 1971 (U). LA RÉUNION: Sine loc., s.coll. (L, 2 échantillons); Cirque de Cilaos, sentier du Taïbit, 1800 m, Gimalac 75 R 912, mai 1975 (herb. Onraedt, U); id., au Grand Maratum, 1450 m, Onraedt 74 R 8090 et 8092, janvier 1974 (herb. Onraedt, U); id., ravine du Benjoin, 1500 m, Onraedt 8093, décembre 1973 (herb. Onraedt, U); Plaine des Cafres, au Piton Desforges, 1800 m, Onraedt 69 R 92, décembre 1969 (herb. Onraedt, U); Cirque de Mafate, plaine des Tamarins, 1750 m, Gimalac 75 R 0913, avril 1975 (herb. Onraedt, U); Anse des Cascades, 10 m, Onraedt 76 R 1507, janvier 1976 (herb. Onraedt, U); au SW de Saint-Benoît, 400 m, J.L. De Sloover 17830 bis, décembre 1973 (NAM, BR).

fo. *verrucosa:* MADAGASCAR: Province de Tananarive, au lac de Mantasoa, 1400 m, Onraedt 74 M 8079 (type) et 2104, mars 1974 (herb. Onraedt).

b. var. *integra*: MADAGASCAR: Région orientale de l'île, au pK 300, épiphyte sur des branchettes, Tixier 10145, décembre 1976, type (BR); Ambatofitorahana, à 34 km au S. d'Ambositra, sur les arbres d'une forêt primaire dégradée, 1650 m, Onraedt 71 M 5374, août 1971 (herb. Onraedt, U).

c. var. *bidentata*: MADAGASCAR: Province de Tananarive, au lac de Mantasoa, sur les branches d'un *Philippia* dans un fourré, 1400 m, Onraedt 74 M 2129, mars 1974 (herb. Onraedt, BR, U); id., vallée de la Mandraka, route de Tananarive à Moramanga, 1100 m, Onraedt 74 M 2012, février 1974 (herb.

Onraedt, U); Province de Diégo-Suarez, Montagne d'Ambre, sur un arbre dans la forêt, 1000 m, Cremers 2755, août 1973 (herb. Onraedt, U). LA RÉUNION: Entre Saint-Pierre et Saint-Benoît, à Terre Carrère, sur des arbres isolés en bordure d'une rivière et de la route, 800 m, Onraedt 71 R 9275, septembre 1971, type (U, herb. Onraedt, herb. Grolle). ILE MAURICE: Sine loc., Rodriguez s.n., ex herb. Renauld, sub *Acrojeunea borgenii* det. Stephani (PC).

2. **Schiffneriolejeunea fragilis** Gradst. et E.W. Jones Fig. 8

Journ. Bryol. 12: 45, fig. 4 (1982).

Type: Gabon, Poungui, Le Testu s.n., novembre 1929 (BR holotype, PC, U).

Plante dioïque, brun jaune à l'état sec, à tiges feuillées longues de 1-2 cm et larges de (0,8-)1-1,4(-1,6) mm. Rameaux apparemment toujours du type '*Lejeunea*'; diamètre: 100-165 µm; mérophyte ventral large de 4-5 cellules. Feuilles imbriquées, étalées, squarreuses; lobe ovale, obtus à arrondi au sommet, entier, plan ou à bord ventral un peu involuté, souvent fragile, 0,4-0,7(-0,8) mm × 0,5-0,9(-1) mm; lobule ovale lorsque bien développé, à dent apicale unicellulaire et obtuse, 0,14-0,17 mm × 0,2-0,3 mm, souvent plus petit et long seulement de 0,15 mm environ. Cellules foliaires subhexagonales-subrectangulaires, à parois présentant des trigones noduleux à 2 côtés convexes et à un côté concave ainsi que des épaississements intermédiaires noduleux; cellules au centre du lobe: 16-18 µm × 23-25 µm; cellules basilaires atteignant une longueur de 30 µm; cellules apicales: environ 10 µm × 10-15 µm. Amphigastres contigus à imbriqués, spatulés, approximativement aussi larges que hauts ou plus hauts que larges, plans ou à partie apicale un peu squarreuse, très largement arrondis ou tronqués au sommet, cunéés ou rarement un peu auriculés à la base; une bosse médiane peu prononcée; ligne d'insertion arquée; dimensions: 0,25-0,4 mm × 0,35-0,5 mm.

Andrécie au sommet d'un rameau, souvent long, du type '*Lejeunea*', devenant intercalaire, à 5-10 paires de bractées hypostatiques; partie apicale du lobule allongée, arrondie au sommet, à bord distal formant un angle aigu avec le bord ventral du lobe; bractéoles semblables aux amphigastres. Gynécie au sommet d'un rameau généralement long, du type '*Lejeunea*'. Bractées et bractéole précédées de 1-2 paires de feuilles et amphigastres modifiés, formant un involucre enveloppant le périanthe, fragile, souvent déchiré; bractées dépourvues de carène; lobe plus long que le périanthe, environ 0,6 mm × 1,5 mm, aigu ou largement acuminé au sommet; lobule plus long à approximativement aussi long que le périanthe, environ 0,15 mm × 0,1 mm, étroitement ovale avec un acumen triangulaire; bractéole ovale ou obovale, environ 0,7 mm × 1,7 mm, souvent épaulée des deux côtés par une dent obtuse, à sommet brusquement rétréci et bilobé jusqu'au 1/6-1/4 de la longueur de la bractéole, à lobes acuminés et souvent inégaux entre eux. Périanthe pyriforme, enflé, lisse, dépourvu de carènes ou pourvu d'esquisses de carènes dans la partie tout-à-fait apicale de l'organe, à sommet habituellement ombiliqué; dimensions: 0,6-0,75 mm × 1-1,1 mm; bec cylindrique, haut de 4-6 assises de cellules.

DISTRIBUTION ET OBSERVATIONS: Sierra Leone, Ghana, Nigéria, Cameroun, République congolaise, Zaïre; 0-750 m. — "It is apparently confined to the forest

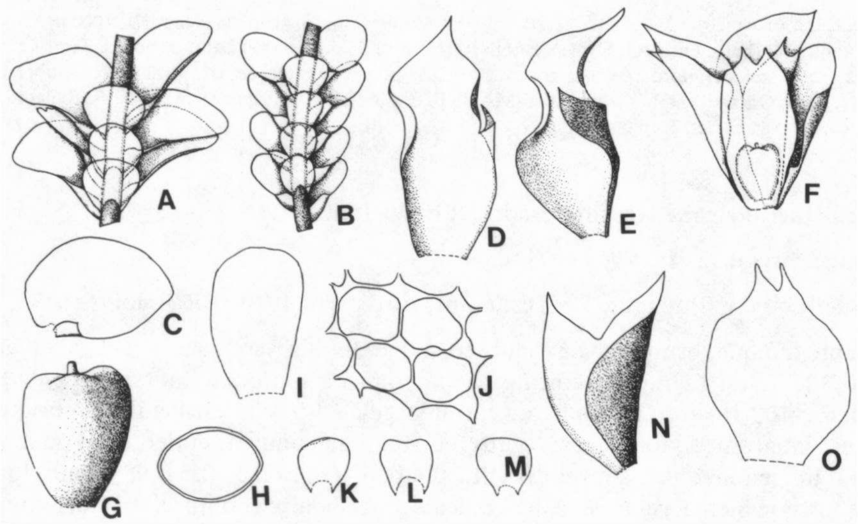

Fig. 8. *Schiffneriolejeunea fragilis.*

A et B: Fragments de tiges feuillées, en vue ventrale (×22). C: Feuille détachée de la tige et étalée (×22). D et E: Bractées ♀ (×22). F: Gynécie avec un périanthe juvénile, en vue ventrale (×22). G: Périanthe (×22). H: Section transversale dans un périanthe, à mi-hauteur (×22). I: Bractéole involucrale ♀ située immédiatement sous la bractéole interne (×22). J: Cellules du périanthe (×370). K, L et M: Amphigastres (×22). N: Bractée ♀ (×22). O: Bractéole ♀ (×22).

A-H et K-L: E.W. Jones 1517 a. I et M-O: Le Testu s.n. (type).

districts of lowland tropical West Africa and the Congo Basin. Probably all the recorded localities are below 750 m alt., and most are very much lower. It is closely related to *S. pappeana* (Nees) Gradst., which is widely distributed in South and East Africa and extends to Cameroon Mountain, but is not known with certainty from further west. *S. pappeana* is more montane, rarely occurring in tropical Africa below 1000 m alt. *S. fragilis* shares with *S. pappeana* the terete eplicate perianth and other features of the gynoecium and the squarrose leaves, but it is easily distinguished by its smaller size and usually by the brittleness of leaves and bracts- it is very difficult to dissect perfect female bracts and bracteole... The brittleness of the leaves, though characteristic, is not a constant character of *A. fragilis*; unbroken well developed leaves may sometimes be found at shoot bases or on main stems, and occasionally none of the leaves are fragile. On the other hand fragile leaves are not entirely lacking in *S. pappeana,* as they were observed on branches of an otherwise typical specimen of *S. pappeana* from the lower mountains of Zaïre (Betongwe, 1000 m alt., Jean Louis 4508, BR).

Where the habitat has been adequately recorded *S. fragilis* has been on boughs in the inner parts of the crowns or on the upper parts of the boles of large forest trees or (in Jones 802) on the bole of a roadside tree. It sometimes grows mixed with *S.*

polycarpa (Nees) Gradst. (e.g. in E.W. Jones 802 and 1515), which might cause confusion if mature perianths are not present. The underleaves of *S. polycarpa*, like those of *S. fragilis*, have cuneate bases without auricles but are rounder in shape; the lobe of the leaf also has a rounder apex, is never brittle and when moist not squarrose (rarely slightly so)." (Jones 1982: 46-47).

Exemplaires examinés (*S. fragilis*): SIERRA LEONE: Loma Mts., Seredu, E.W. Jones 1516a, mars 1971 (herb. E.W. Jones, U); id., 1517a (herb. E.W. Jones, BR). NIGERIA: Benin, Okomu Forest Reserve, E.W. Jones 195B, février 1948 (K in BM, herb. E.W. Jones). CAMEROUN: Ekundu Ndene, Dusén s.n., janvier 1891 (U, UPP). GABON: Poungui, Le Testu s.n., septembre 1929, type (BR, PC, U). REPUBLIQUE CONGOLAISE: Brazzaville, Matala, Assel 408, janvier 1966 (EGR, U). ZAIRE: Mayombe, Luki, E.W. Jones 832 (herb. E.W. Jones, U); Kisantu-Kwango, Haute Nsele, Vanderyst 14097 (BR, U); Maniema, Kindu, E.W. Jones 802 (herb. E.W. Jones, U).

3. **Schiffneriolejeunea madagascariensis** (Steph.) Gradst. Figs. 9, 10

Journ. Hattori Bot. Lab. 38: 333 (1974). *Ptychocoleus madagascariensis* Steph., Spec. Hep. 5: 27 (1912).

Lectotype: Madagascar, sine loc., Forsyth Major 505 (BM). Paratype: id., Forsyth Major 1000 (BM).

Plante dioïque, corticole, formant des gazonnements brun marron foncé appliqués contre le substrat; rameaux feuillés, apparemment toujours du type '*Lejeunea*', larges de 1,7-2(-2,4) mm. Tige longue de 1-2,5 cm; diamètre: 150-300 µm; anatomie de la coupe semblable à celle décrite chez *S. pappeana* mais à nombre de cellules souvent plus élevé que chez cette espèce; mérophyte ventral large de 10-12 cellules.

Feuilles fortement imbriquées, étalées-dressées, nettement concaves ventralement; lobe ovale-suborbiculaire, à bord dorsal fortement convexe, à base dorsale tronquée ou faiblement convexe, parfois subauriculée, ne débordant pas la tige ou la débordant faiblement, à bord ventral entièrement involuté, à sommet obtus-arrondi et souvent cucullé, 0,93-1,4 mm × 1,1-1,8 mm; lobule relativement grand, 0,32-0,37 mm × 0,47-0,6 mm lorsque étalé, enflé en fuseau le long de la carène, à partie distale appliquée contre le lobe; dent apicale peu proéminente, unicellulaire et arrondie, d'un diamètre de 15 µm environ; papille hyaline fugace, claviforme, interne, longue de 45-60 µm; bord libre convexe-sinué, généralement pourvu d'une deuxième dent bien apparente, à 1(2) cellules, subaiguë ou obtuse, longue de 15-20 µm. Cellules foliaires subhexagonales-allongées, à parois pourvues de grands trigones à 2 côtés convexes et à un côté concave; cellules au centre du lobe: (16-)18-22(-25) µm × 25-30(-32) µm; cellules de la zone marginale du lobe nettement plus petites et devenant subrectangulaires, celles des 2-3 rangées les plus externes mesurant 14-20 µm × 15-21 µm; cellules basilaires à peine plus grandes que les cellules centrales, longues jusqu'à 36 µm.

Amphigastres imbriqués, environ 4 fois aussi larges que la tige, subrectangulaires-réniformes, plus larges que hauts, fortement concaves ventralement, à bord étroitement révoluté sur le pourtour de l'organe ou sur la plus grande partie de ce

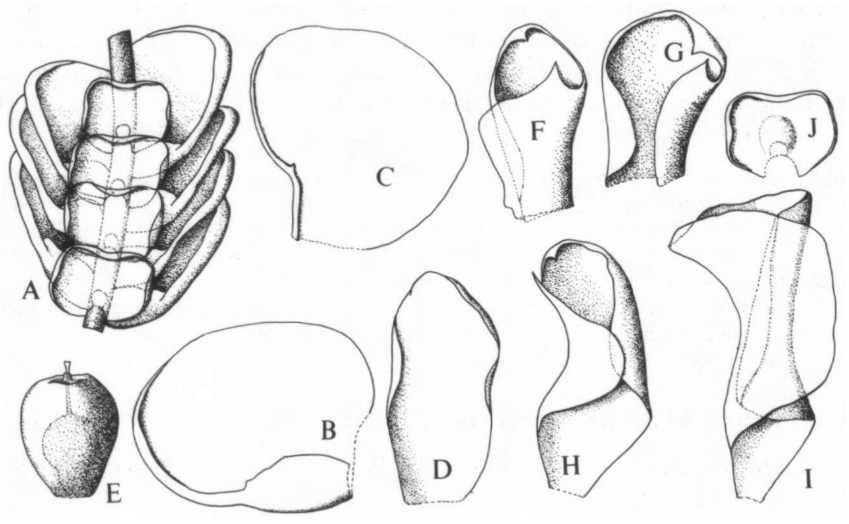

Fig. 9. *Schiffneriolejeunea madagascariensis.*

A: Fragment de tige feuillée, en vue ventrale (×22). B: Feuille détachée de la tige et étalée (×22). C: Bractée involucrale ♀ située immédiatement sous les bractées internes (×22). D: Bractéole involucrale ♀ située immédiatement sous la bractéole interne (×22). E: Périanthe (×22). F, G et H: Bractées ♀, en vue ventrale (×22). I: Bractéole ♀, en vue dorsale (× 22). J: Amphigastre, en vue ventrale (×22). A-J: Tixier 9619.

pourtour; de petites oreillettes à la base; une bosse médiane; dimensions des amphigastres: (0,46-)0,54-0,72 mm × (0,67-)0,7-0,9 mm; éventuellement un disque radicellifère grand et épais de 3-4 cellules (chez *S. pappeana:* 2 cellules!), les rhizoïdes étant insérés environ 200 µm au-dessus de la ligne d'insertion de l'amphigastre.

Andrécie au sommet d'un rameau du type '*Lejeunea*' plus ou moins allongé, proliférant et devenant intercalaire, souvent de forme ovoïde, plus étroite que les rameaux feuillés, à 4-5(6) paires de bractées imbriquées; celles-ci à carène hémicirculaire; bractéoles tout le long de l'andrécie, souvent plus petites et moins concaves que les amphigastres; parfois une verrue au centre de la face externe des cellules du lobule des bractées. Deux anthéridies subglobuleuses à l'aisselle de chacune des bractées; diamètre: 180-210 µm.

Gynécie au sommet d'un rameau latéral du type '*Lejeunea*'; pas d'innovations du type '*Radula*'. Bractées et bractéole précédées de 4-5 paires de feuilles et amphigastres fortement imbriqués entre eux et plus grands que les feuilles et amphigastres végétatifs; partie inférieure de cet involucre en forme de manchon enveloppant étroitement le périanthe, contracté immédiatement au-dessus de celui-ci; partie supérieure étalée ou dressée-étalée; bractées à lobe ovale, fortement concave, à bord dorsal partiellement involuté, à sommet parfois cucullé, aigu ou arrondi et apiculé,

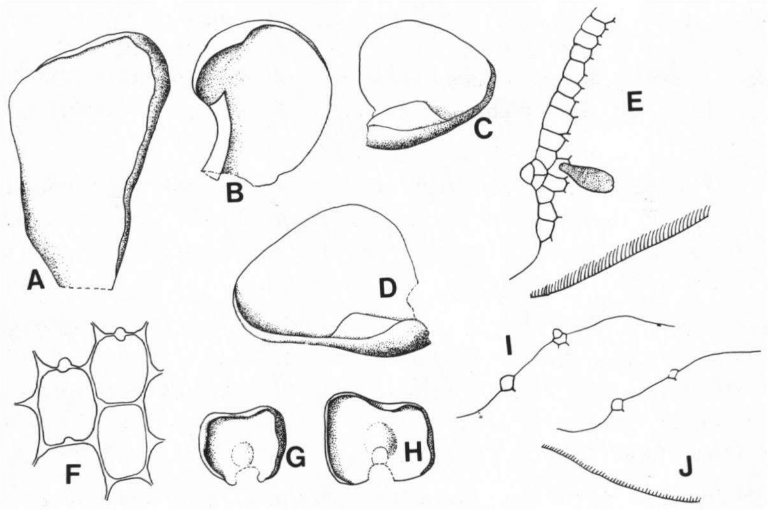

Fig. 10. *Schiffneriolejeunea madagascariensis.*

A: Bractéole ♀ (×22). B: Bractée involucrale ♀ située sous les bractées internes (×22). C et D: Feuilles détachées de la tige et étalées (×22). E: Face interne d'un lobule foliaire avec la dent apicale et la papille hyaline (×230). F: Cellules du périanthe (×300). G et H: Amphigastres, en vue ventrale (×22). I et J: Bord libre de deux lobules foliaires, avec la dent apicale et une dent supplémentaire (×115).

A, B, F et H: Tixier 9619. C, D, G, I et J: Onraedt 74 M 2216. E: Forsyth Major 505 (type).

0,9-1,2 mm × 1,2-1,85 mm; lobule très variable, subrectangulaire à hémicirculaire, environ 0,6 mm × 0,6-1 mm, à sommet toujours aigu, à carène très obtuse; bractéole obovale, arrondie-sinuée au sommet ou pourvue de quelques dents irrégulières, fortement concave, enroulée autour du périanthe, à base très étroite, 1-1,2 mm × 2-2,2 mm. Périanthe obovoïde, tronqué ou rétus au sommet, dépourvu de carènes, formé de cellules à face externe subrectangulaire et lisse, à parois présentant des trigones irrégulièrement noduleux et quelques épaississements intermédiaires noduleux; périanthe petit, 0,72-0,8 mm × 1-1,05 mm; bec cylindrique, long de 100-135 μm, haut de 7-8 assises de cellules à face externe subcarrée, environ 15 μm × 15 μm; ouverture entière, dépassée par le sommet du col de l'archégone.

DISTRIBUTION ET ÉCOLOGIE: L'espèce a été observée exclusivement dans la partie orientale de Madagascar, dans des districts particulièrement humides, vers 1400 m d'altitude. Elle croît en épiphyte dans des stations bien éclairées, notamment dans les forêts dégradées et les fourrés à *Philippia.*

Observations:

1. Le lobule foliaire, chez *Schiffneriolejeunea madagascariensis,* porte souvent deux dents. La dent proximale, par rapport à la tige, est formée de 1(2) cellules et est bien apparente; elle est située au sommet d'un angle obtus qui brise la courbe régulière de la partie proximale du bord libre du lobule. La deuxième dent, située entre la dent

proximale et le bord ventral du lobe, n'est que faiblement proéminente; elle est apparemment toujours unicellulaire et sa face libre est arrondie. Cette deuxième dent est la dent apicale car c'est sous elle que la papille hyaline est insérée sur la face interne du lobule. Une 3e et même une 4e dent sont rarement observées sur le bord libre du lobule.

2. A la suite de la diagnose de *Ptychocoleus madagascariensis*, Stephani (1912) indique simplement 'Madagascar' comme lieu de récolte de la plante qu'il vient de décrire; il n'y a pas de nom de récolteur. Il est donc nécessaire de proposer un lectotype de l'espèce.

L'herbier Stephani (G) contient 8 échantillons étiquetés *Acrolejeunea madagascariensis* Steph., taxon probablement publié en 1912 sous le nom de *Ptychocoleus madagascariensis* Steph. Tous ces échantillons, dont des doubles sont conservés dans l'herbier de Londres (BM), répondent à la diagnose de *Schiffneriolejeunea pappeana* (Nees) Gradst.

Les dessins de Stephani représentant *Acrolejeunea madagascariensis* se rapportent pourtant à une espèce différente de *S. pappeana* (Icones Ined. G 008271). L'échantillon dessiné est une plante femelle récoltée à Madagascar par Forsyth Major; il porte le numéro 535. Or, le Forsyth Major 535 conservé à Genève est une plante mâle et relève de l'espèce *S. pappeana*!

Gradstein a examiné un échantillon Forsyth Major 505 récolté à Madagascar et conservé Londres (BM) sous le nom de *Acrolejeunea madagascariensis*. Il s'agit d'une plante femelle dont les caractères sont ceux figurés et décrits par Stephani. Dans ces conditions, on peut croire à une erreur de numérotation et il est légitime de choisir le Forsyth Major 505 comme lectotype de *Schiffneriolejeunea madagascariensis*. Un autre échantillon authentique de cette espèce, Forsyth Major 1000 (BM), moins bien développé, avec des périanthes jeunes, est considéré comme paratype.

Exemplaires examinés (*S. madagascariensis*): MADAGASCAR: Sine loc., Forsyth Major 505, lectotype (BM); id. 1000, paratype (BM); Province de Tananarive, au lac de Mantasoa, 1400 m, Onraedt 74 M 2216, mars 1974 (herb. Onraedt, U); Andosibe, Tixier 9619, novembre 1970 (BR).

4. **Schiffneriolejeunea parviloba** (Steph.) Gradst. Fig. 11

Journ. Hattori Bot. Lab. 38: 335 (1974). *Acrolejeunea parviloba* Steph., Bot. Gaz. 15: 286, pl. 18, fig. 8 (1890). *Ptychocoleus parvilobus* (Steph.) Steph., Spec. Hep. 5: 31 (1912); E.W. Jones (1954: 397, fig. 1).

Type: Ile Maurice, Rodriguez s.n., 1892, ex. herb. Renauld (G holotype, BM, PC, W).

Plante dioïque formant des feutrages lâches, brun verdâtre à brun cuivré; tiges feuillées principales longues de 2-4 cm et larges de (0,85-)1-1,8(-2,2) mm. Tige irrégulièrement ramifiée, la plupart des rameaux étant du type '*Lejeunea*', parfois microphylles et larges seulement de 0,72 mm environ; rameaux végétatifs du type '*Frullania*' parfois nombreux; en coupe: 18-25 cellules corticales à parois pigmentées de brun, un peu plus petites à un peu plus grandes que les cellules médul-

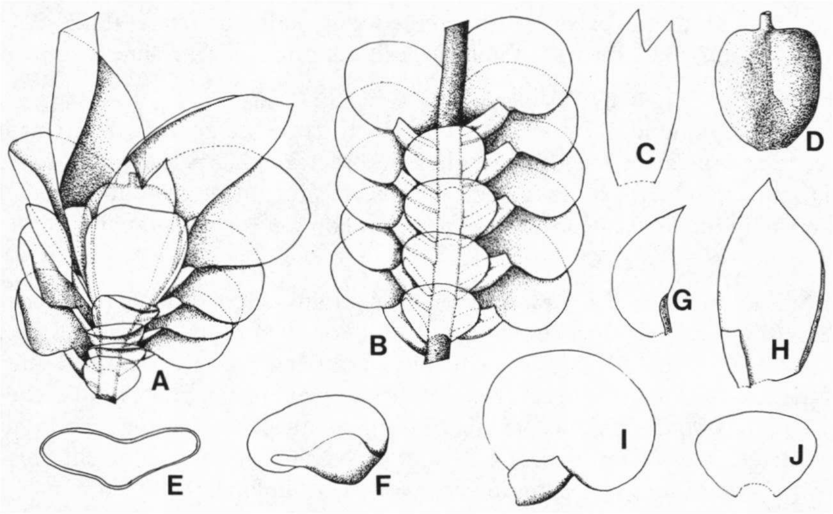

Fig. 11. *Schiffneriolejeunea parviloba.*

A: Fragment de rameau porteur d'une gynécie, en vue ventrale (×22). B: Fragment de tige feuillée, en vue ventrale (×22). C: Bractéole ♀ (×22). D: Périanthe (×22). E: Coupe transversale dans un périanthe, à mi-hauteur (×35). F: Bractée ♀, en vue ventrale (×45). G: Bractée ♀ (×16). H: Bractée ♀ (×22). I: Feuille détachée d'une tige et étalée (×22). J: Amphigastre (×22).

A-D et H-J: Onraedt 73 Ma 328. E-G: Rodriguez s.n. (type).

laires; celles-ci, comme chez *S. pappeana*, à parois non pigmentées; mérophyte ventral large de 6-10 cellules; diamètre des tiges principales: 150-260 µm.

Feuilles imbriquées, étalées, non squarreuses; lobe elliptique à ovale-suborbiculaire, entier, largement arrondi, plan ou un peu incurvé au sommet, à base dorsale largement arrondie débordant un peu la tige ou ne la débordant pas, (0,55-)0,7-1,05 mm × (0,70-)0,9-1,3 mm; lobule ovale lorsque étalé, enflé et subhémicylindrique le long de la carène, à partie supérieure plane et appliquée contre le lobe; carène faiblement arquée formant un angle de 45-60° avec la tige et un angle droit ou obtus (jusque 135°) avec le bord ventral du lobe; dent apicale obtuse, formée de 1-2 cellules, longue de 20 µm environ, rarement accompagnée d'une 2e dent, proximale par rapport à la tige; papille hyaline insérée sur la face interne du lobule, sous la base de la dent apicale; bord libre convexe, entier-sinué; dimensions: 0,16-0,27 mm × 0,26-0,48 mm. Cellules foliaires hexagonales-allongées, régulièrement alignées, à parois pourvues de trigones à 1 côté concave et 2 côtés convexes et souvent d'épaississements intermédiaires noduleux; cellules au centre du lobe: 15-20 µm × 20-30(-35) µm; cellules apicales: 12-15 µm × 12-18 µm; cellules basilaires: 16-20 µm × 30-40 µm.

Amphigastres imbriqués à contigus, obovales-cunéés, plus longs que larges à plus larges que longs, tronqués ou largement arrondis et souvent un peu récurvés au sommet, présentant parfois de petites oreillettes arrondies à la base, (0,25-)0,3-0,4(-0,6) mm × (0,28-)0,32-0,45(-0,7) mm sur les tiges principales; cellules semblables à celles des lobes foliaires, 12-15 μm × 18-25 μm.

Andrécie au sommet d'un rameau latéral, du type '*Lejeunea*', devenant intercalaire, relativement courte, à 5-6 paires de bractées plus petites que les feuilles végétatives; lobule hypostatique à partie apicale plus ou moins allongée, le bord distal formant un angle aigu avec le bord ventral du lobe; bractéoles plus petites que les amphigastres.

Gynécie au sommet d'un rameau plus ou moins allongé du type '*Lejeunea*'. Bractées dressées ou dressées-étalées mais non squarreuses comme chez *S. pappeana*, précédées de 1-2 paires de feuilles modifiées, plus grandes que les feuilles végétatives, faiblement imbriquées entre elles et peu enveloppantes, à carène bien marquée; lobe obovale-oblancéolé, aigu à obtus et apiculé au sommet, à bord dorsal parfois étroitement involuté, 0,52-0,82 mm × 1-2 mm; lobule nettement plus petit que le lobe, moins long que la moitié de la longueur du lobe, 0,12-0,24 mm × 0,45-0,9 mm, subrectangulaire ou oblancéolé, longuement soudé au lobe, à partie libre nulle. Bractéole précédée de 1-2 amphigastres modifiés, oblongue ou obovale, convexe ventralement, à bords latéraux non involutés, n'enveloppant pas le périanthe, terminée par 2 dents ou 2 lobes aigus au sommet; ceux-ci séparés par un sinus plus ou moins profond, atteignant parfois le 1/5 environ de la longueur de la bractéole; dimensions: 0,45-0,63 mm × 1-1,275 mm. Périanthe faiblement enfoui dans l'involucre, obovoïde-comprimé, arrondi ou à faces dorsale et ventrale un peu concaves, dépourvu de carènes, tronqué à rétus au sommet, environ 0,78 mm × 1 mm; parois des cellules présentant des trigones irrégulièrement noduleux ainsi que quelques épaississements intermédiaires noduleux; bec cylindrique, long de 75-150 μm, haut de 5-12 assises de cellules, à ouverture entière.

Variabilité et exemplaires observés: *Schiffneriolejeunea parviloba* n'a été récolté qu'aux Mascareignes et est apparemment une espèce peu variable. MAURICE: Rodriguez s.n., 1892, ex herb. Renauld, type (BM, G, PC, W); id., 1888, stérile (BM, FH, M, PC); Anderson s.n. (BM); H 101, récolteur inconnu (UPP); Curepipe, sur les arbres du Jardin Botanique, 400 m, Onraedt 73 Ma 328, décembre 1973 (herb. Onraedt, U); Curepipe, récolteur inconnu, juin 1906 (L). LA RÉUNION: Rodriguez s.n., ex herb. Renauld (BM, G); de l'Isle s.n., ex herb. Renauld (?) (BM).

Références

ARNELL, S. 1953. Hepaticae collected in 1951. New and little known species. Bot. Notis. 1953: 163-182; ibid. 271-289.

ARNELL, S. 1963. Hepaticae of South Africa. Stockholm.

GRADSTEIN, S.R. 1974. Studies on Lejeuneaceae subfam. Ptychanthoideae I. Nomenclature and taxonomy of *Ptychocoleus, Acrolejeunea* and *Schiffneriolejeunea*. J. Hattori Bot. Lab. 38: 327-336.

GRADSTEIN, S.R. 1975. Studies on Lejeuneaceae subfam. Ptychanthoideae III. A taxonomic monograph of the genus *Acrolejeunea*, with an arrangement of the genera of Ptychanthoideae. Bryophyt. Bibl. 4: 1-216.

GRADSTEIN, S.R. & INOUE, H. 1980. Studies on Lejeuneaceae subfam. Ptychanthoideae V. A review of the species from Ceylon. Bull. Nat. Sci. Mus. Tokyo ser. B, 6: 23-32.

JONES, E.W. 1954. African Hepatics IX. Some species of *Ptychocoleus*. Trans. Brit. Bryol. Soc. 2: 396-407.

PEARSON, W.H. 1892. Lejeuneae Madagascariences. Christiana Vid.-Selksk. Forh. 8: 3-11.

SCHUSTER, R.M. & HATTORI, S. 1954. The oil bodies of the Hepaticae II. The Lejeuneaceae. J. Hattori Bot. Lab. 11: 11-86.

STEPHANI, F. 1912. Species Hepaticorum V, p.p. Geneva.

VANDEN BERGHEN, C. 1976. Deux Lejeunéacées holostipées nouvelles pour la Flore africaine. Rev. Bryol. Lichénol. 42: 923-929.

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BEIHEFT 80 ZUR NOVA HEDWIGIA

9 A Revision of the Genus *Stictolejeunea* (Spruce) Schiffn.

by

S.R. Gradstein

ABSTRACT: *Stictolejeunea* is an epiphytic genus of moist primary lowland and submontane rainforests, especially of tropical America. It is probably one of the most natural genera of Lejeuneaceae. Three species are accepted in this revision: *S. squamata* (= *S. kunzeana* syn. nov), *S. balfourii* (= *S. richardsii* syn. nov.) and *S. iwatsukii*. *S. squamata* is a common neotropical species and constitutes the subgenus *Stictolejeunea*. *S. balfourii* was originally considered an African species but is now reported also from tropical Asia (where it was known as *S. richardsii*) and from tropical America (new). In Suriname a separate variety occurs: *S. balfourii* var. *bekkeri* var. nov. *S. balfourii* and *S. iwatsukii* (Japan) constitute the subgenus *Parastictolejeunea* subg. nov., characterized by the posession of a simplified stem structure and predominantly *Lejeunea*-type (in stead of *Frullania*-type) branching.

The different distributions of *S. balfourii* and *S. squamata* are correlated with different sex distributions, viz. monoicous resp. dioicous conditions, which corroborates the notion that in Lejeuneaceae transoceanic distributions are found only in taxa with bisexual spores. It is postulated that *Stictolejeunea* originated in tropical America and from there migrated to palaeotropical regions, either via ancient land-connections or through long-range air dispersal.

Introduction

The genus *Stictolejeunea* (Spruce) Schiffn., as defined by Spruce (1884) and Evans (1907, 1935), is probably one of the most natural genera of Lejeuneaceae. Characteristic are 1) the numerous, scattered ocelli in leaves, underleaves, bracts and perianths, 2) the small, evenly thickened chlorophyllose leaf cells lacking oil bodies, 3) the entire underleaves, 4) the stem lacking a hyaloderm, 5) the small androecial spikes with reduced bracteoles, 6) the flattened perianth, placed on a very short lateral branch and dilated above into two large, rounded auricles, which like the leaves and underleaves may be bordered by whitish, dead cells, and 7) the "Lejeuneoid" capsule of the sporophyte (Geissler & Gradstein 1981). The peculiar perianth was compared by Spruce with the head and ears of an Andean rodent, the chinchilla!

Stictolejeunea has a 16:4 seta and therefore belongs in the subfamily Ptychanthoideae (Geissler & Gradstein 1981), in which it stands somewhat isolated because of its peculiar leaf areolation. Among Lejeuneaceae a similar leaf areolation is also found

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Studies on Lejeuneaceae subfam. Ptychanthoideae XIV. Also appearing as STUDIES ON THE FLORA FLORA OF THE GUIANAS 9.

in *Rectolejeunea berteroana* (Schuster 1980) and in *Lepidolejeunea* (Schuster 1980a), which has sometimes been confused with *Stictolejeunea*. Sterile *Lepidolejeunea*, when holostipous (*L. graeffii, L. herzogii)*, may indeed resemble *Stictolejeunea*, but is immediately recognised by the 2 cells wide ventral merophyte and the stem hyaloderm.

Stictolejeunea has long been known only by two species from tropical America: *S. squamata* from low elevations and the more robust *S. kunzeana* from higher elevations. In 1950 Vanden Berghen described *S. africana* from Ivory Coast and Rodriguez and in the same year Herzog described *S. richardsii* from Borneo. Jones (1957, 1976) pointed out that *Lejeunea balfourii* Mitt. 1879 from Rodriguez is conspecific with *S. africana* (hence *Stictolejeunea balfourii* (Mitt.) E.W. Jones) and reported several new localities for the species as well as details on its variation and habitat.

New Asiatic localities for *S. richardsii* were recorded by Inoue & Miller (1968) and Grolle (1969). Mizutani (1978) described a further palaeotropic species, *S. iwatsukii*, from the Ryukyu archipelago, southern Japan and provided a key to the above five species of *Stictolejeunea* hitherto recognised. Four further species have been described in *Stictolejeunea: S. herzogii, S. micholitzii* and *S. orientalis*, which belong in *Lepidolejeunea* (see excluded species), and *S. rotundifolia*, which is probably conspecific with *S. squamata.*

The present study attempts at defining the species of *Stictolejeunea* on a worldwide basis. It was instigated by the discovery of *S. balfourii* in Suriname by Miss J. Bekker, in the course of the 1981 bryophyte exploration of the Kabalebo Dam project area (Florschütz-de Waard & Zielman, in prep.).

Taxonomy and Relationships

In this revision three species are accepted in *Stictolejeunea:* the neotropical *S. squamata* (= *S. kunzeana*), the pantropical *S. balfourii* (= *S. richardsii*) and *S. iwatsukii* from southern Japan. Differences are shown in the key. *S. balfourii* and *S. iwatsukii* are evidently very closely related, but their affinity to *S. squamata* is more remote notwithstanding the basic structural similarity of the three species (leaf areolation, androecia, perianth). For an evaluation of the differences between *S. squamata* and *S. balfourii* (and *S. iwatsukii*), the strong morphological variation of *S. squamata* (as opposed to the other species) should particularly be taken into account.

Generally, *S. squamata* is much more robust than *S. balfourii.* Correlated with its larger size is the tendency in *S. squamata* to grow free from the substrate and attain a pendulous habit (*S. balfourii* is always creeping), to produce numerous branches in a regular, pinnate fashion, to develop rigid stems with numerous thickened, brownish pigmented cortical cells in more than one row and to develop large, very broad underleaves. The robust stem seems an adaptation to the pendulous growth habit of this species, because tinier creeping forms usually have thinner stems approaching those of *S. balfourii* (some creeping populations of *S. squamata* have robust stems as well, though).

S. squamata may further be distinguished from *S. balfourii* by its (usually) curved, strongly inflated lobules (straight and less inflated in *S. balfourii*); in both species the lobule shows a tendency for reduction. A difference is also found in the placement of the underleaves: in *S. squamata* underleaves are free, not associated with lateral leaves, whereas in *S. balfourii* the underleaves are almost connate (by one cell) with leaves on one side of the stem. The latter type of underleaf placement is unusual in Ptychanthoideae, but may be more common in other subfamilies of Lejeuneaceae.

An important difference between *S. squamata* and *S. balfourii* is the branching type: vegetative branches in *S. squamata* are always of the *Frullania*-type; in *S. balfourii* they are of the *Lejeunea*-type as a rule, but robust plants may develop occasional *Frullania*-type branches as well. Jones (1970) and Gradstein (1975) have reported a similar branching modality, as found in *S. balfourii*, for other genera of Ptychanthoideae, and apparently this type of branching behaviour is rule rather than exception in the subfamily (see also Thiers, this volume). On the other hand, the exclusive production of *Frullania*-type (rather than *Lejeunea*-type) branches is rare in Lejeuneaceae and apparently constant on the generic or subgeneric level (*Ptychanthus, Tuzibeanthus*).

As regards to branching, *S. squamata* and *S. balfourii* are also different as to the production of innovations. In *S. squamata* each gynoecium produces one innovation, which is usually short and sterile but occasionally may continue to grow and give rise to new gynoecial shoots. Only once I have found in this species a gynoecium without innovation (other gynoecia of the same plant did produce them as usual). In *S. balfourii,* however, the perianth lacks innovations or, when present, the innovation is very short and tiny and occupied by male bracts (never in *S. squamata,* as that species is dioicous).

Perianths are similar in the two species, except for the tendency in *S. squamata* to produce whitish auricle borders.

The sporophyte of *Stictolejeunea* has been studied in two collections of *S. squamata:* Peru, leg. Spichiger (described in Geissler & Gradstein 1981), and Brazil, Sellow s.n., the type of *Lej. squamata* var. *neesii* Gott., and in one collection of *S. balfourii:* Suriname, leg. Bekker 1619b, the type of *S. balfourii* var. *bekkeri.* In all three specimens the capsule is typically Lejeuneoid (valves pale, suberect, with inner and outer thickenings nodulose, the elaters without spirals and the spores narrow rectangular), but in *S. squamata* the thickenings of the inner valve layer may become rather strong above, tending to become coalesced and ± fenestrate. Geissler & Gradstein (1981) recorded a plurifenestrate pattern in the material of *S. squamata* from Peru, but in the Brazilian specimen M. van Slageren and I found only strongly nodulose thickenings tending to form a monofenestrate pattern.

The above differences between *S. squamata* on the one hand and *S. balfourii* and *S. iwatsukii* on the other hand, indicate a rather pronounced evolutionary divergence and are reasons to recognize two different subgenera (Figs. 1, 2, 3): subgenus *Stictolejeunea* (*S. squamata*) and subgenus *Parastictolejeunea* subg. nov. (*S. balfourii* and *S. iwatsukii*).

As to its generic relationship, *Stictolejeunea* is usually considered most closely related to *Neurolejeunea* (Spruce 1884, Evans 1907, Schuster 1963, Gradstein 1975), which has similar gametoecia, small leaf cells (with oil bodies, though), sometimes a few ocelli in a row, and lacks a hyaloderm as well. The seta in *Neurolejeunea* is 16:4 (seen in *N. breutelii*, Cuba, leg. Reyes) as in other Ptychanthoids, and my earlier recording of a 12:4 seta in this genus (cf. Grolle 1983) is erronous. The structure of the capsule is Lejeuneoid as in *Stictolejeunea* (fide M.W. van Slageren, oral comm.). *Neurolejeunea* differs from *Stictolejeunea* in some important traits, though: possession of blackish cell wall pigmentation, oil bodies, two very dimorphic lobule teeth (the first one short and blunt, sometimes reduced and therefore overlooked by previous authors, the second one long and slender, often curved), an elongated gynoecial shoot and two well developed innovations for each gynoecium (Table I). In spite of these differences, *Neurolejeunea* may best be kept in the *Stictolejeunea* complex where Schuster (1963) and Gradstein (1975) placed it.

Affinities of *Stictolejeunea* to other genera of Ptychanthoideae are much more remote. Spruce (1884) suggested an affinity to *Symbiezidium*, with which it shares the abbreviated gynoecial branches, the lack of male bracteoles and the Lejeuneoid capsule. The gametophytes of the two genera are very different, though, as is shown in Table I. Other genera are even more distant (Gradstein 1975). In all, it appears that *Stictolejeunea* is one of the most clearly defined genera of the subfamily.

Table I. A comparison between *Stictolejeunea, Neurolejeunea* and *Symbiezidium*.

	Sticto-lej.	*Neuro-lej.*	*Symbie-zidium*
1. Secondary pigmentation lacking (+) or present (-)	+	-	-
2. Ocelli numerous, scattered (+ +), few in a row (+) or lacking (-)	+ +	+	-
3. Oil bodies lacking (+) or present: segmented (-) or homogeneous (--)	+	-	--
4. Stem cortex enlarged (-) or not (+)	+	+	-
5. Median leaf cells 10-20 µm (+) or 30-40 µm (-)	+	+	-
6. Intermediate thickenings lacking (+) or present (-)	+	+	-
7. Trigones coalescent (+) or free (-)	+	+	-
8. Female bract lobule small (+) or large (-)	+	+	-
9. Perianth keels expanded (+) or not expanded (-)	+	+	-
10. Perianth keels smooth (+) or ciliate (-)	+	+	±
11. Underleaf base bistratose (+) or tristratose (-)	+	+	±
12. Gynoecium on an abbreviated (+) or an elongated (-) shoot	+	-	+
13. Innovations lacking or 1, sterile (+) or 2, well-developed (-)	+	-	+
14. Lobule tooth 1 (+) or 2 dimorphic (-)	+	-	+

Distribution and Dispersal

Stictolejeunea is a characteristic element of primary tropical rain-forests, ranging in altitude from sea leavel up to 2000(-2500) m. The genus is pantropical and has two species in tropical America (*S. balfourii, S. squamata*), one species in tropical Africa and tropical Asia (*S. balfourii*) and one species in southern Japan (*S. iwatsukii*). The following distribution patterns may be distinguished (Fig. 4):

endemic:	*S. balfourii* var. *bekkeri* (Suriname)
	S. iwatsukii (Ryukyu Islands)
neotropical:	*S. squamata*
pantropical:	*S. balfourii* var. *balfourii*

A discussion into the nature and origin of these patterns may focus particularly on *S. balfourii*, which has the most intriguing distribution. *S. balfourii* belongs to an increasingly large group of tropical liverwort species with wide-ranging, transoceanic distributions (the "wide-tropical" element, Gradstein & Weber 1982). A minority among them is truely pantropical; the following Lejeuneaceae are included: *Lopholejeunea subfusca, Stictolejeunea balfourii, Leucolejeunea xanthocarpa, Cheilolejeunea trifaria, Lejeunea flava, Lejeunea cucullata, Diplasiolejeunea cavifolia, Colura tenuicornis, Cololejeunea cardiocarpa* (?), *C. minutissima* (?), *Mastigolejeunea auriculata* (?). In addition, some 30-40 species of Lejeuneaceae are known from at least two continents: Asia and Africa (Pócs 1976), America and Africa (Gradstein et al. 1984) or Asia and America (not yet reviewed).

It should be noted that, although very wide-ranging, *S. balfourii* var. *balfourii* is still only known from relatively few, scattered localities. Presumably, the species has been overlooked as it grows in very sheltered habitats, often mixed among other bryophytes. In contrast, numerous collections are available of *S. squamata*, which in the field is indeed a much more conspicuous plant. During the 1982 BRYOTROP expedition to Peru, in which five bryologists participated myself included, *S. squamata* was frequently seen and collected. None of us realized, however, that *S. balfourii* var. *balfourii* was also in our collections (the first genuine record of this taxon for tropical America), until in the herbarium Dr. Riclef Grolle discovered two small populations among *Symphyogyna* spp. from submontane rain-forest at the roots of the Andes. As similar habitats are (still) plentiful in tropical South America, I would presume that at least in the neotropics *S. balfourii* is much more widespread than the distribution map (Fig. 4) suggests.

How did the vast distribution area of *S. balfourii* var. *balfourii* come about, what do we know about the dispersibility of this taxon? Recent data on transoceanic taxa (e.g. Gradstein et al. 1984) indicate that virtually all of them — including *S. balfourii* — are monoicous or polyoicous, hence may produce bisexual spores, generally considered more suitable for successful long-range dispersal than the unisexual spores of dioicous species (Schuster 1966). In contrast, there are no genuine dioicous species of Lejeuneaceae known to be transoceanic. Apparently, dioicous species of Lejeuneaceae are not fit to cross wide oceans successfully, whereas monoicous species may... This suggests that in this family sex distribution, sometimes considered of little value as a taxonomic character (Gradstein 1975), is of considerable biogeographical significance!

The differences in distribution pattern and sex distribution between *S. balfourii* (monoicous) and *S. squamata* (dioicous) agree with the above correlation, but apparently this generalization does not hold for the endemic taxa (e.g. *S. iwatsukii*) which may also be monoicous. Nor does it hold for other families of leafy liverworts containing transoceanic species, which are often dioicous (see Gradstein et al. 1984). A possible explanation for this discrepancy might be a difference in spore size, Lejeuneaceae having rather large, multicellular spores (with endosporous protonema) — generally considered less suited for long-range air transport — whereas most other members of leafy liverworts have small, unicellular spores.

Little information is available on the actual capacity of the liverwort spores to survive the hazards of transoceanic air transport. This question has been investigated for mosses by van Zanten (1978) and more recently for liverworts in a preliminary fashion (van Zanten 1984). According to van Zanten, spores of tropical rain-forest liver-worts are very poorly drought-resistent, yet have good resistance against wet-freezing (-30.C), which migh permit them to migrate over longer distances via (wet) typhoons or heavy showers. Migration via dry air-streams seems out of the question, however. As spores of Lejeuneaceae were not yet included in these investigations (van Zanten, oral comm.), the above data cannot be extrapolated to the members of that family.

The habitat of *S. balfourii*, finally, should also be considered. Our previous investigations on tropical liverwort biogeography (Gradstein & Weber 1982, Gradstein et al. 1984) indicate that transoceanic species are often found in rather open situations, e.g. low bushes, forest edges, tree crowns or alpine meadows, sometimes being rather weedy, which would allow the spores to become air-born and carried away with the wind. *Stictolejeunea balfourii*, however, is a typical skiophilous element of the ground layer of the tropical rain-forest, hence grows in locations very unsuited for long-distance air dispersal! For this reason, one would be inclined to explain its present-day distribution by assuming step-by-step dispersal via ancient land connections rather than long-range dispersal. In this case one would have to assume a very old age for the species (at least early Tertiary), which would seem unlikely in view of the amount of genetic variability found in general in liverworts on the species level (Szweykowski 1984). On the other hand, fossil records of Lejeuneaceae from Eocenic amber (Grolle 1981) do suggest that forms morphologically very similar to present-day species existed at that time. The scarce evidence, however, barely allows us to conclude in favour of either recent longe-range dispersal or ancient step-by-step dispersal in the case of *Stictolejeunea balfourii*.

To finalize, I would like to present the following evolutionary sketch for *Stictolejeunea*. Presumably, the genus and its two subgenera originated in the rain-forest of tropical America because 1) this is the center of diversity of the group, 2) its relative *Neurolejeunea* and the most primitive species of *Stictolejeunea*, *S. squamata*, are restricted to this area. Primitive traits of *S. squamata* are its branching type and its robust stem (cf. Schuster 1963, Gradstein 1975). Because of its dioicous inflorescence, the species is not expected to occur in the palaeotropics (see above). From tropical America, *S. balfourii* subsequently migrated to palaeotropical regions, via ancient land connections or via long-range air dispersal. The two endemic taxa, *S. balfourii* var. *bekkeri* and *S. iwatsukii*, probably evolved rather recently as segregates from *S. balfourii*. They might be looked upon as "neo-endemics", like *Acrolejeunea allisonii* and *A. mollis* from New Zealand (Gradstein 1975), although a distribution wider than presently known for these two *Stictolejeunea* members would not seem unlikely, as their appearance and habitat is very similar to that of *S. balfourii* var. *balfourii*.

STICTOLEJEUNEA (Spruce) Schiffn.

in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893); Evans (1907: 1); Evans (1935: 4); Schuster (1963: 149); Bischler (1965: 435); Mizutani (1978: 134); Geissler & Gradstein (1982: 128). *Lejeunea* subg. *Stictolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 81 (1884).

Lectotype (Evans 1907): *Stictolejeunea squamata* (Willd. ex Web.) Schiffn.

Plants variable in size, the leafy stem 1-8(-15) cm long, 1-2,5 mm wide, without particular smell or taste, creeping to ascending to pendulous, glossy green to dull olive-green when alive retaining its colour or becoming darker, brownish to blackish when dry, but without secondary pigmentation in the cell walls, irregularly branched to (more characteristically) regularly and often densely (bi)pinnate; vegetative branches *Frullania*- or *Lejeunea*-type, sexual branches *Lejeunea*-type, innovations lacking or single, usually short and sterile, rarely fertile, of the *Radula-Jubula*-type, microphyllous branches lacking.

Stem rigid, of thickwalled cells, (0,07-)1,5-3,5 mm in diam., the ventral merophyte 4-18 cells wide, the dorsal cortex cells in straight longitudinal rows, the lateral merophytes dorsally interlocking; in cross section with 12-75 brownish pigmented or pale, thickwalled cortical cells in 1-3 rows surrounding 15-250 unpigmented, thinnerwalled medullary cells, the cortical cells smaller than the medullary cells (when numerous) or about the same size to slightly larger (when few).

Leaves ± imbricated, widely spreading and flattened, almost unaltered when dry, ovate, oblong or suborbicular, subsymmetric, the dorsal base ± extending across the stem, straight to auriculate, with a very long, linear hyaline papilla, the dorsal insertion line 0,3-0,5 × lobe width; leaf apex broadly rounded to obtuse (rarely), often with a fragile, 1-3 cells wide, whitish border of larger, thinwalled hyaline cells, the border sometimes extending along the dorsal margin, the margins plane, entire or crenulate by eroding border cells, the dorsal margin curved, the ventral margin ± straight, curved at the junction with the keel, the keel very short or lacking. Cells subisodiametric, relatively small, median leaf cells 10-25 × 5-15 μm, ± equally thickened by confluent trigones, intermediate thickenings and oil bodies lacking; ocelli present, scattered throughout leaves, underleaves, bracts and perianth, variable in number, ca. 20-200 per leaf, up to 2 × cell size, isodiametric (never elongated), 20-30 µm in diam., with one large, ± colourless, granulose mass of oil filling the lumen, without chloroplasts. Lobule inconspicuous, up to 1/4 × leaflength but usually smaller, often reduced, when present inflated, ± ovate, straight or curved with the orifice turned backwards to the base of the stem, the free margin usually incurved, the apex without or with one, 1-3 cells long tooth, the hyaline papilla on the inner lobule surface 0-3 cells below the proximal base of the tooth.

Underleaves distant to imbricated, orbicular to reniform, 2-10× stem width, the apex undivided and rounded, plane or recurved, the margins entire, sometimes with a hyaline border 1 cell wide, the bases ± straight, the insertion line transverse to deeply arched, the base in cross section 2 cells thick ("*Stictolejeunea*-type"); rhizoids in short bundles from the bases of the underleaves, sometimes (in ramicolous or epiphyllous plants) forming an adhesive disc.

Dioicous or monoicous. Androecium spicate or capitate, occupying a short-specialized, *Lejeunea*-type branch or short innovation, or terminating an elongated *Frullania*-type branch; male bracts smaller than leaves, in 3-10 series, subequally bifid, hypostatic, each bract embracing 2 sphaerical antheridia; male bracteoles 0-3, restricted to the base of the spike, in short-capitate androecia wanting. Gynoecium on a strongly abbreviated *Lejeunea*-type branch, originating from the main stem or from a primary branch, with or without 1 leaf and underleaf, and with 1 series of bracts and bracteole, with or without one *Radula-Jubula* type innovation; bracts ± smaller than leaves, unequal in size, the inner bract larger, the lobe apex rounded, the margins entire, the lobule much smaller than the lobe, ligulate-obovate, 1/4-1/2× lobe length, elongated beyond the keel; bracteole orbicular to oblong-spathulate, longer than underleaves and covering the lower half of the perianth, the apex rounded, entire. Perianth exerted, when mature often standing upwards and visible only in dorsal view of the plant, up to 2 mm long, obovate-obpyriform, compressed, the dorsal surface smooth and plane, the ventral surface weakly swollen, smooth or (rarely) with 1-2 low, narrow plicae above, the lateral keels entire, considerably expanded beyond the rostrum forming two distinct auricles, the margins of the auricles often whitish-bordered (in *S. squamata*); rostrum short, ca. 3 cells long.

Sporophyte: seta made up in cross section of 4 inner and 16 outer cells, not (?) articulate (fide Geissler & Gradstein 1981), the foot consisting of a few bulging cells; capsule valves pale in colour, remaining suberect after capsule dehiscence, the upper two-thirds of the valves bistratose, the lower third tristratose with thinwalled cells and two very large cells adjacent to the valve margins in the intermediate layer; outer valve cells with irregularly nodulose thickenings, inner valve cells with irregularly nodulose to monofenestrate thickenings (plurifenestrate according to Geissler & Gradstein 1981), the thickenings tending to become strong and coalescent; elaters inserted at valve margins only, pale, with rudimentary spiral, 200-250 µm long, 15 µm wide; spores narrow rectangular with irregularly waving margins, 2-2,5× longer than wide, 40-50 × 15-25 µm, finely spinose; sporeling (Nehira 1984) *Lejeunea*-type (= *Stictolejeunea*-type), the protonema endosporous, cylindrical, the young leafy shoot with ovate primary leaves lacking lobules and saccate inflated juvenile leaves, underleaves (? not seen).

Vegetative reproduction unknown.

DISTRIBUTION AND ECOLOGY: pantropical, ranging in altitude from sealevel to ca. 2000 m. A characteristic hygrophytic epiphyte of shade synusia in tropical lowland and submontane rainforests, usually on bark, rarely on living leaves or rock.

DIFFERENTIATION: important diagnostic characters are shown in Table I. The genus is subdivided into two subgenera, the neotropical subgenus *Stictolejeunea* and the pantropical subgenus *Parastictolejeunea*. Differences are given in the key.

Key

1. Plants creeping, ascending to pendulous, regularly (bi-)pinnate or (when creeping) irregularly branched, vegetative branches always of the *Frullania*-type, sexual-branches of the *Lejeunea*-type. Stem over 1,5 mm in diam., ventral merophyte (4-)8-18 cells wide. Underleaves wider than long, (3-)4-10 × stem width. Widespread in tropical America.................................... .... 1. *S. squamata* (subgenus *Stictolejeunea*)

1. Plants creeping, irregularly branched, vegetative and sexual branches normally of the *Lejeunea*-type, vegetative *Frullania*-type branches occasionally present in robust plants. Stem less than 1,5 mm in diam., ventral merophyte 4 cells wide. Underleaves suborbicular, 2-3,5 × stem width(subgenus *Parastictolejeunea*). . .2

2. Leaves with 150-225 ocelli. Southern Japan................ 3. *S. iwatsukii*

2. Ocelli fewer, less than 100 per leaf.................... 2. *S. balfourii*. . .3

3. Perianth wings greatly expanded, suborbicular, 1/3 × perianth length, leaving a very narrow opening above the rostrum. Pantropical....................... .... 2a. *S. balfourii* var. *balfourii*

3. Perianth wings lower, about 1/5 × perianth length, leaving a wide opening above the rostrum. Suriname....................... 2b. *S. balfourii* var. *bekkeri*

STICTOLEJEUNEA subgenus Stictolejeunea

Plants creeping or, when fertile, ascending from the substrate becoming pendulous. Branching regularly (bi-)pinnate, in creeping plants sometimes irregular. Vegetative branches always of the *Frullania*-type, specialized sexual branches of the *Lejeunea*-type. Stem normally robust, the ventral merophyte (4-)8-18 cells wide, the stem in cross section with (15-)25-75 brownish pigmented, strongly thickened cortical cells in (1-)2-3 rows surrounding numerous thinnerwalled, unpigmented medullary cells. Leaf apex rounded, often with a hyaline border. Lobule when present inflated, the free margin incurved, the orifice usually turned backwards.

Underleaves transversally ovate to reniform, (3-)4-7(-10) × stem width, the apex plane or recurved, the isertion usually arched. Dioicous. Androecia on a short-specialized *Lejeunea*-type branch or on a longer, *Frullania*-type branch. Gynoecium with one sterile or female innovation, the innovation rarely lacking. Perianth wings strongly expanded, usually with a whitish border.

DISTRIBUTION: tropical America.

1. **Stictolejeunea squamata** (Willd. ex Web.) Schiffn. Fig. 1

Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893); Evans (1907: 5, pl. 1); Evans (1935: 195, fig. 313); Geissler & Gradstein (1981: 128, pls. 4-6). *Jungermannia squamata* Willd. ex Web., Hist. Musc. Hepat. Prodr.: 33 (1815); Nees (1833: 347); Montagne (1835: 310). *Lejeunea squamata* (Willd. ex Web.) Nees ex Mont., Ann. Sci. Nat. Paris, sér. 2, 3: 210 comb. inval. in synon. *Lejeunea squamata* (Willd. ex Web.) Nees, in Gottsche, Lindenb. & Nees, Syn. Hep.: 322 (1845); Spruce (1884: 82). *Symbiezidium squamatum* (Willd. ex Web.) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat., ser. 3, 4: 403 (1877). *Lejeunea squamata* (Willd. ex Web.) Nees var. *willdenowiana* Gott., in Gottsche, Lindenb. & Nees, Syn. Hep.: 322 (1845) art. 26 ICBN. *Stictolejeunea squamata* (Willd. ex Web.) Schiffn. var. *macrior* (Spruce) Herz., Rev. Bryol. Lichénol. 20: 130 (1951); *Lejeunea squamata* (Willd. ex Web.) Nees var. *macrior* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 83 (1884) nom. superfl. illeg. (art. 63 ICBN).

Type: West Indies, "In corticibus Myrti caryophyllatae", sterile, unknown collector (S, STR, W hb. Lindenberg 6171 & 6172).

Heterotypic synonyms:

Phragmicoma ocellulata Nees & Mont., in Montagne, Ann. Sci. Nat. Bot. sér. 2, 19: 159 (1843). *Lejeunea squamata* (Willd. ex Web.) Nees var. *squamata* ("*willdenowiana* Gott.") fo. *ocellulata* (Nees & Mont.) Gott., Lindenb. & Nees, Syn. Hep.: 322 (1845).

Type: Dominica, "inter muscos in insula Dominicensi lecto mecumque a Boryo communicatos inveni" (PC-Mont. holo, STR).

Stictolejeunea kunzeana (Gott.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893); Evans (1907: 7); Evans (1935: 193). *Lejeunea squamata* (Willd. ex Web.) Nees var. *kunzeana* Gott., in Gott., Lindenb. & Nees, Syn. Hep.: 322, 819 (1845). *Lejeunea kunzeana* (Gott.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 83 (1884).

Lectotype: Chile, Pöppig s.n., "misit Kunze 1832" (S hb. Lehmann, iso in STR). Paratype: Peru, Pöppig s.n., "misit Kunze" (PC-Mont., S hb. Lehmann). According to the original publication, authentic material of the two syntype collections is in the hb. Lehmann (S) and the hb. Lindenberg (W). However, we did not find authentic material among the specimens received from W. Among the material from

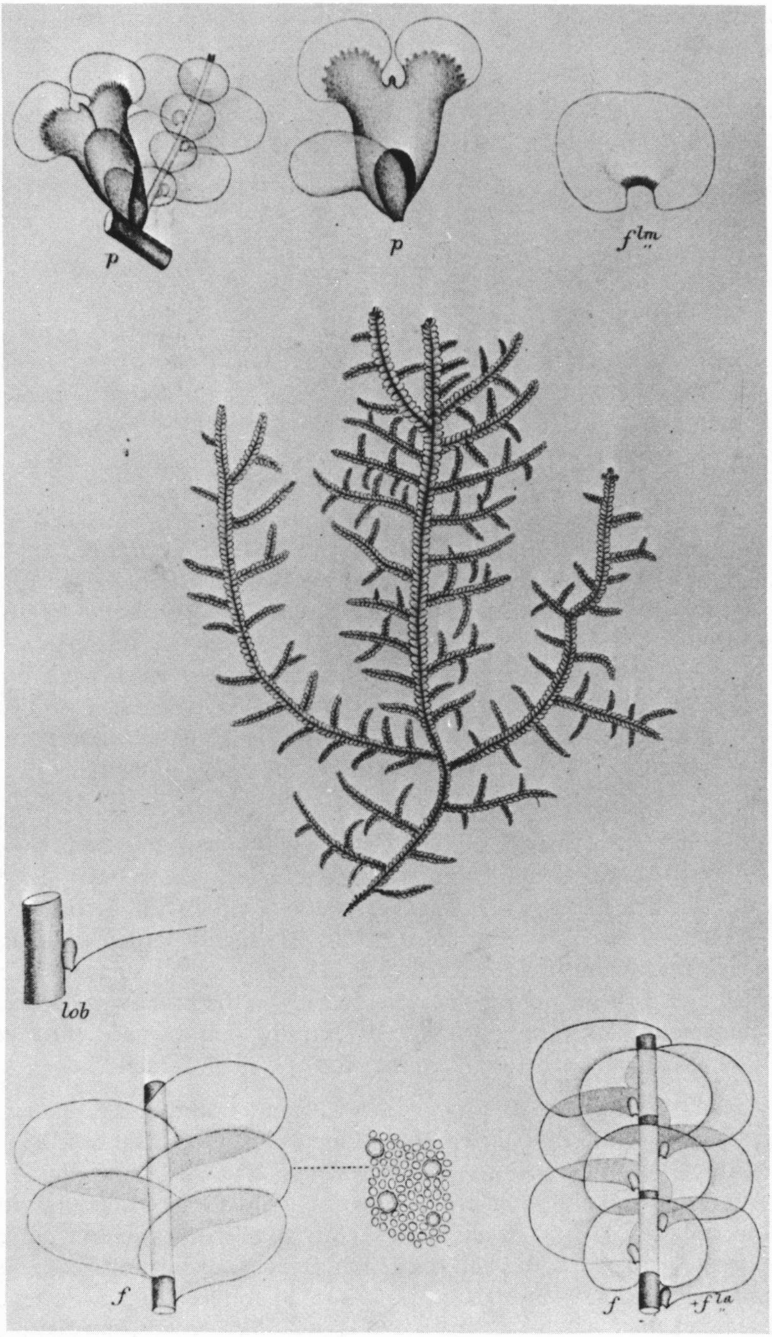


Fig. 1. *Stictolejeunea squamata* (Web.) Schiffn. After Spruce (1884).

S, the syntype collection from Chile is somewhat more copious and therefore chosen as the lectotype

Lejeunea squamata (Willd. ex Web.) Nees var. *neesii* Gott., in Gottsche, Lindenb. & Nees, Syn. Hep.: 322, 819 (1845); Spruce (1884: 83).

Lectotype: Brazil, Rio de Janeiro, Sellow s.n. (STR lectotype, W hb. Lindenberg 6170).

?*Stictolejeunea rotundifolia* Steph., Spec. Hep. 6: 556 (1924); Stephani, Icones Ined. nr. 009742 (G).

Type: West Indies, Broadway s.n. (not seen). According to Dr. P. Geissler, Geneva (in litt.), the type specimen lacks in the Stephani herbarium. Stephani's illustration of a leaf and underleaf in his Icones, a copy of which was kindly provided by Dr. Geissler, indicates that *S. rotundifolia* is probably a synonym of *S. squamata*.

Plants medium-sized to robust, the leafy stem 1,5-8(-15) cm long, 1,2-2,5 mm wide, glossy pale-green becoming dull-green tinged with white to olive when dry, creeping to ascending to pendulous with the outgrown shoots hanging free from the substrate, usually regularly and (when fertile) densely pinnate to bipinnate, more sparsely branched, in sterile, creeping plants, with elongated vegetative branches of the *Frullania*-type and shorter, specialized sexual branches of the *Lejeunea*-type, the *Frullania*-type branches usually spatiated, the fertile plants with one to several *Lejeunea*-type branches between two adjacent *Frullania*-type branches.

Stem usually robust, 0,2-0,35 mm in diam., the ventral merophyte 8-18 cells wide; in weak creeping plants stem occasionally thinner, 0,15 mm in diam., the ventral merophyte only 4-6 cells wide (branch characteristics); ventral cortical cells in surface view long and narrow; stem in cross section (7-)10-15 cells across with 25-75 cortical cells in (1-)2-3 rows surrounding (30-)100-250 slightly larger medullary cells, the cortical cells uniform in size, 12-20 × 8-15 μm, the walls strongly thickened, 2-4 μm thick and ± brownish pigmented especially in the primary middle lamella, the thickening somewhat more pronounced ventrally than dorsally, the medullary cells 20-30 × 15-20 μm, less strongly thickened, the walls 1,5-2 μm thick, yellowish.

Leaves ovate-suborbicular, 0,8-1,6 × 0,6-1,2 mm, on branches smaller, often orbicular, the dorsal insertion line ca. 0,4× lobe width, the dorsal base truncate to auriculate, the apex and dorsal margin often with (1-)2-3 cells wide whitish border of larger, fragile, dead cells, the margins entire or crenulate by eroding border cells. Median leaf cells 14-24 × 10-16 μm, cells slightly smaller towards leaf margin and slightly larger towards base, the wall thickening ± even, distinct or weak; ocelli ca. 20-150 per leaf lobe, 20-30 μm in diam. Lobule small or absent, on branches usually better developed than on stems, up to 1/5(-1/4)× leaf length, normally ca. 80-120 μm wide, 100-160 μm long, inflated and usually curved with the orifice turned backwards to the base of the stem, more rarely straight, the free margin entirely incurved or, in large lobules, plane near apex, the apical tooth 1-3 cells long, straight or curved, usually invisible without dissection.

Underleaves contiguous or imbricated, transversally ovate to reniform, (3-)4-7(-10) × stem width, on branches usually narrower, (0,4-)0,6-1,6 mm wide, 0,3-1 mm long, ± plane, the margins entire, green or with a 1-2 cells wide hyaline margin of fragile, dead, thinwalled cells, the apex plane or recurved and sometimes undulated, the bases straight, the insertion line arched, up to 0,2 mm deep.

Dioicous. Androecia capitate or spicate, occupying a short-specialized *Lejeunea*-type branch or terminal (rarely intercalary) on a longer, *Frullania*-type branch. Gynoecium on a very short *Lejeunea*-type branch, without (rarely) or with one innovation, the innovation usually short and sterile but occasionally elongated and bearing one or more gynoecial shoots (innovation than closely resembling the adjacent *Frullania*-type branch!). Bracts and bracteoles as in the genus, with or without ocelli. Perianth 1,5-2 mm long, with or without ocelli, the lateral keels expanded up to 0,5 mm beyond the rostrum and almost touching each other, each auricle usually with a conspicuous whitish border of dead cells, the border 2-10 cells wide.

Sporophyte as in the genus, but inner capsule valve cells rather strongly nodulose, the thickenings tending to become coalescent forming an irregular, ± fenestrate pattern.

DISTRIBUTION AND ECOLOGY: Mexico, Guatemala, Costa Rica, Cocos I., Panama, Cuba, Jamaica, Haiti, Puerto Rico, St. Kitts, Guadeloupe, Dominica, St. Vincent, Trinidad, French Guiana, Suriname, Guyana, Brazil, Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile; ranging from 0-2400 m alt. In wet lowland rainforests and submontane cloud forests in shaded locations, on truncs of trees, on twigs, living leaves, lianas and on decaying wood. Occasionally on moist (calcareous) rock. Most records are from the lower cloud forests at 400-1500 m, but under very favourable moisture conditions the species descends to sea level, e.g. in the Guianas, along the Pacific coast of Costa Rica, Colombia and northern Ecuador, and in igapó forest along the Amazon, Rio Negro and its tributaries. On islands the species tends to occur, as may be expected, at rather low altitudes but on Cuba the species reaches up to the summits of the Sierra Maestra at 1800 m.

VARIATION: *S. squamata* varies considerably in size and growth habit, lobule and underleaf size and shape, as well as in the development of the whitish border on leaf, underleaf and perianth (see descr.). The size variation correlates to some degree with altitude and growth habit, and was reason for previous authors to distinguish two species (Spruce 1884, Evans 1907): at lower altitudes *S. squamata*, characterized by small statue, creeping habit, densely pinnate branching, well developed lobule and perianth without hyaline borders; at higher altitudes *S. kunzeana*, a more robust, pendulous and laxly pinnate plant with smaller lobule and conspicuous whitish perianth borders. My study of the variation in *S. squamata* revealed that the differences between *S. squamata* and *S. kunzeana* are by no means sharp (as Herzog 1952 already noted) and do not allow for the distinction of two different species. Although certain trends are obvious (Table II), I have refrained from distinguishing infraspecific taxa in *S. squamata*, even more so because in the herbarium it is sometimes difficult to determine the growth form of the plant.

Table II. Morphological intergradation between *Stictolejeunea squamata* and *S. kunzeana* as related to altitude (altitudes for type specimens approximated, because unknown). 1: Plant robustness, as expressed by underleaves wider than 1 mm (+) or distinctly smaller. 2: Perianth with whitish border (+) or without (?: perianth not seen). 3: leaves with whitish border (+) or without.

	1	2	3
a. 0-500 m alt.			
?West Indies, type of *S. squamata*		?	+
Cuba, Pócs 9063/BU		+	+
Cuba, Pócs 9063/BO			+
Guadeloupe, Le Gallo 633		?	
Cocos I., Weber 549		?	+
French Guiana, Leprieur s.n.	+	+	
French Guiana, Degelius s.n.	+	+	
Guyana, Tutin 321		+	+
Brazil, Manaus, Griffin 786		?	+
Acre, Maas P13267			
Acre, Reese 13157		?	+
Sao Paulo, Schiffner 1963		+	+
Rio Grande do Sul, Vianna s.n.	+	?	
Colombia, Chocó, Bischler 155	+	+	
Ecuador, Los Rios, Harling 2109	+	+	
b. 500-1000 m alt.			
Cuba, Léon & Clemente 186			+
Cuba, Bisse & Köhler 6479		+	+
Costa Rica, Standley 44756	+	+	
Suriname, Bekker 1069		?	
Colombia, von Sneidern s.n.	+	+	
Peru, Frahm et al. div. nrs.		+	+
Bolivia, Buchtien s.n.	+	+	
c. above 1000 m alt.			
Cuba, Pócs 9210	+	?	+
Cuba, Lippold 16690		?	+
Costa Rica, Standley 50623		+	
Venezuela, Griffin 58	+	?	
Colombia, Killip 11145	+	+	
Ecuador, Chimborazo, Spruce s.n.	+	+	
Peru, Frahm et al. div. nrs.	+	+	
?Chile, lectotype of *S. kunzeana*	+	?	

It appears that the lowland plants of *S. squamata* are more often creeping while the more robust pendulous form is especially common in the cooler, submontane rainforest where there is excessive moisture due to fog. It also appears that the pendulous form is more frequently fertile and often lacks a whitish border along the leaves (although this border may still be present on the underleaves). The whitish perianth border never lacks in robust plants but in small, creeping plants it may be present too (e.g. Cuba, Lippold 16690); the width of the perianth border varies considerably, though. Plants with and without hyaline perianth borders have been collected by Pócs and Reyes (9063) in Cuba in the same locality. In this case, the whitish perianth border was only seen in more luxuriant, loosely growing plants while in more appressed and weaker plants borders were lacking.

Lobule reduction is common in older parts of the plants and on main stems. The underleaf apex may be recurved or plane, and does not allow for distinguishing infraspecific taxa as the authors of the Synopsis Hepaticarum believed. In one specimen (Cuba, Lippold 12238a) I found plane underleaves, ca. 5 × stem width, on shoot portions with lobules, while on shoots lacking lobules the underleaves were much bigger, ca. 10 × stem width, with recurved apices.

In robust, montane forms the underleaves are always plane and often very large, up to 1,6 mm wide. The largest specimen of *S. squamata* was collected by Spruce near the base of Mt. Chimborazo at 1000 m. (BM), measuring 15 cm long. This was the collection which he based his description and illustration of *S. kunzeana* on (cf. Fig. 1). In contrast, small lowland plants, even when fertile, may measure not more than 1,5 cm long (e.g. Brazil, Maas et al. P13267). *S. squamata* is not infrequently epiphyllous, but I never found reproductive organs in plants growing on leaves.

Specimens examined (*S. squamata*): MEXICO: Chiapas, Munch s.n., 1907 (S). GUATEMALA: vicinity Guatemala city, s.coll., ex hb. Levier (BM). COSTA RICA: prov. Cartago, Peji valle, Standley & Valerio 47166 (JE); prov. Guanacaste, near Tilarán, Standley & Valerio 44756a & 45403, I.1926 (JE); prov. Heredia, Cerros de Zurqui, Standley & Valerio 50623 (JE); prov. Limón, Rio Reventazon below Cairo, Standley & Valerio 48716, II.1926 (JE); Cocos I., Chatham Bay, Weber 549, III.1964 (COLO, U). PANAMA: prov. Chiriqui, Boquote forest near David, Hélion s.n., VI. 1906 (L, S, U). CUBA: St. Clara, Banao Mts., Léon & Roca 149, 180 & 186, VIII.1915 (HAC); Loma S. Juan, Hiroram 12374, VII.1934 (HAC); Sierra de Escambray, Pócs & Borhidi 9005 (HAC); Sierra Maestre, Gran Piedra, Ekman 8818, XI.1917 (S); ibid., Reyes 830, 841, 842, 847 & 850 (HAC); ibid., Pócs & Reyes 9210/C, XI.1980 (HAC, EGR, U); Moa, Lippold 12238a (JE); Guantanamo, Baracoa, Natenson 324, VII.1935 (HAC); ibid., Bisse & Köhler 6479, III.1968 (JE); ibid., Pócs & Reyes 9063 (HAC, EGR, U). JAMAICA: s.l., MacFadyen 1 (BM); s.l., misit Hooker (S, W). HAITI: NE of Basse Terre, Leonard 12481a, III.1929 (JE). PUERTO RICO: s.l., Pagan 965 (HAC). ST. KITTS: Breutel s.n. (BM). GUADELOUPE: Grand Etang de Capsterre, Le Gallo 633, 1960 (JE). DOMINICA: s.l., Bory a.n., type of *Phragmicoma ocellulata* Mont. et Nees (PC, STR). ST. VINCENT: "misit Hooker" (W). TRINIDAD: s.l., Broadway s.n., 1929 (G). FRENCH GUIANA: Gabaret river, Leprieur s.n. (PC-Mont., STR, W); Comté river, near Belizon, Degelius s.n., VI.1958 (S); Saül, Cremers 4160, XII.1976 (JE); confluent Sinnamary crique Maronina, Cremers 5471, II.1979 (JE). SURINAME: Paramaribo, Wullschlaegel s.n. (BM); Brownsberg, Florschütz 4757, I.1976 (U); ibid., Bekker 1069, XI.1981 (U); Lely Mts., Lindeman et al. 86a & 88a, IX.1975 (U); Kabalebo Dam area, Bekker 1619a, 1711, 1722 p.p., IX.1981 (U, BBS). GUYANA: Cuyuni river, Oko cr., Tutin 321, VII.1933 (BM); Essequibo river, near Rockstone, Maas et al. 3943 (U). BRAZIL: *Amapa,* upper Rio Oyapock, Lützelburg 20283, 20385 & 21222, VII.1927 (JE, S); *Amazonas,* Manaus, Griffin et al. 786, VII.1974 (FLAS, U); *Acre,* Rio Branco to Abuna 15 km, Reese & McPherson 13157, II.1978 (NY, U); *Acre,* Cruzeiro do Sul, Maas et al. P13267, V.1971 (NY, U); *Minas Gerais,* Rio de Janeiro, Hell 502, 1963 (JE); ibid., Sellow s.n., lectotype of *Lejeunea squamata* var. *neesii* Gott. (STR, W); *Sao Paulo State,* Rio Branco, Schiffner 1963, IX.1901 (S); Rio Mambu, Schiffner 735, VI.1901 (S); *Rio Grande do Sul,* Torres, Vianna s.n. (ICN 0677), IX.1970 (ICN, U). VENEZUELA: Zuila, trail to Topochalito, Griffin 58, VII.1975 (FLAS, U). COLOMBIA: Chocó, near Quibdo, Bischler 151 & 155. IV.1957 COL, JE, PC, U); Valle, Buenaventura-Buga, Bischler 357, 1958 (COL, JE, PC, U); La Cumbre, Killip 11145a, IX.1922 (JE); Dagua valley, Killip 5087 (JE); Cauca, El Tambo, K. von Sneidern s.n., III.1938 (S). ECUADOR: Esmeraldas, Rio San Miguel, Harling 4670, 1959 (S); Los Rios, Samama, Hac. Clementina, Harling 2109, 2112 & 2162 (JE), ibid. 2128, 2144 & 2257 (S); Chimborazo, Spruce s.n. (BM); Santiago-Zamora, Mendez, Harling 2212a, 1947 (S); Yurupaza, Harling 2249 & 2252

(JE). PERU: s.l., Pöppig s.n. (PC-Mont., S); Loreto, Puccalpa to Lima km 80, Spichiger s.n., V.1980 (G); near Iquitos, Hegewald 6377, VII.1973 (hb. Hegewald, U); San Martin, Yurimaguas to Tarapoto ca. km 95, Frahm et al. 1435, 2043, 1411 & 1789 (Bryotrop expedition), IX.1982 (B, U); Chachapoyas to Moyabamba ca. km 400, Frahm et al. 20, 467, 1314 & 2166, IX.1982 (B, U). BOLIVIA: Tutuhuancana, Espirito Santo, Buchtien s.n., VI. 1909 (S). CHILE: s.l., Pöppig s.n., lectotype of *S. kunzeana* (Gott.) Schiffn. (S, STR).

Also recorded from several localities in Puerto Rico by Evans (1907) and Amazonia by Spruce (1884). There are no genuine records from the palaeotropics, although the species has been recorded from the East Indies and from Hawaii, as Evans (1907) has pointed out. The Hawaiian specimen, present in Stockholm, belongs to *Stictolejeunea balfourii.*

STICTOLEJEUNEA subgenus Parastictolejeunea subg. nov.

Type species: *Stictolejeunea balfourii* (Mitt.) E.W. Jones

A subg. *Stictolejeunea* differt statura humiliora, caule tenuiore irregulariter ramosa, ramis vegetativis plerumque *Lejeunea*-type, amphigastriis parvioribus, inflorescentia monoica.

Plants creeping. Branching irregular, vegetative and sexual branches of the *Lejeunea*-type, an occasional vegetative *Frullania*-type branch present in vigorous plants. Stem rather thin, zig-zag with the underleaves ± connate by one cell with leaves on one side of the shoot, the ventral merophyte 4 cells wide, the stem in cross section with 12-16 cortical cells in 1 row surrounding a similar number of medullary cells, cortical cells as large as or slightly larger than medullary cells, all stem cells moderately thickwalled, without pigmentation. Leaf apex rounded to obtuse, occasionally with a hyaline border. Lobule when present inflated, the free margin barely incurved, the orificice directed towards leaf apex. Underleaves suborbicular, 2-3,5 × stem width, the apex plane, the line of insertion transverse. Monoicous. Androecia on a short-specialized branch or innovation, occasionally on a longer vegetative branch. Gynoecium without innovation or with one short innovation occupied by male bracts. Perianth wings expanded to varying degree, without whitish border.

DISTRIBUTION: pantropical.

2. Stictolejeunea balfourii (Mitt.) E.W. Jones Figs. 2, 3

J. Bryol. 9: 50 (1976).

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

2a. Stictolejeunea balfourii var. balfourii

Lejeunea balfourii Mitt., Philos. Trans. Roy. Soc. London 168: 398 (1879) "*balfouri*". *Symbiezidium balfourii* (Mitt.) Steph., Spec. Hep. 5: 99 (1912).

Type: Rodriguez I., I.B. Balfour s.n. (K in BM).

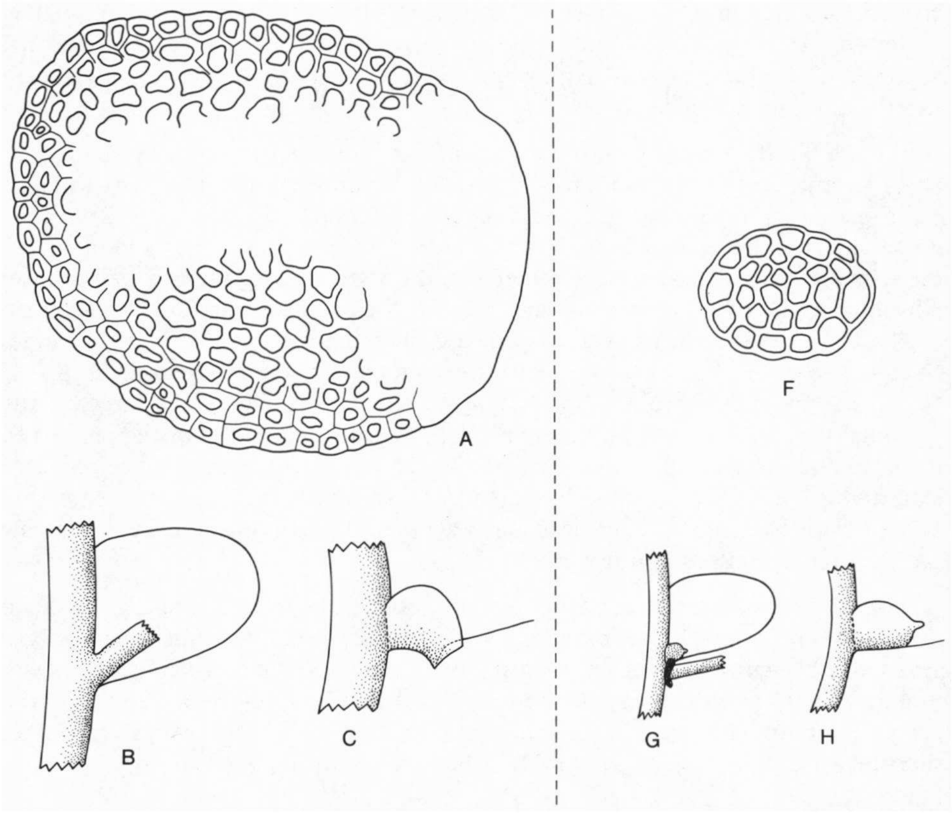


Fig. 2. A comparison between *Stictolejeunea* subgenus *Stictolejeunea* (left) and subgenus *Parastictolejeunea* (right).

A, F: stem in cross section. B, G: vegetative branch. C, H: lobulus.

Heterotypic synonyms:

Stictolejeunea africana Vand.Bergh., Bull. Jard. Bot. Etat (Bruxelles) 20: 15 (1950), syn. fide Jones (1976).

Syntypes: Ivory Coast, Chevalier 17 (not seen); Rodriguez I., Balfour s.n. (not seen). The syntype from Rodriguez is a topotype of *S. balfourii.*

Stictolejeunea richardsii Herz., Trans. Brit. Bryol. Soc. 1: 318 (1950) syn. nov.; Inoue & Miller (1968: 5); Grolle (1969: 143).

Type: Borneo, Sarawak, Mt. Dulit, among *Megaceros celebensis* on rotten log in shade and in spray of waterfall, P.W. Richards 2618, anno 1932 (JE holo).

Plants relatively small, the leafy stem 1-3 cm long, 1-1,5 mm wide, dull olive green to dark brownish or blackish when dry, growing in small, appressed mats or creeping among other bryophytes, sparingly to irregularly, rarely weakly pinnately branched, the branches of the *Lejeunea*-type, in vigorous plants an occasional vegetative *Frullania*-type branch may be present; innovations lacking or single, very short and occupied by male bracts.

Stems typically zig-zag with the underleaf bases on one side ± attached to leaf bases by one cell, ca. 70-140 μm in diam., the ventral merophyte 4 cells wide, in cross section as in the subgenus. Leaves ovate to oblong, 0,5-0,9 × 0,3-0,7 mm, the dorsal insertion line only 0,25-0,3 × leaf width, the dorsal base not extending across the stem and not dilated above the insertion, the apex rounded to narrowed-obtuse, a hyaline border of 1-2 cells sometimes present. Median leaf cells 10-20 × 5-15 μm, ocelli ca. 25-75 per leaf, up to 2 × cell size. Lobule up to 1/4 × lobe length, sometimes entirely reduced, when present ovate-subquadrate, the free margin ± plane, the apex truncate, with one 1-3 cells long tooth, the hyaline papilla large, at the proximal base of the tooth on the inner surface. Underleaves distant, appressed to the stem and one side ± connate, by one single cell, with the base of the adjacent leaf, about 2-3,5 × stem width, 0,2-0,35 mm wide, plane, the margins often with a 1-2 cells wide hyaline border of dead and fragile, thinwalled cells, the bases straight, the line of insertion nearly transverse.

Monoicous. Androecia capitate or spicate, occupying a short specialized branch or innovation, sometimes terminating a longer vegetative branch, the bracts in 2-10 series, much smaller than leaves, almost globose. Gynoecium on a very short lateral branch without or with a very short male innovation; bracts and bracteole as in the genus. Perianth with ocelli, ca. 1 mm long, the oblong-obovate wings very large, suborbicular, ca. 1/3-2/5 × perianth length, almost touching each other.

SPOROPHYTE: see var. *bekkeri*.

DISTRIBUTION AND ECOLOGY: Peru, (?) Honduras (sterile), Sierra Leone, Ivory Coast, Ghana, Nigeria, Cameroun, Central African Republic, Reunion, Rodriguez, Borneo, Papua New Guinea, Solomon Islands, New Caledonia, Caroline Is., Hawaii (?); 0-800 m alt. *S. balfourii* seems characteristic for rather wet, natural lowland and lower submontane rainforests, where it grows in appressed mats among other bryophytes on tree bases, roots, lianas, living leaves and rotten logs as well as on rocks in very moist and sheltered locations close to the ground. Its small statue, dull colour, preference for shaded localities close to the ground and tendency to grow sparingly or in thin mats, may be reasons why the species was so little collected notwithstanding its vast range. Most records are from islands or mainland areas not too far from the coast. The species is normally epiphytic but the type specimen from Rodriguez was apparently saxicolous "on the moist clay rocks at the sides of the stream. In dull olive brown to blackish patches" (Mitten 1879: 398). Also the specimen from Ponape was from rock.

VARIATION: *S. balfourii* var. *balfourii* is much less variable than *S. squamata*, yet some interesting variation is observed. The type from Rodriguez is a relatively robust blackish-brown plant, with leaves up to 1 mm long and underleaves ca. 3,5 × stem width. The ventral merophyte never exceeds 4 cells in width, though. It grows in much thicker mats than other specimens, as Jones (1976) noticed, which may be an adaptation to the rheophytic habitat. A hyaline border is usually present on the underleaves and occasionally on the leaves as well; it may be fragmentary or lacking altogether, though, and is by no means a character of taxonomic relevance as Mizutani (1978) thought it to be.

The male bracts are on short-specialized, *Lejeunea*-type branches (in the types of *S. balfourii* and *S. richardsii*), on short innovations (collections from New Guinea, Caroline Is. and Peru) or on both (some colls. from W. Africa), although in the latter case the occurrence on innovations is exception rather than rule (fide E.W. Jones in litt.). In addition, some West African collections have short male spikes on elongated branches. The latter condition was never found in Asiatic populations, which, in turn, more frequently develop androecial innovations. Moreover, androecial innovations are found in *S. balfourii* var. *bekkeri* (see below).

The observed variation in placement of the androecia is summarized in Table III. The presence of androecial innovations in *S. balfourii* has been overlooked by previous workers and may have caused some of them (e.g. Vanden Berghen 1951) to believe that the plants are dioicous. It should be noted that these tiny innovations of *S. balfourii*, when present, are always male!

The mature perianth in this variety always has huge auricle-like wings, as contrary to the plant from Suriname described here as a separate variety. Mitten's illustration of a perianth with very low wings in the type of *S. balfourii* is erronous, as Jones (1976) has pointed out; my study of the type material confirms this. Similarly, Inoue

Table III. Placement of the androecia in the fertile collections of *Parastictolejeunea* examined. 1: androecia on innovations. 2: androecia on short-specialized lateral branches. 3: androecia on elongated branches. (): rarely present. ?: material not seen, record based on the description (refers to Vanden Berghen's record of innovations in *S. africana* from Ivory Coast).

	1	2	3
a. *S. balfourii* var. *balfourii*			
Caroline Is., leg. Miller	+		
Solomons Is., leg. Dennis	+		
New Guinea, leg. Schuster	+		
Borneo, leg. Richards		+	
Rodriguez, leg. Balfour		+	
Nigeria, Jones 870	(+)	+	
Ghana, Jones 1217	(+)	+	
Ghana, Jones 1343	(+)	+	
Ivory Coast, leg. Chevalier	+?		
Sierra Leone, leg. Arnell			+
Peru, Frahm et al. 1691b	+		
b. *S. balfourii* var. *bekkeri*			
Suriname, leg. Bekker	+		(+)
c. *S. iwatsukii*			
Japan, leg. Mizutani		+	

& Miller's illustration of an (apparently mature) perianth with low wings in material from Ponape (Inoue & Miller 1968, fig. 1: 5) is wrong, as I found an ordinary perianth with huge auricles in this material as well.

Specimens examined (var. *balfourii*): PERU: Dept. San Martin, road Yurimaguas - Tarapoto ca. 95 km., submontane forest 500-700 m, between *Symphyogyna* spp., Frahm et al. 1691b & 2046b (Bryotrop expedition), IX.1982 (B, hb. Grolle, U). (Furthermore placed in this variety with some doubt, is a fragmentary, sterile neotropical specimen from HONDURAS: Dept. Atlantida, near Tela, Lancetilla valley, Standley 55741 p.p., 1927-1928 (JE)). SIERRA LEONE: Freetown, Mt. Oriel, Arnell 2349 & 2368, XII. 1951 (S). IVORY COAST: Abidjan, Banco Nat. Park, van Eijndhoven 75-6 (U). GHANA: Western Region, Krokosua Hills Forest Reserve, Jones 1392 p.p. (hb. Jones); Pra Suhien Forest Reserve, Jones & Hall 1343, II. 1971 (hb. Jones); Eastern Region, Kade Agric. Res. Station, Jones & Hall 1217, I.1971 (hb. Jones, S). NIGERIA: Benin prov., Ehor Forest Reserve, Jones 870, X.1955 (hb. Jones). REUNION: Takamaka, Colville Barclay 2024, XI.1970 (hb. Jones, MAU 14435). RODRIGUEZ: Balfour s.n., type (BM, K). BORNEO: Sarawak, Dulit, Richards 2618, 1932, type of *Stictolejeunea richardsii* Herz. (JE). PAPUA NEW GUINEA: Morobe Distr., Markham river, near Lae, Schuster 67-6015, VI.1967 (JE). SOLOMON IS.: Guadalcanal, Mataniko river headwaters, Dennis 20011, IV.1965 (S). NEW CALEDONIA: Tao Forest, Franc 245/b, 1910, ex hb. Grolle (JE). CAROLINE IS.: Ponape, Mt. Nahnaland, Miller 9245, IV.1965 (TNS). HAWAII: s.n., "repens ad *Radula pallens*", ex hb. Hooker, as *Lejeunea squamata* (S hb. Lehmann).

2b. **Stictolejeunea balfourii** var. **bekkeri** var. nov. Fig. 3

A var. *balfourii* differt carinis perianthiae brevioris.

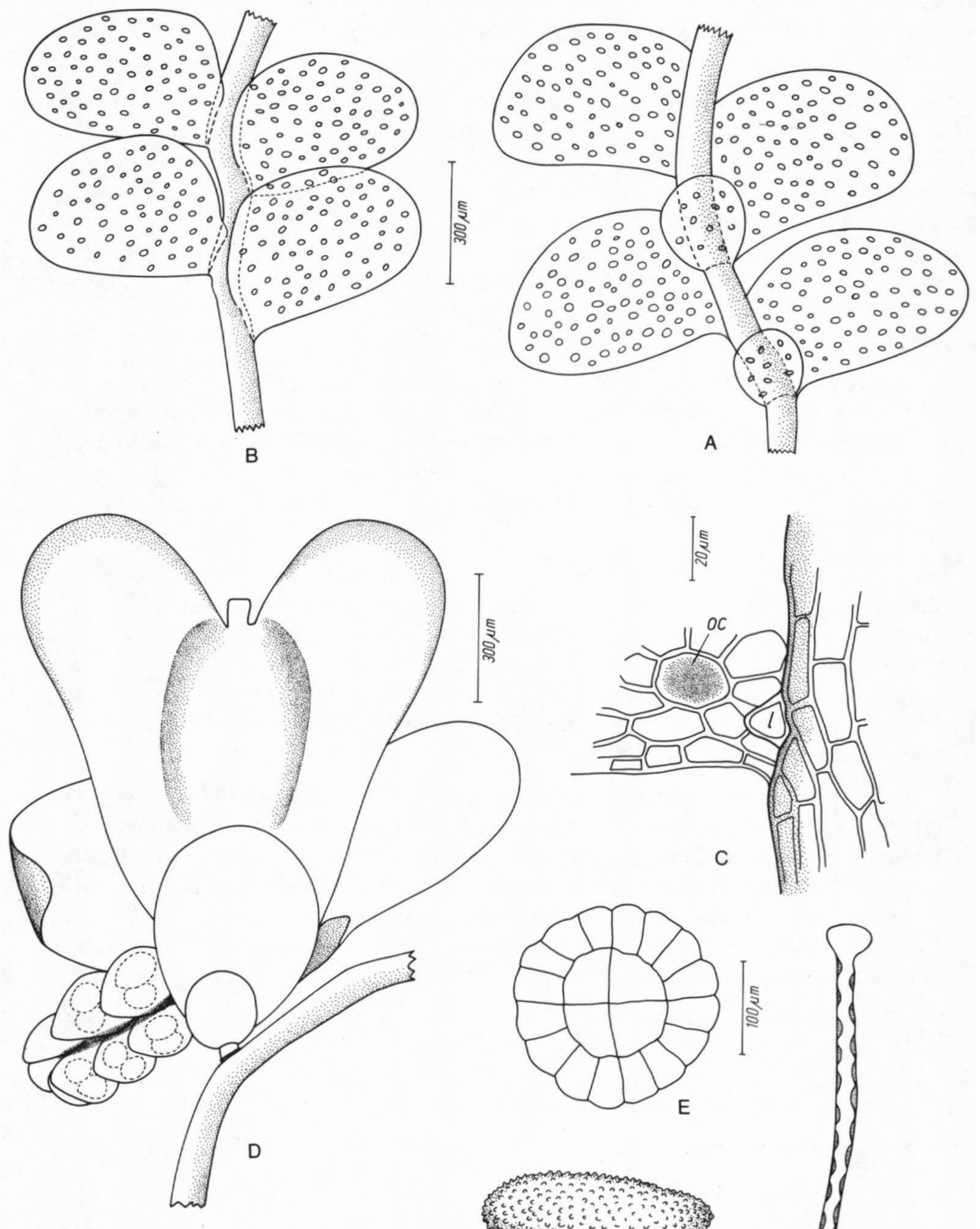
Type: Suriname, Distr. Nickerie, Kabalebo Dam project area, line opp. camp road km 212, alt. 0-50 m, rainforest with *Astrocaryum skiophilum*, on bark of living tree, in shade, with *Stictolejeunea squamata*, J. Bekker 1619b, 20.XI.1981 (U holo, BBS, hb. Jones, hb. Grolle).

Plants creeping over bark in small mats, the leafy stem up to 1,5 cm long, 1-1,3 mm wide, dull olive-green to brownish, at shoot apices yellowish-green, irregularly branched with *Lejeunea*-type branches and tiny, male innovations, the vegetative branches elongated, the sexual branches very short. Stems as in the subgenus, ca. 70-80 μm in diam. Leaves imbricated, widely spreading, ovate-oblong, 0,5-0,7 × 0,3-0,4 mm, the dorsal insertion line only 1/4× leaf width, the dorsal base not dilated above the insertion, the dorsal margin slightly curved, the ventral margin straight, the apex rounded, lacking a hyaline border. Median leaf cells 12-20 × 10-16 μm, ocelli 50-90 per leaf, up to 2× cell size. Lobule reduced to a single cell at the ventral base of the leaf. Underleaves as in var. *balfourii*, ca. 2,5× stem width, with a one cell wide hyaline border.

Monoicous. Androecia occupying a tiny innovation at the abaxial base of the perianth or, occasionally, on an elongated branch, the bracts in 4-6 series, bracteoles 1-2, limited to the base of the spike. Gynoecium on a very short *Lejeunea*-type branch without or with one short, male innovation; bracts and bracteole as in the

Fig. 3. *Stictolejeunea balfourii* (Mitt.) E.W. Jones var. *bekkeri* Gradst.

A: habitus ventral. B: ibid. dorsal. C: ventral leaf insertion (l = lobulus, here reduced to a single cell; oc = ocellus). D: perianth and male innovation. E: cross section of the seta. F: spore. G: elater. All from the type.


B
300 µm
A
20 µm
oc
l
C
D
300 µm
E
100 µm
G
F
20 µm

genus. Perianth obovate-obtrapezoid, 1 × 0,75 mm, the lateral keels elevated to ca. 0,2 mm above the rostrum, sinus between the wings broad and rounded, the inflated portion of the ventral perianth surface sometimes with a low, sharp fold at the edges.

Sporophyte: seta 16: 4, capsule valves pale, the outer side made up of elongated cells with small, cordate to confluent trigones, the inner size of larger, elongated cells, thinwalled in the lower half, irregularly thickened in the upper half with nodulose thickenings, the valve margins in the upper half bordered by short rectangular cells with nodular thickenings on the cross walls in a very regular fashion, forming a zip-pattern. Elaters colourless, ca. 8-10 per valve, inserted at valve margins, the spiral rudimentary. Spores rectangular with irregularly waving margins, ca. 40 × 15 μm, finely punctate-papillose, without rosettes. Sporeling not seen.

DISTRIBUTION AND ECOLOGY: *S. balfourii* var. *bekkeri* is only known from the type locality in Suriname, where it grows in lowland rain forest dominated by *Astrocaryum skiophilum* and in marsh forest, on lower portions of tree truncs, rotten logs and roots in deep shade, together with *Stictolejeunea squamata, Lopholejeunea subfusca, Lophocolea, Radula* and *Plagiochila* spp. It was also found at the edge of the forest near falls.

Note: *S. balfourii* var. *bekkeri* agrees with var. *balfourii* in all respects except for the perianth, which is obovate-obtrapezoid in outline (usually oblong in var. *balfourii*) and has much lower wings. Moreover, the ventral perianth surface may develop two low plicae, which I did not observe in var. *balfourii.* Male bracts are largely restricted to innovations, which in var. *balfourii* is commonly seen in Asiatic populations as well as in the plants from Peru, but is unusual in the African populations (see under var. *balfourii,* Table III).

In the type collection var. *bekkeri* grows mixed with *S. squamata,* the latter being rather small, creeping and sterile here, and therefore habitually rather similar to *S. balfourii. S. squamata* is easily recognised, however, by its very conspicuous hyaline leaf border and its *Frullania*-type branches. When well developed, *S. squamata* is the more robust plants, with larger underleaves and broader ventral merophyte and a rather loose, ascending to procumbent growth, but in the weaker, creeping, sterile populations these differences tend to disappear.

Specimens examined (var. *bekkeri*): SURINAME: Distr. Nickerie, Kabalebo Dam project area. Bekker 1619a, XI.1981, type (hb. Grolle, hb. Jones, BBS, U); ibid. 1693a (BBS, FLAS, U); ibid. 1593, 1712a, 1713 (BBS, U).

3. **Stictolejeunea iwatsukii** Mizut.

J. Hattori Bot. Lab. 44: 134, fig. 7 (1978).

Type: Japan, Ryukyu Is., Iriomote I., forest on south-facing slope of Bt. Gozadake, west of Otomi, alt. 20 m., on rock, Z. Iwatsuki 2909, 2.I.1977 (NICH holo, U).

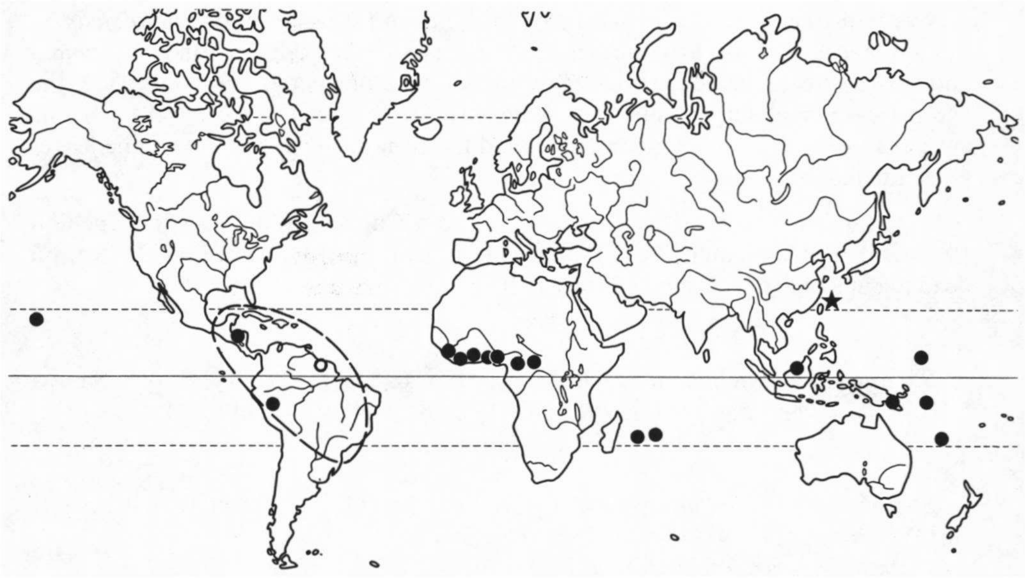


Fig. 4. The distribution of *Stictolejeunea* (Spruce) Schiffn.

Dots: *S. balfourii* var. *balfourii*. Circle: *S. balfourii* var. *bekkeri*. Star: *S. iwatsukii*. Broken line: *S. squamata*.

S. iwatsukii was adequately described and illustrated by Mizutani (l.c.). It resembles *S. balfourii* but differs by the remarkably high number of ocelli, ca. 150-225 per leaf lobe. As a result, the ocelli often border each other, forming groups of 2-3 (in *S. balfourii* they are isolated or occasionally in groups of 2). The chlorophyllose leaf cells in *S. iwatsukii* are rather variable in form (isodiametric to elongate) and on average are smaller than in *S. balfourii*: 9-16 × 7-11 μm. At leaf base they are distinctly enlarged, measuring up to 35 × 15 μm.

The perianth, according to Mizutani, has low wings (the portion of the type that I examined had only juvenile perianths), innovations are lacking and androecia are on short-specialized lateral branches. The lack of a hyaline border on leaves and underleaves was taken as a character to distinguish between *S. iwatsukii* and *S. richardsii* (= *S. balfourii*) by Mizutani (l.c.). In *S. balfourii*, however, this border is by no means constant (Jones 1957) and may lack altogether as well.

DISTRIBUTION AND ECOLOGY: *S. iwatsukii* is only known from the type collection.

Excluded Species

1. *Stictolejeunea herzogii* Buchloh, Nova Hedwigia 3: 515 (1961). Type: Peru, "Nebelwald im Gebiet von Taulis bei 2100 m", Rauh 2779 (not seen, material not available). Paratype: Peru, Quincemil, 800 m, Rauh P2530 (JE)
= *Lepidolejeunea herzogii* (Buchloh) Grolle & Gradst. comb. nov.

A very distinct species, which may be easily taken for a species of *Stictolejeunea,* though, because of its entire underleaves, its small curved lobule as in *S. squamata* and its scattered ocelli. However, the ventral merophyte is only two cells wide, the leaf cells are much larger as in *Stictolejeunea,* with distinct trigones, and the plants are glossy brownish in colour rather than dull green or olive. Moreover, the leaves are denticulate.

L. herzogii is known from Peru (type), from Chocó, Colombia (fide Buchloh 1961) and from Panama: prov. Panama, la Eneida, Cerro Jefe region, 750 m, on dead log in low forest, Maas & Dressler 691 (U, JE).

2. *Stictolejeunea micholitzii* Steph., Spec. Hep. 6: 556 (1924). Type from Samoa
= *Lepidolejeunea graefii* (Jack & Steph.) Schust. (fide Mizutani 1970)

3. *Stictolejeunea orientalis* Pears., in Setchell, Pap. Dept. Marin Biol. Carnegie Inst. Washington 20: 412 (1924). Type from Samoa
= *Lepidolejeunea integristipula* (Jack & Steph.) Schust. (fide Grolle 1979)

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References

Bischler, H. 1965. Recherches sur l'anatomie de la tige chez les Lejeuneaceae II. Les sous-familles Lejeuneoideae, tribu Ptychantheae, Nipponolejeuneoideae et Myriocoleoideae. Revue Bryol. Lichénol. 33: 399-458.

Buchloh, G. 1961. Einige species novae und Neufunde von Moosen aus den Anden von Peru. Nova Hedwigia 3: 507-516.

Crandall, B.J. 1969. Morphology and development of branches in the leafy Hepaticae. Beih. Nova Hedwigia 30: 1-261.

Evans, A.W. 1907. Hepaticae of Puerto Rico VII. *Stictolejeunea, Neurolejeunea, Omphalanthus* and *Lopholejeunea.* Bull. Torrey Bot. Club 34: 1-34.

Evans, A.W. 1935. The anatomy of the stem in the Lejeuneaceae. Bull. Torrey Bot. Club 62: 187-214.

Geissler, P. & Gradstein, R. 1981. On a small collection of living Lejeuneaceae from Peru. Candollea 36: 119-130.

Gradstein, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea.* Bryophyt. Bibl. 4: 1-162.

Gradstein, S.R. & Weber, W.A. 1982. Bryogeography of the Galapagos Islands. J. Hattori Bot. Lab. 52: 127-152.

GRADSTEIN, S.R., PÓCS, T. & VÁNA, J. 1984. Disjunct Hepaticae in tropical America and Africa. Acta Bot. Hung. 29: 127-171.

GRADSTEIN, S.R. 1984. Transoceanic Hepaticae of Tropical America. Acta Bot. Neerl. 33: 248.

GROLLE, R. 1969. Novae Guineae Hepaticae Schusteranae I. J. Hattori Bot. Lab. 32: 140-144.

GROLLE, R. 1979. Miscellanea hepaticologica 181-190. J. Hattori Bot. Lab. 45: 173-184.

GROLLE, R. 1981. On hepatics in baltic amber, present knowledge and promisings. In: J. Szweykowski (ed.), New perspectives in bryotaxonomy, p. 83-88. Poznan.

GROLLE, R. 1983. Nomina Generica Hepaticarum; references, types and synonymies. Acta Bot. Fenn. 121: 1-62.

HERZOG, T. 1950. Hepaticae Borneenses. Trans. Brit. Bryol. Soc. 1: 275-326.

INOUE, H. & MILLER, H.A. 1968. Noteworthy Hepaticae from Micronesia. Bull. Nat. Sci. Mus. 11: 1-12.

JONES, E.W. 1957. African Hepatics XII. Some new or little known Lejeuneaceae. Trans. Brit. Bryol. Soc. 3: 191-207.

JONES, E.W. 1970. African Hepatics XXII. *Dicranolejeunea* and *Marchesinia*. Trans. Brit. Bryol. Soc. 6: 72-81.

JONES, E.W. 1976. African Hepatics XXIX. Some new or little-known species and extensions of range. J. Bryol. 9: 43-54.

MITTEN, W. 1879. Hepaticae. In: I.B. Balfour, The Botany of Rodriguez. Philos. Trans. 168: 396-401.

MIZUTANI, M. 1970. Lejeuneaceae, subfamilies Lejeuneoideae and Cololejeuneoideae from Sabah (North Borneo). J. Hattori Bot. Lab. 33: 225-265.

MIZUTANI, M. 1978. Lejeuneaceae from Ishigaki and Iriomote Islands of Ryukyu Archipelago. J. Hattori Bot. Lab. 44: 121-136.

NEHIRA, K. 1984. Spore germination, protonema development and sporeling development. In: R.M. Schuster (ed.), New Manual of Bryology, p. 343-385. Nichinan.

SCHUSTER, R.M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae I. Introduction; annotated keys to subfamilies and genera. Nova Hedwigia Beih. 9: 1-203.

SCHSUTER, R.M. 1966. The Hepaticae and Anthocerotae of North America Vol. I. New York.

SCHUSTER, R.M. 1980. Ibid. Vol. IV. New York.

SCHUSTER, R.M. 1980a. New combinations and taxa of Hepaticae I. Phytologia 45: 415-437.

SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Jubuleae. Trans. Proc. Bot. Soc. Edinburgh 15: i-xi, 1-308.

SZWEYKOWSKI, J. 1984. Genetische Variabilität in Bryophyten Populationen. Herzogia 6: 395-410.

VANDEN BERGHEN, C. 1950. Le genre *Stictolejeunea* (Spruce) Schiffn. en Afrique. Bull. Jard. Bot. Etat, Bruxelles 20: 15-18.

ZANTEN, B.O. van 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. J. Hattori Bot. Lab. 44: 455-482.

ZANTEN, B.O. van 1984. Some considerations on the feasibility of long-distance transport in bryophytes. Acta Bot. Neerl. 33: 231-232.

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NOTES ADDED IN PROOF: 1. A second South American locality has become known for *Stictolejeunea balfourii* var. *balfourii:* COLOMBIA, Dept. Meta, Villavicencio, forest of S.A. Bavaria, 600 m, on wood near running water in deep shade, leg. S.R. Gradstein, IX.1984 (COL, GRO, U). Fertile material is now being cultured in the laboratory of Dr. van Zanten, University of Groningen, to test dispersibility by means of spore germination experiments.

2. In a recent issue of Phytologia (vol. 56: 70, 1984) the following new names have been established in *Stictolejeunea:*

S. sect. *Macrocellularia* Schust. Type: *S. herzogii* Buchloh. This name should be transferred to *Lepidolejeunea* (see "excluded species"). *S.* subg. *Leptostictolejeunea* Schust. Type: *S. iwatsukii* Mizut. This name antedates *Parastictolejeunea* Gradst. (this paper) and therefore has priority.

BEIHEFT 80 ZUR NOVA HEDWIGIA

10

A Revision of the Genus *Symbiezidium* Trevis.

by

S.R. Gradstein and J. van Beek

ABSTRACT: *Symbiezidium* Trevis. is a well-defined epiphytic genus with two species widespread in tropical America (*S. barbiflorum* (Lindenb. & Gott.) Evans and *S. transversale* (Sw.) Trevis.) and one species restricted to Madagascar and the Seychelles (*S. madagascariensis* Steph.). The genus is a characteristic element of moist lowland and submontane rainforests and lacks in the more mesic areas.

By its gametophytic characters *Symbiezidium* is remotely allied to *Lopholejeunea* and *Marchesinia* but the sporophyte — newly described here — and the androecia are as in *Stictolejeunea* and *Neurolejeunea*. *S. transversale* is the most polymorphic species and is subdivided into the widespread subsp. *transversale* (with two varieties) and sthe subsp. *dentatum* (Herz.) comb. nov. from Pacific Colombia and Ecuador. *S. madagascariensis* is considered the most primitive species and is placed in a separate subgenus, *Eosymbiezidium* subg. nov., because of its different perianth and underleaf anatomy. The peculiar disjunction between the subgenera may be explained by assuming a western Gondwanalandic origin and subsequent extinction on mainland Africa due to the past deterioration of the African climate.

Introduction

The genus *Symbiezidium* is a common element among the liverworts of the neotropical lowland rainforests and one of the more easily distinguished groups. Among Lejeuneaceae it is probably one of the most natural genera and its circumscription has hardly changed since Spruce (1884). Very problematical, however, has been the delimitation of the species, which has been tackled by several authors, including — most recently — Fulford (1942) in her "Studies on American Hepaticae IV — A revision of the Genus *Symbiezidium*". Fulford recognized six species in tropical America but her results were not fully satisfactory as she explains herself:

> "The genus is extremely variable in all its characters, the leaves, lobules, underleaves and their mode of attachment, the female bracts and bracteoles, the configuration of the ventral surface of the perianth, the width of the wings, and in the numbers and distribution of the lacinia or cilia. This variability, which has already been pointed out by Stephani, Evans and Verdoorn, is so great, sometimes even on one stem, that it is often very difficult to clearly delimit the species. In the treatment of the species which follows, the shape of the female bracteole, i.e. whether it is bifid with acute teeth, or whether it is round, has been used as a character of major significance; and following that, the shape of the ventral keel of the perianth and the characteristics and position of its cilia or laciniae have served to separate the species within the two groups. Unfortunately, even these characters are not always so clear cut as one would wish, for very often there is considerable variation in the outline of the female bracteoles and the perianths among the several inflorescences on one stem" (p. 294).

Studies on Lejeuneaceae subfam. Ptychanthoideae XV. Also appearing as STUDIES ON THE FLORA OF THE GUIANAS 10.

In the course of our work on neotropical Lejeuneaceae we have indeed encountered many difficulties in keying out materials of *Symbiezidium*. Following current species concepts, material with mature gynoecia is required for species recognition and even then a positive identification often cannot be made. As Fulford's study was mostly limited to material from North American herbaria and included very few authentic specimens, we have undertaken a study of the genus based as much as possible on all available materials. The few palaeotropical records for the genus have also been taken into account; most of them are in fact doubtful or belong elsewhere.

History

The generic concept of *Symbiezidium* was established by Spruce (1884), in his masterly Hepaticae of the Amazon and the Andes, under the name *Lejeunea* subgenus *Platylejeunea* Spruce (= *Platylejeunea* (Spruce) Schiffn. 1893). The characters by which *Platylejeunea* was distinguished from its ally *Lopholejeunea* according to Spruce were the large size of the plant, the brownish colour, the long, little branched, creeping stems, the broadly lingulate leaves with very small, pouched lobules, the large, deeply inserted entire underleaves and, especially, the inconspicuous, lateral gynoecia with small, subequally bifid bracts, a short vegetative innovation and a flattened perianth without or with rudimentary ventral keels and with conspicuous cilia or laciniae on the lateral keels as well as, sometimes, on the ventral surface.

This circumscription of *Platylejeunea* has proven quite adequate for the neotropical representatives of the genus (= *Symbiezidium* subgenus *Symbiezidium*). Some further differential characters have been added by later authors, viz. the androecium with bracteoles limited to the base of the spike (Evans 1908), the stem hyaloderm (Bischler 1965), the tristratose underleaf base (Winkler 1970) and the *Bazzania*-type oil bodies (Gradstein et al. 1981).

Evans (1908) showed that the generic name *Platylejeunea* is antedated by *Symbiezidium* Trevisan 1877 — through the choice of *Symbiezidium transversale* (Sw.) Trev. as the lectotype — which therefore has priority. As contrary to *Platylejeunea, Symbiezidium* in its original sense (= *Lejeunea* sect. Phragmicomoideae Gott., Lindenb. & Nees 1845) was a very unnatural group containing 35 species now placed in 12 different genera: *Symbiezidium, Dicranolejeunea, Lopholejeunea, Marchesinia, Neurolejeunea, Leucolejeunea, Archilejeunea, Thysananthus, Acrolejeunea, Stictolejeunea, Omphalanthus* and even *Cololejeunea*. Only 6 species actually belong in *Symbiezidium*.

The oldest species name in *Symbiezidium* was introduced about 200 years ago when Swartz (1780) recognized *Jungermannia transversalis* sp. nov. among his materials collected in Jamaica. *S. transversale* is in fact one of the first species of Hepaticae that have become known from tropical America and its type specimen is still well preserved in the Swartz herbarium in Stockholm. A second specimen of

Symbiezidium was collected in 1801 by Alexander von Humboldt in the Colombian Andes, at the base of Mt. Tolima, and described by Kunth (1822) as *Jungermannia subrotunda* Kunth. This species is now placed in the synonymy of *S. transversale* although its identity cannot be determined with certainty by lack of mature perianths. Nees von Esenbeck (1833) added a third species, *Jungermannia granulata* Nees, collected by Sellow somewhere along the Amazon river. This plant has also proven to be a synonym of *S. transversale.*

In the Synopsis Hepaticarum (Gottsche, Lindenberg & Nees 1845) *J. transversale, J. subrotunda* and *J. granulata* are classified in *Lejeunea* sect. Phragmicomoideae together with 35 other holostipous species, among them two further genuine elements of *Symbiezidium: Lejeunea hobsoniana* Lindenb. (= *S. transversale*) and *L. vincentina* Gott. (= *S. transversale* var. *hookeriana*), both from the West Indian island St. Vincent. *L. transversalis* was the first species treated in this section and collections from various parts of the world were attributed to it. Three varieties were distinguished, two of which are excepted in this treatment (var. *transversale* and var. *hookeriana* Gott.).

Further species names were created by a.o. Lindenberg & Gottsche, Mitten, Spruce, Stephani, Evans and Herzog but all of these have fallen into synonymy except for *Lejeunea barbiflora* Lindenb. & Gott. (type from Suriname), *Symbiezidium dentatum* Herzog from Pacific Colombia and Ecuador, and *S. madagascariensis* Steph. from E. African islands, which is the only genuine palaeotropical representative of *Symbiezidium.*

Taxonomy and Relationships

Fulford (1942) recognised 6 species in neotropical *Symbiezidium,* based primarily on characters of the gynoecium (perianth and female bracteole). The female bracteole served to distinguish two groups of species, one with bracteole bifid and one with the bracteole entire. Checking through our materials, we have found great variation in the shape of the bracteole apex which may often be bifid and entire in single populations, for instance in authentic material of *S. barbiflorum* (Fig. 3). Consequently, this character could not be used for species recognition. Sex distribution (autoicous or dioicous) is another character which proved less constant as previous authors believed, although *S. barbiflorum* indeed seems to be consistently monoicous.

In tropical America we have been able to distinguish only two closely related, yet distinct species: *S. transversale* and *S. barbiflorum.* Most binomina seem to fall under the single, variable species *S. transversale* which is readily distinguished from *S. barbiflorum,* as has been shown previously, by the perianth which has cilia or laciniae restricted to the keels (see key). In addition we found that *S. barbiflorum* is normally smaller in size than *S. transversale* which would facilitate species identification when sterile material or material with immature gynoecia is at hand. The size difference is not entirely trustworthy, however, as some overlap in measurements has been found. In general, *S. transversale* is a more variable species as delimited here than *S. barbiflorum*. As to androecia, for instance, they are always short lateral in *S. barbiflorum* while in *S. transversale* they may also occur in elongated shoots. Three infraspecific taxa can be recognized in *S. transversale*, most distinct being the form with denticulate leaves (*S. transversale* ssp. *dentatum*).

S. madagascariensis Steph. from Africa is the third species in *Symbiezidium* which we have been able to recognize. It stands out by its perianth, which is completely smooth and by its underleaves, which are much smaller as in the neotropical species and less deeply inserted. The latter difference serves to distinguish species in many other genera of Lejeuneaceae, e.g. *Brachiolejeunea densifolia* and *Br. corticalis*, *Marchesinia mackaii* and *M. brachiata*, etc. In addition we found a further difference in the cross section of the stem: while all neotropical material investigated has the tristratose underleaf base described by Winkler (1970), *S. madagascariensis* has the underleaf base thinner, only two layers thick.

The very different perianth and underleaf seem sufficient reasons to place *S. madagascariensis* in a separate subgenus: *Symbiezidium* subg. *Eosymbiezidium* subg. nov. As the characters by which the subgenus *Eosymbiezidium* is distinguished are more commonly met in the other genera of the subfamily related to *Symbiezidium*, we consider this the more primitive group which, in view of its geographic isolation, became probably separated from the subgenus *Symbiezidium* long ago (see below). Admittedly, ciliate-laciniate perianths as in subg. *Symbiezidium* are also characteristic for *Lopholejeunea*, the genus probably closest to *Symbiezidium*, but this character is not constant as recently *Lopholejeunea* species with smooth perianths have also been discovered, viz. *L. erugata* Thiers and *L. gradsteinii* Awasthi & Udar.

Symbiezidium is allied to *Lopholejeunea* and *Marchesinia* (Gradstein 1975) and has been placed in the *Lopholejeunea* complex or in a generic complex of its own, the *Symbiezidium* complex (Schuster 1963). This classification was based on the gametophyte only, as sporophytes were unknown in *Symbiezidium* and some other genera of the subfamily Ptychanthoideae. Mature sporophytes proved indeed quite rare in *Symbiezidium:* among about 200 collections investigated we have found only one with mature sporophytes, collected by the first author in Colombia (*S. barbiflorum*, Gradstein 3606). Surprisingly, we found that in contrast with *Lopholejeunea* and *Marchesinia*, which have the usual Ptychanthoid capsule with fenestrate inner valve thickenings (Geissler & Gradstein 1982), *S. barbiflorum* has a capsule as found in the Lejeuneoideae with the inner valve layer thickenings nodular and elaters marginal and without spiral (Fig. 4). This difference indicates that *Symbiezidium* is less closely allied to *Lopholejeunea* and *Marchesinia* than assumed by Gradstein (1975), and approaches *Stictolejeunea* and *Neurolejeunea* instead, with which it shares the Lejeuneoid sporophyte and Lejeuneoid androecia with bracteoles limited to the base of the spike. Leaf areolation, oil bodies and stem anatomy, however, sharply separate *Symbiezidium* from *Stictolejeunea* and *Neurolejeunea*. For that reason it may be best to classifiy *Symbiezidium* in a complex of its own, the *Symbiezidium*-complex (following Schuster 1963), with affinities to the

Table I. A comparison between *Symbiezidium*, *Lopholejeunea* and *Marchesinia*.

	Symbiezidium		*Lopho.*	*March.*
	subg. *Symb.*	subg. *Eosymb.*		
Growth prostrate (+) or ascending (-)	+	+	+	-
Ventral cortex cells larger (+) or not larger (-) than medulla	+	+	+	-
Lobule strongly (+) or weakly (-) inflated	+	+	+	-
Lobule teeth 1 (+) or more (-)	+	+	+	-
Oil bodies segmented (-) or homogeneous: *Massula*-type (+) or *Bazzania*-type (+ +)	+ +	?	+	±
Underleaf insertion deeply arched (+) or curved only (-)	+	-	-	±
Underleaf base tristratose (+) or bistratose (-)	+	-	-	-
Innovations lacking (-), 1 (+) or 2 (+ +)	+	+	-	+ +
Gynoecium an abbreviated (+) or an elongated (-) shoot	+	+	-	-
Perianth keels ciliate (+) or smooth (-)	+	-	±	-
Male bracteoles reduced (+) or well developed (-)	+	+	-	-
Capsule valves Lejeuneoid (+) or Ptychanthoid (-)	+	?	-	-
Elaters without (+) or with spirals (-)	+	?	-	-

Stictolejeunea-complex (sporophyte!) and the *Lopholejeunea*-complex (gametophyte!). Data on the sporophyte of *S. madagascariensis* would be needed to verify the assumed generic relationships. Differences between *Symbiezidium, Lopholejeunea* and *Marchesinia* are summarized in Table I. For a detailed comparison between *Symbiezidium* and *Stictolejeunea/Neurolejeunea* see Gradstein, A revision of the genus *Stictolejeunea* (this volume).

Distribution

Symbiezidium has a typical "peri-Afroamerican" distribution (Stearn 1971), with two species (*S. barbiflorum* and *S. transversale*) in America and one remote ally, *S. madagascariensis,* in Madagascar and the Seychelles but lacking in mainland Africa (Fig. 5). The phenomenon that tropical American plant groups occur in Lemuria, while being absent in continental Africa, occurs also in other bryophytes and is also well known in phanerogams (Gradstein et al. 1984). There seem to be two moss genera following the same pattern, viz. *Potamium* and *Adelothecium,* and one further genus of Lejeuneaceae, *Bryopteris* (the African records of this genus remain old and unconfirmed, however; cf. Stotler & Crandall-Stotler 1974).

Among phanerogams the peri-Afroamerican disjunction is known in ceroxyloid palms, grasses (*Echinochlaena*), composites (*Oliganthes*), *Carpodiptera* (Tiliaceae), *Oplonia* (Acanthaceae), *Phenax* (Urticaceae), *Rheedia* (Clusiaceae) and *Ravenala* (Musaceae); the disjunctions are normally among species or higher infrageneric categories. Stearn (1971) has argued that these groups should have developed before the dissection of the Afro-American part of Gondwanaland and, at the time of the dissection, were lacking in the interior of this land mass where drastic continental climate changes made them extinct. Therefore coastal areas of this former supercontinent, especially Madagascar, are particularly rich in these old, now disjunct Gondwanalandic elements. The same phenomenon is known in the distribution of some animal groups, e.g. reptiles.

In tropical America the species of *Symbiezidium* occur as epiphytes in moist tropical lowland and submontane forests, but they are lacking in the more mesic areas. For instance, the genus is common on Cocos Island (Costa Rica), where there is plenty of moist forest, but lacks entirely on the more mesic Galapagos Islands (Gradstein & Weber 1982). As perianths with (immature) sporophytes are frequently seen, dispersal is likely to take place by spores but little can be said about its effectivity by lack of observations on spore dispersal. Vegetative reproduction is unknown in *Symbiezidium*.

The great morphological divergence between the African and American representatives of *Symbiezidium* indicates a long-time separation of the two groups, and suggests a Gondwana origin of the genus. Thus, we believe that the peculiar disjunction in *Symbiezidium* is better explained by an early evolution in the western portion of Gondwanaland and subsequent extinction on mainland Africa after dissection of the old continent, rather than by more recent long-range dispersal, in which case its absence from mainland Africa would be more difficult to explain. Of course, the possibility that *Symbiezidium* does exist there but has not yet been collected, cannot be ruled out. Occurrence on mainland Africa is even more likely in view of the frequent occurrence of monoicous inflorescences in the species of *Symbiezidium*, monoicous conditions being particularly characteristic for widespread, often transoceanic species in Lejeuneaceae (Gradstein 1975, Gradstein et al. 1984).

SYMBIEZIDIUM Trevis.

Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 402 (1877); Evans (1908) 533; Stephani (1912) 97 "*Symbyezidium*"; Fulford (1942) 293; Bischler (1965) 436; Schuster (1963) 58; Gradstein et al. (1984) 76. *Lejeunea* sect. Phragmicomoideae Gott., Lindenb. et Nees, Syn. Hep.: 310 (1845).

Lectotype (Evans 1908): *Jungermannia transversalis* Sw. (*Symbiezidium transversale* (Sw.) Trevis.).

Heterotypic synonym:

Platylejeunea (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130 (1893, preprint); Evans (1900) 416. *Lejeunea* subg. *Platylejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 124 (1884) "*Platy-lejeunea*"; Stephani (1890) 6, 13.

Lectotype (nov.): *Lejeunea* (subg. *Platylejeunea*) *taeniopsis* Spruce (*Symbiezidium taeniopsis* (Spruce) Fulf.). Among the five species described by Spruce (1884) in *Lejeunea* subg. *Platylejeunea* Spruce (*L. subrotunda, L. taeniopsis, L. hobsoniana, L. vincentina* and *L. pogonoptera*), *Lejeunea taeniopsis* Spruce fits best the original subgeneric description and, moreover, is known from characteristic female material.

Plants monoicous or dioicous, yellowish-brown to blackish-brown, growing in appressed mats, usually relatively large, the stems creeping and up to 20 cm long, simple or sparsely branched with elongated vegetative branches of the *Lejeunea*-type or the *Frullania*-type, and with short-sexual *Lejeunea*-type branches (often hidden below leaves).

Stem rigid, 0,15-0,3 mm in diam., in transverse section circular, with 10-25 cortex cells surrounding 15-75 medullary cells, the cortical cells 1,5-2× larger than the medullary cells, dorsally somewhat larger than ventral or subequal, the cell walls colourless, thickened in varying degree.

Leaves incubous, imbricated, with a large dorsal lobe and a very small ventral lobule in situ hidden behind the underleaf, lobes ± concave and widely spreading both when dry and moist, ovate-oblong to ligulate, at opposite sides of the stem often of different sizes, dorsally attached to the stem over 3/4-1/1 the length of the merophyte, usually auriculate at base and arching beyond the stem, the apex rounded to apiculate, sometimes decurved, the margins entire or (rarely) with a few irregular teath near the apex (*S. transversale* ssp. *dentatum*), plane, the keel ± curved and very short, making a wide angle with the ventral margin of the lobe; lobe cells isodiametric, with ± triradiate trigones and one intermediate thickening on each longer cell wall, the primary lamella usually with blackish pigmentation; oilbodies *Bazzania*-type, 5-7 per cell, homogeneous, ellipsoid and relatively large, ca. 7 × 17 μm., colourless (seen in *S. barbiflorum*). Lobule small, 0,15-0,3× lobe length, inflated throughout or at the base only, becoming plane above, sac-like with the free margin ± incurved, with one-celled tooth or ± notched with 2 projecting cells and one cell bearing the hyaline papilla in the notch in between the projecting cells, the hyaline papilla curved inwards and hidden within the watersac.

Underleaves imbricated, relatively large, 4-6× the stem width, orbicular or wider than long, undivided, the bases widely rounded, straight or cuneate, decurrent, the line of attachment deeply arched or slightly curved only (*S. madagascariense*), the underleaf bases consisting of 2 or 3 cell-layers.

Androecia occupying short specialized *Lejeunea*-type branches or terminal to intercalary on longer branches or stems, occasional besides the perianth on the innovation; bracts in 5-12 series, hypostatic, diandrous; bracteoles ± restricted to the base of the male spike, very much reduced or lacking above.

Gynoecium on a very short *Lejeunea*-type branch, usually hidden behind stem leaves, without or with one short, sterile or male innovation of the *Radula-Jubula*-type. Bracts and bracteoles in one series only, much smaller than the vegetative stem leaves and underleaves, the bract subequally bifid, lobe and lobule rounded, the bracteole rounded to short bifid. Perianth emergent, obovate to obpyriform, 0,5-1,7 mm long, dorsiventrally flattened, with 2 sharp lateral wings and 0-2 small plicae on the ventral surface visible as lines, the lateral wings normally with numerous ciliae and laciniae in the upper half, in *S. madagascariense* completely smooth, the ventral surface smooth or with short or long laciniae which are either randomly distributed over the surface or restricted to the small plicae (hence in 1-2 rows).

Sporophyte (Fig. 4): seta ptychanthoid (16: 4), articulate; capsule valves after splitting suberect, colourless, bistratose, the outer cells with small nodulose cell wall thickenings, the inner cells with large, irregular, colourless, nodulose thickenings which become smaller towards valve margin; elaters 5-6 per valve, inserted only at valve margin, 325-430 µm long, 14-15 µm wide, with one colourless spiral of 7-9 µm wide; spores green, angular-elongated, 65-85 µm long, covered by numerous small papillae and a few rosettes.

Notes:

1. Although *Frullania*-type branching is rare, we have occasionally found plants with vegetative branches purely of the *Frullania*-type, e.g. in *S. transversale* var. *hookeriana* from Peru (BRYOTROP collections). The same may be found in other genera of Ptychanthoideae in which *Lejeunea*-type branches dominate, e.g. *Acrolejeunea, Lopholejeunea, Schiffneriolejeunea.* We agree with Jones (1969) that the occurrence of *Frullania*-type branching in these groups is probably mainly the result of vigorous growth.

2. A peculiarity of *Symbiezidium* not previously recorded for Lejeuneaceae (as far as we know) is the marked asymmetric development of the leaves in many populations, the leaves of one side of the stem being much shorter for a distance. We have also observed this in *Archilejeunea parviflora* occasionally; published observations of this phenomenon are available for *Calypogeia miquelii* Mont. and its ally (synonym?) *C. amazonia* (Spruce) Steph. from northern S. America, in which it is very characteristic. An explanation for the asymmetry of the leaves cannot be given.

3. By its very small, pouched lobule *Symbiezidium* approaches *Stictolejeunea,* to which it otherwise bears no close relationship. In *Stictolejeunea* the keel of the lobule is usually shorter than the lobule width, while in *Symbiezidium* it is usually slightly longer. Further similarities among the two genera, e.g. the male spike with bracteoles limited to the base and the lateral perianth with short, sterile innovation, are probably the results of parallel development.

4. Gradstein, Matsuda & Asakawa (1981) studied the terpenoid chemistry of *Symbiezidium barbiflorum.* Many compounds could be detected by gaschromatography-mass spectrometry, most of them hitherto undescribed and of unknown structure. The main components are the sesquiterpene hydrocarbon bicyclogermacrene, which is widely distributed in the Hepaticae, various sesquiterpenes acetates

and what seemed to be an oxygenated diterpene (M^+ 352). No special chemotaxonomic relationship to other Lejeuneaceae investigated could as yet be detected, as contrary to other groups, e.g. the *Brachiolejeunea* complex, in which distinct chemical affinities among species were demonstrated.

Key

1. Underleaf insertion-line shallowly curved (<100 μm deep), the underleaf base not decurrent, at rhizoid disc bistratose. Perianth keels smooth. East African Islands.. 1. *S. madagascariense*

1. Underleaf insertion-line deeply arched (ca. 200 μm deep), the underleaf base decurrent, at rhizoid disc tristratose. Perianth keels laciniate. Tropical America. ....subg. *Symbiezidium*...2.

    2. Leaf apex entire (rounded or apiculate)................................ 3.

    2. Leaf apex denticulate. Pacific coast of Colombia and Ecuador............. .... 2b. *S. transversale* ssp. *dentatum*

3. Ventral surface of the perianth covered randomly with laciniae or spines, in addition 1-2 rows of laciniae may be present. Plants relatively small, the stem with leaves 1,5-3 mm wide, the ventral merophyte 4 cells wide. Monoicous. From sea level up to 2800 m.................................. 3. *S. barbiflorum*

3. Ventral surface of the perianth smooth or with laciniae in 1-2 rows only. Plants variable in size but normally rather large, the stem with leaves 2,5-5 mm wide, the ventral merophyte (4-)6 cells wide. Monoicous or dioicous. From sea level up to 1700 m......................... 2a. *S. transversale* ssp. *transversale*...4.

    4. Ventral surface of the perianth smooth.................. var. *transversale*

    4. Ventral surface of the perianth with laciniae in 1-2 rows.... var. *hookeriana*

SYMBIEZIDIUM subgenus **Eosymbiezidium** subg. nov.

A subgenere *Symbiezidium* differt amphigastriis parvis, basi bistratosis, perianthiis laevis.

Type: *S. madagascariense* Steph.

A monotypic subgenus, known only from the East African islands.

1. **Symbiezidium madagascariense** Steph. Fig. 1

Spec. Hep. 5: 99 (1912).

Type: East Madagascar, St. Marie, on bark, Voltzkow s.n., 1904 (G 17555 holo, G 17554 iso). The two specimens are evidently duplicates but G 17555 is the more copious one and includes Stephani's personal annotation on the label. The type is

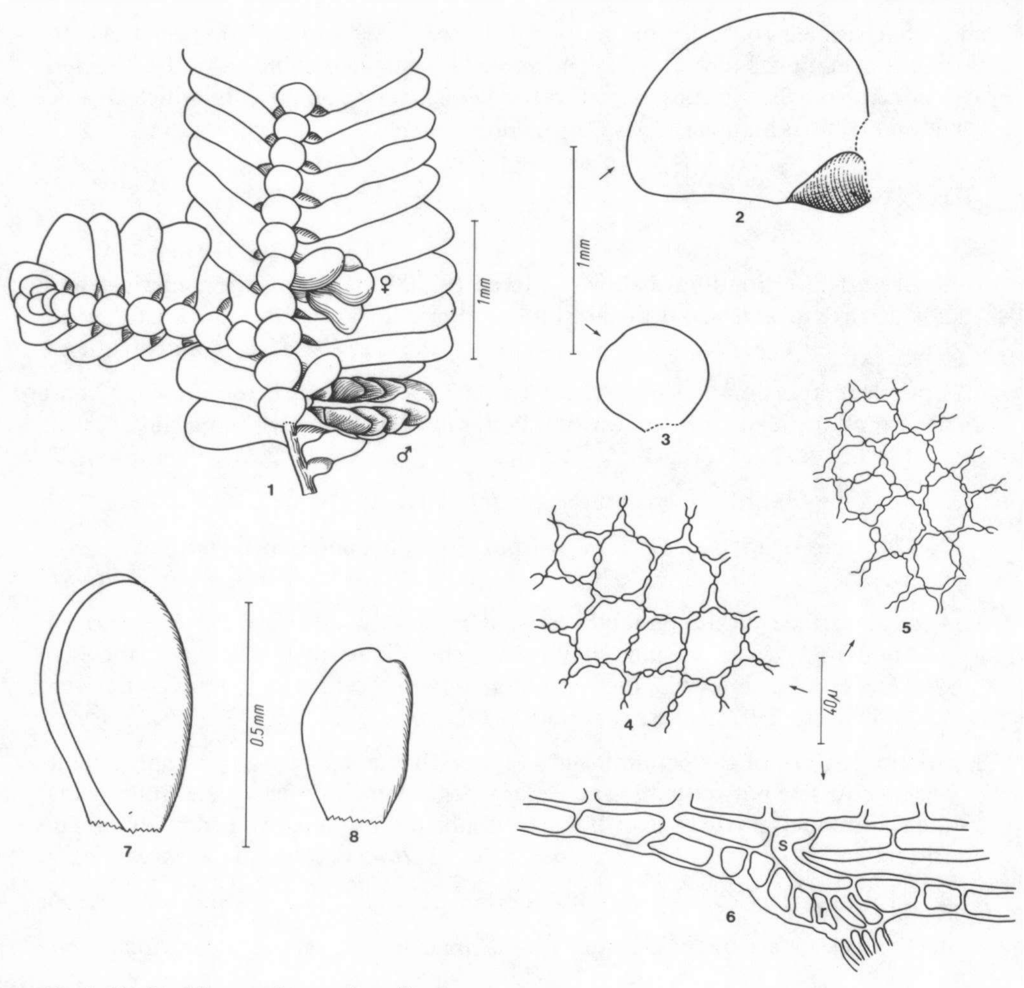


Fig. 1. *Symbiezidium madagascariense* Steph.

1. habitus. 2-3. leaf, underleaf. 4. leaf cells. 5. underleaf cells. 6. stem in longitudinal section showing underleaf base (s = superior central cell, r = rhizoid disc initial cell).

1-6 from Norkett 17485, Seychelles.

clearly monoicous and contains androecia and some juvenile gynoecia, although Stephani characterised it as "dioica" and described only the androecia.

Plants monoicous, brownish, relatively small, the stem with leaves up to 2,5 mm wide, branching of the *Lejeunea*-type or (innovation) *Radula-Jubula*-type. Stem 180 µm in diameter, the ventral merophyte 4 cells wide (8 cells long), in transverse section 9 cells high, cortical cells 30-35 × 20-30 µm, medullary cells 18-20 µm.

Leaves ovate, sometimes of different sizes at opposite sides of the stem, the lobe 1-1,3 × 0,8-1,1 mm, the dorsal base auriculate and slightly arching beyond the stem, the dorsal margin arched and the ventral margin straight, the apex broadly rounded; cells isodiametric, 34-40 µm, trigones conspicicious, 10-12 µm in diam., triradiate, intermediate thickenings 1-2 per cell.

Lobule ca. 0,3 × lobe length or less, saccate but flattened towards apex with a bluntish, one-celled tooth beyond a shallow sinus, the hyaline papilla at the base of the sinus.

Underleaves imbricated, transversally ovate to suborbicular, ± 5 × the stem width, plane, the apex rounded, the insertion line arched, the bases cuneate but ± not decurrent, the base at the rhizoid disc consisting of 2 cell layers. Androecia on short, subglobose to elongated *Lejeunea*-type branches or on innovations, with 4-6 pairs of bracts, the bracteoles 2-3 at the base of the spike.

Perianth relatively small, 0,5 mm long, dorsiventrally flattened, entirely smooth; bracts subequally bifid with rounded apices; bracteoles rounded, with entire apex; one short sterile or male *Radula-Jubula*-type innovation present.

DISTRIBUTION AND ECOLOGY: *S. madagascariense* has only been found on Madagascar and the Seychelles, on tree bark at low elevation.

Specimens examined: MADAGASCAR, Voltzkow s.n., the type (G); SEYCHELLES, Mahé I., upper Trois Frères stream, 180 m, Norkett 17485 (BM, hb. Grolle, U).

SYMBIEZIDIUM subg. Symbiezidium

Underleaf insertion line deeply arched, the base decurrent, at rhizoid disc tristratose. Perianth variously laciniate. Tropical America.

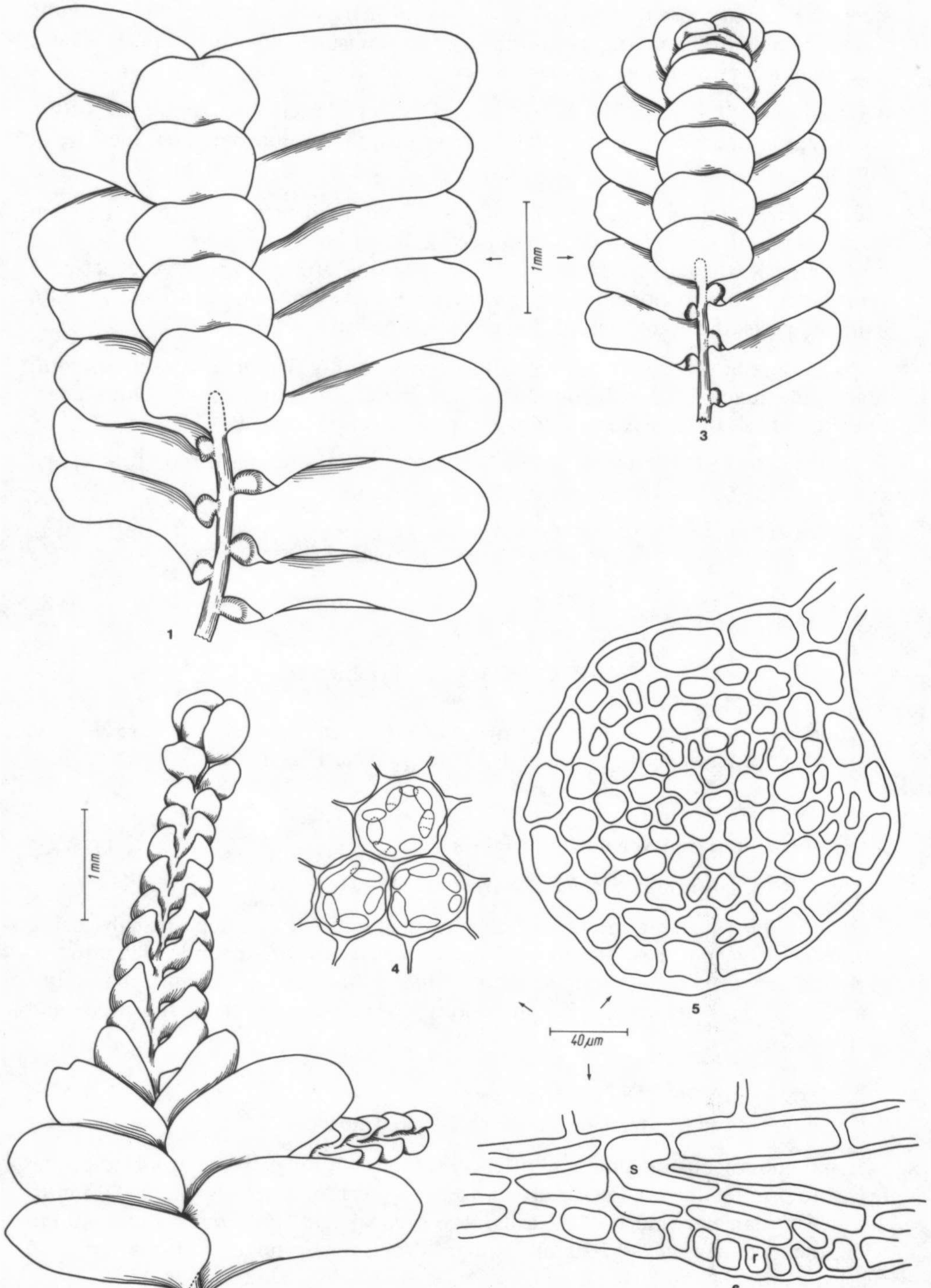
2. **Symbiezidium transversale** (Sw.) Trevis. Figs. 2-3

Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877).

A rather polymorphic species, which is divided into two ± allopatric subspecies: ssp. *transversale* and ssp. *dentatum*. Ssp. *transversale* is further subdivided into two varieties, var. *transversale* and var. *hookeriana*, on the basis of perianth characters. For descriptions, literature, synonyms and type species see under the subspecies and varieties.

2a. **Symbiezidium transversale** (Sw.) Trevis. ssp. **transversale**.

Plants monoicous or dioicous, often tall, to 10 cm long, the stem including the leaves to 5 mm wide; yellowish-brown to olive-green or blackish. Stem 140 µm to 290 µm in diameter (mostly 9-13 cells), the cortical cells 15-25 µm high, 20-40 µm wide, the medullary cells 15-30 µm. in diam. Ventral merophyte 9-14 cells long, 4-6 cells wide, the cells 40-80 µm long.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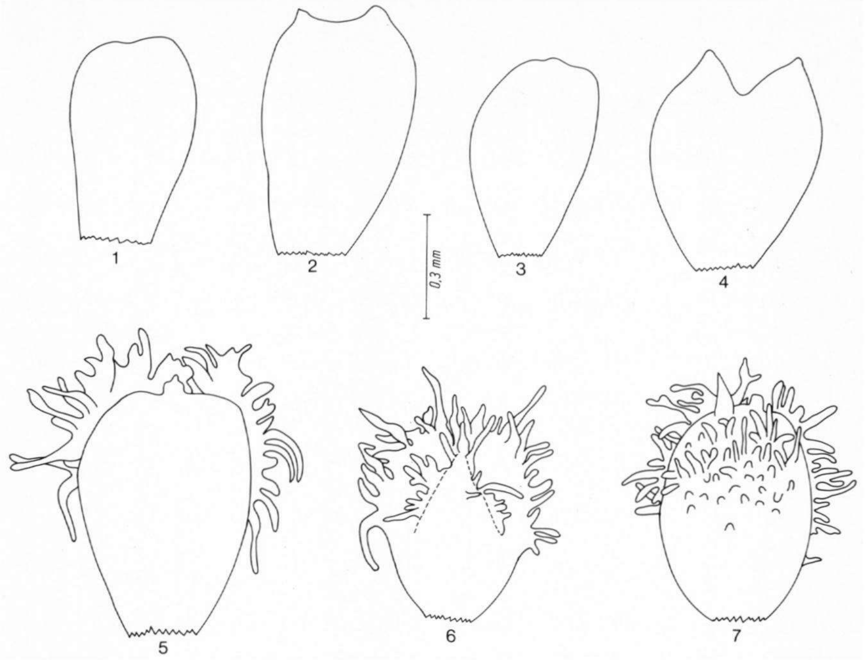


Fig. 3. Gynoecium characters in *Symbiezidium transversale* (Sw.) Trevis. and *S. barbiflorum* (Lindenb. & Gott.) Evans.

1-2. female bracteole in *S. transversale*. 3-4. ibid. in *S. barbiflorum*. 5. perianth in *S. transversale* var. *transversale*. 6. ibid. in *S. transversale* var. *hookeriana*. 7. ibid. in *S. barbiflorum*.

1-2 from the type. 3-4 from the type of *S. pogonopterum*. 5 from Broadway 5418, Trinidad. 6 from Griffin et al. 184, Brazil. 7 from Yano 466, Brazil.

Leaves imbricated, the lobe to 2,5 mm long, sometimes even larger, to 1,4 mm wide, attached over the whole length of the merophyte or nearly so, the apex entire. Median leaf cells 30-46 μm, the trigones (7-)10-16 μm, intermediate thickenings 0-3 per cell. Lobule very variable, as in *S. barbiflorum*, but often larger, 0,15-0,25 × the length of the lobe.

Underleaves imbricated, 0,5-1,6 mm long, to 1,7 mm wide, the underleaf cells not or only slightly differing from the leaf cells. Androecia on short lateral branches and/or on longer branches or stems, terminal or intercalary, then often a larger

Fig. 2. *Symbiezidium transversale* (Sw.) Trevis. and *S. barbiflorum* (Lindenb. & Gott.) Evans.

1-2. *S. transversale* var. *hookeriana*. 1. habitus ventral. 2. portion of stem in dorsal view. 3-4. *S. barbiflorum*. 3. habitus ventral, showing asymmetric development of leaves. 4. oil bodies. 5-6. *S. transversale* var. *transversale*. 5. stem cross section. 6. stem longitudinal section at underleaf base.

1-2 from Lisboa 660, Brazil. 3 from Griffin et al. 46, Venezuela. 4 from Gradstein 3606, Colombia. 5-6 from Pagan 216, Puerto Rico.

series of bracts, usually 8-15 pairs, the bracteoles only in the lower part of the spike well developed, at the top often absent.

Gynoecium terminally on a short lateral branch, with or without one short sterile innovation of the *Radula-Jubula*-type, the perianth dorsi-ventrally flattened, the ventral surface smooth or with 1-2 rows of laciniae, with or without 1-2 angles.

Symbiezidium transversale ssp. *transversale* is widespread in tropical America, occuring in lowland and submontane forests up to 1200 m. It can be recognised by its large, oblong, entire leaves (sometimes with apiculate apex), and by its large size, measuring over 3 mm in width. Smaller plants, with stems only 2,5-3 mm wide, have occasionally been found, however. Such specimens cannot be distinguished from *S. barbiflorum* when perianths are lacking. The two varieties of ssp. *transversale,* var. *transversale* and var. *hookeriana,* can only be distinguished when perianths are available. Among the numerous collections examined, there are a few intermediates (see under "Specimens examined") which have two kinds of perianths on the same stem: with smooth ventral surface or with lacinia in 1-2 rows on the surface. Such specimens may turn up in localities where both varieties occur.

S. transversale approaches *S. barbiflorum* by its var. *hookeriana,* which sometimes, e.g. in the type from Guadeloupe, may develop an occasional lacinia on the perianth surface between the two rows. Such specimens should, however, remain distinct from *S. barbiflorum* which produces laciniae much more densely and is always of small stature. The two varieties have been described in the literature under many different names and the synonymy is rather confusing and complex. For instance, Fulford (1942) in her revision described the var. *hookeriana* under 3 names: *S. subrotundum, S. taeniopsis* and *S. laceratum.* There are two names which we have not been able to identify on varietal level by lack of perianths: *S. subrotundum* and *S. cordistipulum.* The full citation for these names, which may be placed here under *S. transversale* ssp. *transversale,* is as follows:

Symbiezidium subrotundum (Kunth) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877); Stephani (1912) 104; Fulford (1942) 298; Gradstein & Hekking (1979) 131. *Jungermannia subrotunda* Kunth, Syn. Pl. Aequin.-Orb., Nov. sect. 5, 1: 41 (1822). *Lejeunea subrotunda* (Kunth) Hook. ex Gott., Lindenb. et Nees, Syn. Hep.: 312 (1845); Spruce (1884) 125. Type: Colombia, "Mt. Quindio, inter Ibagué et Carthago in boragine ocebrada de Tochecito, alt. 1350 hex.", Humboldt et Bonpland s.n., 1801 (K in BM holo, MANCH, NY, S).

Stephani (1912) described perianths of the *barbiflorum*-type in this species while Fulford (1942) claims them to be of the *hookeriana*-type. We have examined both the holotype in the Hooker herbarium (BM) as well as various duplicates, including the specimens in NY that Fulford studied, but failed to find any mature perianth. All specimens that we saw contain only juvenile gynoecia. The original description also lacks information on the perianth. Since the plant is robust, with stem and leaves ca. 4 mm wide, we do not hesitate to place this type in the synonymy of *S. transversale.*

Symbiezidium cordistipulum Steph., Spec. Hep. 5: 101 (1912). Type: Costa Rica, Boruca, Tonduz 15560, 1891 (G 18833 holo).

The specimen is sterile but fits *S. transversale* because of its large size. *S. cordistipulum* stands out by its remarkably large, reniform underleaves with recurved margins and large auricles. We have not seen such large auricles in other specimens in *Symbiezidium* but because the plant is fully sterile and because of the great gametophyte plasticity of *S. transversale,* we refrain from recognizing *S. cordistipulum* as a separate taxon.

Possibly also belonging here is a specimen from southern Venezuela: Casiquiare, Capiguara, 120 m, on palm trunc, mixed with *Symbiezidium barbiflorum,* K. Mägdefrau 205, 27 January 1958 (herb. Mägdefrau, U).

The synonymy for the two varieties is as follows:

2a1. **Symbiezidium transversale** var. **transversale**

Jungermannia transversalis Sw., Prodr. Fl. Ind. Occ.: 144 (1788); Weber (1815) 34; Nees in Martius (1833) 354 pro parte.

Collections cited by Nees 1833 belong to this species (the type), to *Phragmicoma bicolor* Nees var. *paraënsis,* fide Syn. Hep.: 294 (Para, leg Martius), to *Neurolejeunea catenulata* (fide Syn. Hep.: 323) and to ? (Cape, S. Afr., leg. Ecklon).

Phragmicoma transversalis (Sw.) Nees, Naturg. Eur. Leberm. 3: 248 (1838). *Lejeunea transversalis* (Sw.) Nees, in Gott., Lindenb. et Nees, Syn. Hep.: 310 (1845) "var. *α*"; Spruce (1884) 124; Stephani (1890) 13. *Symbiezidium transversale* (Sw.) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877); Evans (1908) 537, pl. 31 (1-10); Stephani (1912) 105; Fulford (1942) 295, figs. 1-5.; Gradstein & Hekking (1979) 131. *Platylejeunea transversalis* (Sw.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893).

Type: West Indies. Jamaica, Swartz s.n. (S holo, NY, S (ex hb. Aongstr., Weber, Lehmann), STR, MANCH? (ex hb. Taylor)).

Heterotypic synonyms:

Lejeunea transversalis (Sw.) Nees var. *laxior* Lindenb. & Gott., Linnaea 24: 269 (1851).

Type: Suriname, Kegel s.n. (not seen; judging from the description this synonymy should probably be correct).

Phragmicoma baccifera Tayl., London J. Bot. 5: 387 (1846); Gott., Lindenb. et Nees (1847) 742. *Marchesinia baccifera* (Tayl.) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 405 (1877). *Platylejeunea baccifera* (Tayl.) Evans, Trans. Conn. Acad. 10: 417 (1900). *Lejeunea baccifera* (Tayl.) Steph., Hedwigia 29: 140, XIV (1890). *Symbiezidium bacciferum* (Tayl.) Steph., Spec. Hep. 5: 107 (1912); Verdoorn (1934) 237.

Type: "New Holland, Hook. Herb." (K in BM holo, BM, MANCH, NY, S, STR (atypical)).

This species has been reported from Australia (the type) and Hawaii (Evans 1908); the Hawaiian record is based on a collection made by Menzies in 1793. We assume that these records are based on erroneous labels (see also sub *S. cryptocarpum*), as more recent collections of *S. transversale* from outside tropical America are lacking. Perianths in the holotype (Hooker Herbarium) are of the var. *transversale*-type but a duplicate in the Nees herbarium in Strassburg has a perianth of the var. *hookeriana*-type. We did not see the specimen in the Taylor herbarium. As the original description does not indicate the presence of laciniae on the ventral surface of the perianth, we consider the present synonymy as correct.

Lejeunea hobsoniana Lindenb., in Gott., Lindenb. et Nees, Syn. Hep.: 313 (1845). *Platylejeunea hobsoniana* (Lindenb.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893). *Symbiezidium hobsonianum* (Lindenb.) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877); Stephani (1912) 99; Fulford (1942) 295 sub *S. transversale.*

Type: West Indies. St. Vincent, in mount St. Andrews, ex hb. Hooker (isotypes MANCH (ster.), NY (female), S (ster.)).

Lejeunea cryptocarpa Mitt., in Seeman, Fl. Vitiensis: 413 (1871). *Platylejeunea cryptocarpa* Steph., Bull. Herb. Boissier 5: 842 (1897); (non Evans (1900) 418 = *S. transversale* var. *hookeriana*). *Symbiezidium cryptocarpum* (Mitt.) Steph., Spec. Hep. 5: 107 (1912); Verdoorn (1934) 238.

Lectotype (fide R. Grolle 1973 in sched.): "Owykee, Menzius, on *Leptogium azureum*", syntype of *Lejeunea transversalis* var. *hookeriana* Gott. (Hawaii) (NY; isolectotypes in BM, NY, S). As *Symbiezidium* has not been found on Hawaii since Menzius collected it there in 1793 (fide Evans 1900), the Hawaiian record most likely represents a case of mislabelling. We could not find perianths in the type material but an original drawing by Mitten accompanying the lectotype specimen and his description indicate that this synonymy is correct, although Evans (1900) claims that the perianth has ciliae on the ventral surface as in var. *hookeriana.*

The other collections of *L. cryptocarpa* cited by Mitten (l.c.), from Samoa, Powell s.n. (NY) and the Isle of Pines, Strange s.n. (NY), belong to *Pycnolejeunea graeffii* (Jack & Steph.) Steph. (fide R. Grolle in sched.).

Jungermannia granulata Nees, in Martius, Fl. Bras. 1, 1:352 (1833); Montagne (1835) 211. *Phragmicoma granulata* (Nees) Nees, Naturgesch. Eur. leberm. 3: 248 (1838). *Lejeunea granulata* (Nees) Nees ex Mont., Ann. Sci. Nat. Paris, sér. 2, 3: 211 (1835); Gott., Lindenb. et Nees (1845) 311. *Symbiezidium granulatum* (Nees) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877); Stephani (1912) 102.

Type: Brazil. Amazon River, Sellow s.n. (STR holo, W). The type specimens have perianths, although in the original description they are not mentioned. The species has not been investigated by Spruce, Evans and Fulford, yet represents the oldest type of *Symbiezidium* from mainland South America.

Symbiezidium grandifolium Steph., Spec. Hep. 5: 101 (1912); Fulford (1942) 295 sub *S. transversale.*

Lectotype (nov.): Costa Rica. Tonduz 15671 p.p., 1893 (G 18834 female). Paratype: Ecuador, Wallis s.n. (G 18835 male).

DISTRIBUTION AND ECOLOGY (var. *transversale*): Belize, Costa Rica, Panama, Cuba Puerto Rico, Jamaica, Martinique, Trinidad, French Guyana, Suriname, Brazil (Amazonia only), Venezuela, Colombia, Ecuador, Peru, Bolivia (?sterile). From sealevel up to 1250 m in moist lowland and submontane forests, mainly in natural forests but occasionally also on roadside trees. Epiphyte on tree truncs and branches, on twigs and on decayed wood.

2a2. **Symbiezidium transversale** (Sw.) Trevis. var. **hookeriana** (Gott.) comb. nov.

Lejeunea transversalis (Sw.) Nees var. *hookeriana* Gott., Syn. Hep.: 311 (1845), ibid.: 819 (1847); Evans (1900) sub *Platylejeunea cryptocarpa;* Evans (1908) sub *Symbiezidium barbiflorum;* Fulford (1942) ibid.

Lectotype (nov.): "Guadeloupe, Hooker misit s.n. 1837" (STR; isolectotypes in NY and S).

Four syntype collections are cited in the Synopsis: Guadeloupe, s.c.; Guiana, leg. Parker; Hawaii, s.c.; Tasmania, s.c.. The collections from Hawaii and Tasmania (probably based on erroneous labels, see elsewhere) belong to var. *transversale* and are the types of resp. *S. cryptocarpum* (Mitt.) Steph. and *S. bacciferum* (Tayl.) Steph. The collection from Guiana is sterile. Evans (1908) and Fulford (1942) reduced this variety to synonymy under *S. barbiflorum* but none of the syntype collections have that type of perianth. We have chosen the Guadeloupe specimen as the lectotype because it is more copious and unambiguous. Unfortunately, the original description fails to give information on the perianth.

Heterotypic synonyms:

Lejeunea incrassata Tayl. ex Besch. et Spruce, Bull. Soc. Bot. France 36: 179 (1889); Evans (1908) 540 sub *S. barbiflorum;* Stephani (1912) 101 ibid.; Fulford (1942) 297 ibid.

Type: Guadeloupe, Marie s.n. (MANCH). The species was reduced to synonymy of *S. barbiflorum* by all later authors (cf. Evans 1908) but the type has perianths as in var. *hookeriana.*

Symbiezidium laceratum Evans, Bull. Torrey Bot. Club 35: 386, Pl. 28, 15-20 (1908); Fulford (1942) 303.

Type: Haiti, Plaisance to Marmelade, 800 m, Nash 654, 23.VIII.1903 (YU holo, NY).

Lejeunea taeniopsis Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 126 (1884); Stephani (1888) 286 sub *Platylejeunea granulata;* Stephani (1912) 102 sub *Symbiezidium granulatum. Symbiezidium taeniopsis* (Spruce) Fulf., Lloydia 5: 302 (1942).

Lectotype (nov.): Brazil, Para, Spruce L 140, 18.VII.1849 (MANCH, YU). Since Spruce described the perianth as having two ventral keels with cilia, we have selected as lectotype the specimen that fits this description best. Other authentic Spruce materials of *Lej. taeniopsis* have perianths as in var. *transversale* or are sterile.

Lejeunea vincentina Gott., in Gott., Lindenb. et Nees, Syn. Hep.: 313 (1845); Spruce (1884) 127 sub *Platylejeunea. Symbiezidium vincentinum* (Gott.) Trevis., Mem. Real. Ist. Lomb. Sci. Mat. Nat. ser. 3, 4: 403 (1877); Evans (1908) 542; Stephani (1912) 100; Fulford (1942) 299 sub *Symbiezidium subrotundum. Platylejeunea vincentina* (Gott.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 131 (1893).

Type: St. Vincent, ex hb. Hooker (isotypes in W hb. Lindenberg 6127 and G 20055). The type should be in the hb. Lehmann (fide descr. orig.) but we could not find it among the Stockholm materials examined. The fertile isotypes in W and G and the original description indicate that the present synonymy is correct.

Platylejeunea cryptocarpa sensu Evans (1900) 418, non Mitt.

DISTRIBUTION AND ECOLOGY (var. *hookeriana*): Belize, Costa Rica, Cuba, Haiti, Jamaica, Puerto Rico, St. Kitts, Guadeloupe, Martinique, St. Vincent, Dominica, Trinidad, French Guiana, Suriname, Guyana, Brazil, Peru (Amazonia only). From sealevel up to 1200(-1700) m, ecology as var. *transversale.* In the Andes region the variety has thus far only been collected around Tarapoto and Moyabamba, Peru (leg. S.R. Gr. and other members of the 1982 BRYOTROP expedition) where it is a frequent element in submontane rainforest at 500-900 m on hillsides bordering the Amazon basin. It grows here on large, smooth truncs in partly shaded or exposed locations, together with *Lopholejeunea subfusca, Mastigolejeunea auriculata, Lejeunea laetevirens, Hygrolejeunea recurvistipula* and *Ceratolejeunea* spp. Much less frequently, the variety was found in the moister, epiphyll-rich lower montane rainforest from 1100 to its upper limit at 1700 m, on truncs together with *Ceratolejeunea* spp, *Neurolejeunea breutelii* and *Omphalanthus filiformis.*

2b. **Symbiezidium transversale** (Sw.) Trevis. ssp. **dentatum** (Herz.) comb. nov.

Symbiezidium dentatum Herz., Feddes Rep. Sp. Nov. 57: 175 (1955).

Type: Colombia, Dept. El Valle, Santa Rosa, Dagua Valley, forest along Rio Caballate, 200-300 m, on leaf of Gesneriaceae, E.P. Killip 11544 p.p., 22.IX.1922 (JE holo).

The type is sterile but fertile specimens have a *transversale*-type gynoecium, with smooth ventral surface. The plants are robust and agree in all respects with ssp. *transversale* but the leaf apex is erose-denticulate with 4-10 teeth, each tooth 1(-2) cells long.

DISTRIBUTION AND ECOLOGY: Only known from a few lowland localities along the Pacific coast of Colombia (Chocó, El Valle) and northern Ecuador (Esmeraldas). The few specimens are from a wide variety of habitats: from tree trunks, roadside rock or soil, and even from living leaves (the type!).

Ssp. *transversale* and ssp. *dentatum* are apparently allopatric except in the Chocó where both taxa have been found around Quibdo, in separate localities, however. Future collecting should show whether subspecific status is appropriate for *S. dentatum*. By its denticulate leaves, this is the most easily recognised neotropical taxon in *Symbiezidium*.

Leaves of *S. transversale* are sometimes invaded by fungal hyphae, which may grow so vigorous as to give a "hairy" appearance to leaf surface and margins. In some cases, the leaf apex becomes erose, suggesting the presence of irregular, small teeth. Careful examination of these leaves under the microscope would easily reveal the difference between such fungal artefacts and true teeth.

3. **Symbiezidium barbiflorum** (Lindenb. et Gott.) Evans Figs. 2-4

Bull. Torrey Bot. Club 34: 540, Pl. 31 (11-14) (1908); Stephani (1912) 100; Fulford (1942) 297, figs. 6-7.; Gradstein et al. (1981) 242, fig. 1(3). *Lejeunea barbiflora* Lindenb. et Gott., Linnaea 24: 630 (1851); Stephani (1888) 282; Stephani (1890) 13.

Typey: Suriname, Paramaribo, "in ramis *Psidii*", Kegel s.n., (not seen).

The type was not available among the materials received on loan from GOET, W and other herbaria. The original description of the perianth "facie ventrali media dense spinulosovillosis" leaves no doubt, however, about the identity of this species.

Heterotypic synonyms:

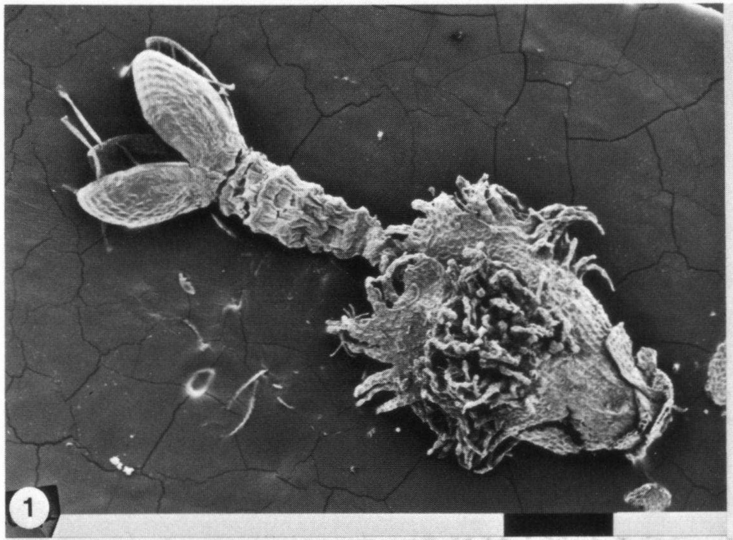
Lejeunea barbiflora Lindenb. et Gott. var. *depauperata* Lindenb. et Gott., Linnaea 24: 630 (1851).

Type: Suriname, Paramaribo, "oude rijweg", Kegel s.n., aug. 1857 (GOET).

Lejeunea transversalis (Sw.) Nees var. *fluminensis* Gott., Syn. Hep.: 311 (1845).

Type: Brazil, Rio de Janeiro, unknown collector (S iso).

Lejeunea (subg. *Platylejeunea*) *pogonoptera* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 128 (1884). *Symbiezidium pogonopterum* (Spruce) Steph., Spec. Hep. 5: 103 (1912); Fulford (1942) 299 sub *Symbiezidium subrotundum*.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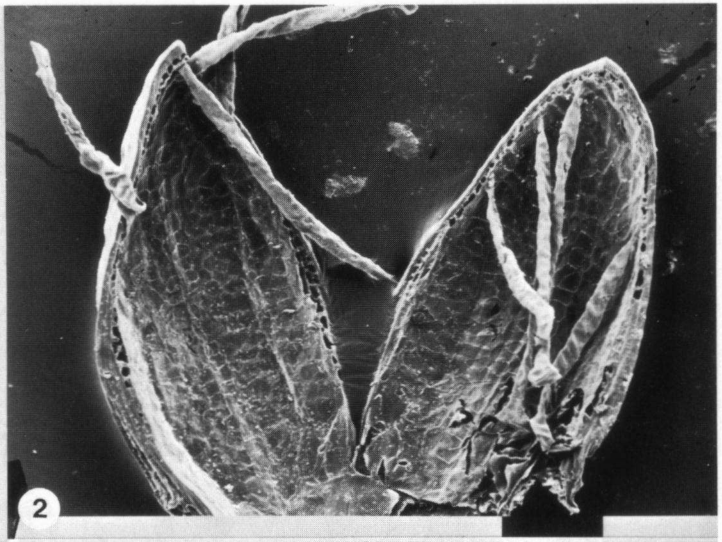
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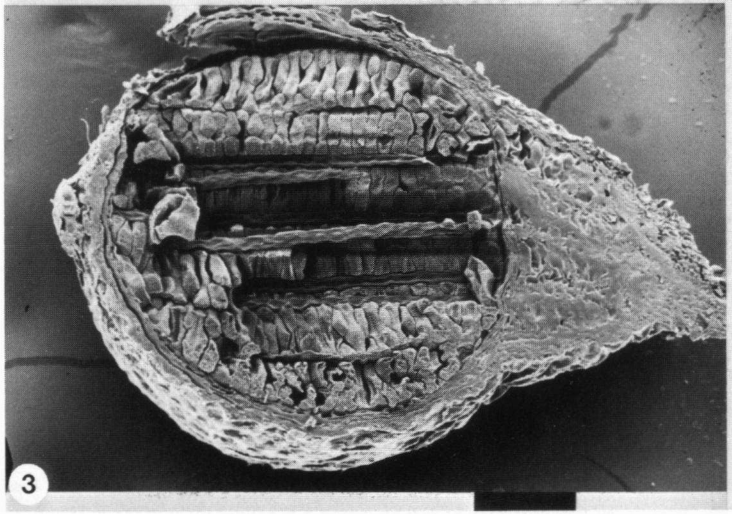
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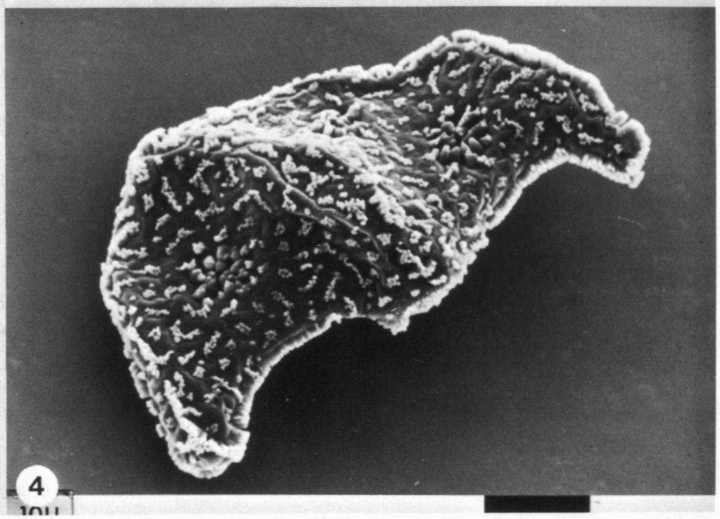
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Lectotype (nov.): Brazil. Pará. Caripi, Spruce L 523, aug.1849 (MANCH 13371; isolectotypes: MANCH 13372, 13374, 13375 and G 20053). Paratype: Peru. "Ad flumen Huallaga", Spruce L 513 (MANCH). According to Spruce (l.c.) perianths in the Pará collections have two weak ventral keels and smooth ventral intersurfaces, whereas in the Peru specimens keels are more pronounced and the interspace rough. However, these observations are not supported by the authentic materials of *L. pogonoptera* in the Spruce herbarium, which have all perianths ± rough on the ventral surface. We have chosen the Pará collection as the lectotype because it is more copious.

Lejeunea (subg. *Platylejeunea*) *setosa* Steph., Hedwigia 29: 14 (1890). *Symbiezidium setosum* (Steph.) Steph., Spec. Hep. 5: 104 (1912).

Type: Mexico, Hacienda de Jovo, Liebmann s.n., "hb. Lindenberg 6125, 6126" as *Lejeunea hobsoniana* var. *β confertior* (G 20052 holo, C).

Lejeunea hobsoniana var. *β confertior* Gott., Lindenb. et Nees, Syn. Hep.: 748 (1847); Gottsche (1863) 181 (preprint) or 277.

Lectotype (nov.): Mexico. Vera Cruz, Hacienda de Mirador, 3000 ft., Liebmann 372b (C). Paratypes: Hacienda de Jovo, Liebmann 570b, 559c, 588d, 542d, the type of *Lejeunea setosa* (C).

Platylejeunea kroneana Steph., Hedwigia 35: 117 (1896). *Symbiezidium kroneanum* (Steph.) Steph., Spec. Hep. 5: 102 (1912); Fulford (1942) 300 sub *S. setosum*.

Type: Brazil. St. Catharina, Krone s.n., 1887 (G 18817 holo, MANCH, YU). The perianth in this plant is small and finely erose-denticulate along the margins and on the ventral surface, approaching the smooth perianths of *S. madagascariense*!

Lejeunea hobsoniana auct. non Lindenb.,: cf. Spruce (1884) 127. *Lejeunea transversalis* var. *hookeriana* auct. non Gott.: cf. Evans (1908) 540. *Lejeunea incrassata* auct. non Tayl. ex Besch. et Spruce: cf. Evans (1908) 540.

Plants monoicous, relatively small, the stem including the leaves 2-3 mm wide, brownish or sometimes olive-green. Stem seldom more than 160 μm in diam. (8-10 cells), the cortical cells 15-26 μm high, 20-40 μm wide, the medullary cells 12-20 μm in diam. Ventral merophyte 8-10 cells long, seldom more than 4 cells wide, the cells 40-70 μm long.

Fig. 4. SEM analysis of the sporophyte of *Symbiezidium* Trevis.

1. Perianth, showing ventral laciniae, and sporophyte, showing articulate seta and valves (bar = 400 μm). 2. Two valves inner surface, showing marginal elaters (bar = 100 μm). 3. Capsule length section showing spore storage in situ (bar = 100 μm). 4. Spore (bar = 10 μm). 1-3 from Pócs & Reyes 9055/BD, Cuba. 4 from Pócs & Borhidi 9004/A, Cuba.

1-4 *S. barbiflorum* (Lindenb. & Gott.) Evans.

Leaves imbricated, the lobe to 1,6 mm long, to 1,1 mm wide, attached over whole length of merophyte or sometimes over only 3/4, the apex rarely with one tooth. Median leaf cells 30-40 μm, the trigones 8-12 μm, intermediate thickenings 0-2 per cell. Oil bodies *Bazzania*-type, ca. 4-7 per cell, large, ellipsoid, 10-20 × 4-6 μm, homogeneous or, rarely, with a few septations (Gradstein et al. 1981: 242).

Lobule very variable in dimensions, up to 370 μm long and 370 μm wide, usually 0,15-0,25 × the length of the lobe.

Underleaves imbricated, 450-1000 μm long, to 1500 μm wide, the underleaf cells with 1-4 intermediate thickenings, otherwise as the leaf cells.

Androecia on short lateral branches or innovations, 4-10 pairs of bracts, the bracteoles reduced or absent in the upper part of the spike.

Gynoecium terminal on a short lateral branch, with or without one short sterile or male innovation of the *Radula-Jubula*-type. Perianth dorsiventral flattened, the ventral surface with or without 1-2 angles, at least partly covered with spines or longer laciniae.

The main character to distinguish *S. barbiflorum* from the other species is the ventral keel of the perianth covered randomly with laciniae, and the smaller stature of the plants as compared with the usual condition in *S. transversale*. Small *S. transversale* has occasionally been found, however; such specimens cannot be distinguished from *S. barbiflorum* except by the perianth. The species varies considerably in size, some plants resembling a *S. transversale*, and in the characters of the gynoecium. The apex of the bracteole can be rounded or bifid, but all intergradations can be found, even in a single plant (e.g. the type of *S. pogonopterum*). As for the ventral keel of the perianth, there are plants with laciniae randomly covering (a part of) the ventral keel and also plants with additional laciniae on 1-2 angles of the ventral keel. The plants previously named as *S. kroneanum* belong mostly to the second type, but since here also intergradations are found and other distinguishing characters are not available, *S. kroneanum* remains a synonym of *S. barbiflorum*.

DISTRIBUTION AND ECOLOGY: Mexico, Belize, Honduras, Costa Rica, Cuba, Puerto Rico, Jamaica, Dominica, Martinique, Trinidad, Suriname, Brazil (Amazonia and S.E. Brazil), Venezuela, Colombia, Ecuador, Peru.

From sealevel up to 2800 m in the Venezuelan Andes. In the Andes apparently always above 1000 m. Epiphyte on tree trunks, branches and twigs, and on rotten logs in (primary) lowland and mountain forests.

S. barbiflorum is the most widely distributed species of *Symbiezidium* and contrary to *S. transversale* has also been found in Mexico and in S.E. Brazil where it is in fact rather common. In the Andes *S. barbiflorum* and *S. transversale* seem to almost exclude each other, *S. barbiflorum* being the montane plant and *S. transversale* predominantly the lowland plant, but in Amazonia, the West-Indies and Central America the two species are sympatric. In the Central Cordillera of Colombia, the first author has found *S. barbiflorum* on smooth bark of large trunks together with *Archilejeunea parviflora*, in moist (not too wet) submontane forest patches on hillsides at about 1500 m.

Selected Specimens Examined (subg. *Symbiezidium*):

barbiflorum = *S. barbiflorum* (Lindenb. et Gott.) Evans

dentatum = *S. transversale* (Sw.) Trevis. ssp. *dentatum* (Herz.) comb. nov.

hookeriana = *S. transversale* (Sw.) Trevis. var. *hookeriana* (Gott.) comb. nov.

hookeriana/transversale = specimen with characters of var. *hookeriana* and var. *transversale* (the two different kinds of perianth on the same plant).

transversale = *S. transversale* (Sw.) Trevis. var. *transversale.*

ssp. *transversale* = *S. transversale* (Sw.) Trevis. ssp. *transversale* s.l. (lacking perianths).

p.p. = pro parte
s.c. = sine collector
s.l. = sine loco
s.n. = sine numero

MEXICO *barbiflorum:* Mirador, Liebmann 372b, the type of *Lej. hobsoniana* var. *confertior* (C); Hacienda de Jovo, Liebmann 570b, 372b, 559c, 588d, 542a, syntypes of *S. setosum* (C, G); cf. *barbiflorum:* Chiapas, Lagunas de Montebello, Eggers & Frahm 922447, III.1979 (hb. Frahm, U).

BELIZE *barbiflorum:* Punta Gorda, s.c., ex MO (hb Fulford). *hookeriana:* Ibid. *transversale:* Ibid., 5 colls.

HONDURAS *barbiflorum:* Lancetilla Valley, Stanley 55553 (S).

COSTA RICA *barbiflorum:* San Domingo, Tonduz s.n., 1896 (G, NY, YU); Cocos I., Weber 550c & 561, 1964; ibid. Itow 7 p.p., 1964 (COLO). *hookeriana:* Cocos I., Itow 7 p.p., 1964 (COLO). *hookeriana/transversale:* Cocos I., Weber 523, 1964; ibid., Itow 7 p.p., 1964 (COLO). *transversale:* Flumen Naranjo, Tonduz s.n., 1893 (NY); Cocos I., Weber 549 (COLO).

PANAMA *transversale:* s.l., Mannée & Gorgone s.n. (YU).

CUBA *barbiflorum:* Sierra de Escambray, Pócs & Bohridi 9004, X.1978 (HAC); Sierra de Nipe, Pócs & Reyes 9055, XI.1978 (HAC); Sierra de la Gran Piedra, Pócs & Reyes 9111 & 9124, XI.1978 (HAC); Sierra Maestra, Pócs & Duany 9079 (HAC); Mt. El Yunque, Underwood & Earle 316, 323, 356 (NY, YU); Baracoa, Pócs & Reyes 9065, XI.1978 (HAC). *hookeriana:* Habana, Sierra del Rosaria, Pócs & Reyes 9042, X.1978 (HAC). *transversale:* Banao Mt., Léon & Clément 5556a, 1915; ibid. 8358, 1918 (HAC, NY, YU); Dept. Holguin, Reyes 968 (HAC); Mt. El Yunque, Underwood & Earle 1018, III.1903 (MANCH, NY, YU).

HAITI *hookeriana:* Plaisance to Marmelade, Nash 654, the type of *S. laceratum* (NY, YU).

JAMAICA *barbiflorum:* Mt. Diabolo, Maxon 2223 (YU). *hookeriana:* s.l., Evans 538, 845 (YU); Chopstown, Bower s.n., VIII.1909 (MANCH). *transversale:* s.l., Swartz s.n., the type of *S. transversale* (MANCH, NY, S); Troy, Marble 663, IX.1906 (YU); Dullwood, Evans 505 (YU); Mansfield, Maxon 967 (YU); St. Catherine's Peak, Baxter 50, V.1956 (hb. Fulford); Portland, Griffin s.n., VI. 1968 (U).

PUERTO RICO *barbiflorum:* Luquillo Mts., Heller 779 & 797 (NY); Maricao, Pagán 239, VII.1937 (HAC, YU). *hookeriana:* Maricao, Pagán 226a (HAC, NY); La Mina, Fulford et al. 282 & 291, VII.1967 (hb. Fulford). *transversale:* Luquillo Mts., Heller 784, 1144, 1159 & 1161 (NY, YU); El Yunque, Evans 25, 67 & 126 (NY, YU); Torito Mts., Pagán 272 (NY); Maricao, Pagán 216, II.1937 (HAC, NY, YU); Sierra de Naguabo, Sintenis s.n., 1885 (NY, YU).

ST. KITT'S *hookeriana:* Molyneaux Estate, Britton & Cowell 689 (NY).

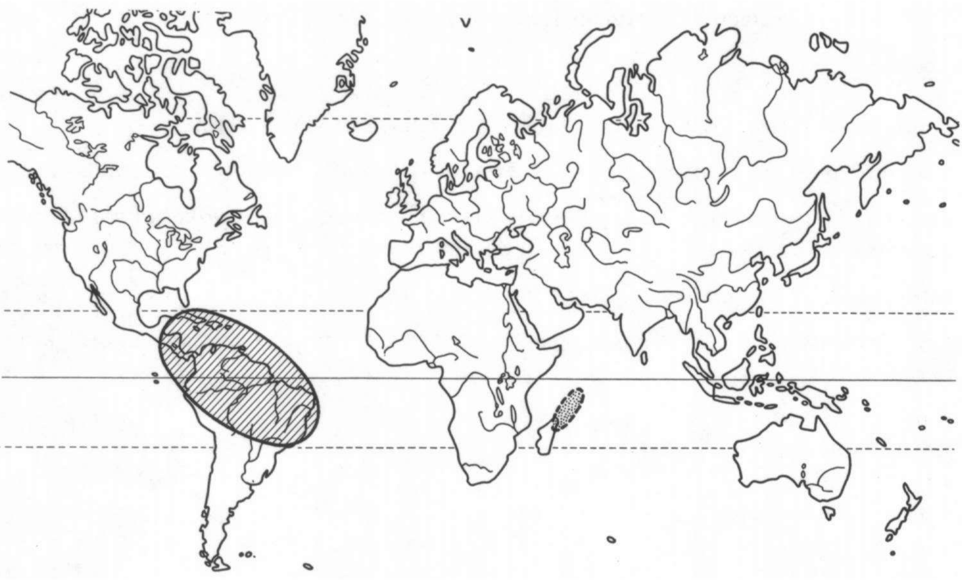

Fig. 5. The distribution of *Symbiezidium* Trevis. Continuous line: subgenus *Symbiezidium (S. barbiflorum* and *S. transversale)*. Broken line: subgenus *Eosymbiezidium (S. madagascariense)*.

GUADELOUPE *hookeriana:* s.l., ex hb. Hooker, lectotype of *S. transversale* var. *hookeriana* (NY, S, STR); s.l., Marie s.n., the type of *Platylejeunea incrassata* (MANCH); s.l., Husnot Pl. des Antilles 226, 1868 (BM, L, MANCH).

DOMINICA *hookeriana:* s.l., Elliot 2160 (YU); St. George, Griffin s.n., VII.1968 (U).

MARTINIQUE *barbiflorum:* s.l., Hahn s.n. (NY). *hookeriana:* Mt. Pelée, Duss 269 & 699, 1899-1901 (NY).

ST. VINCENT *hookeriana:* s.l., ex hb. Hooker, the type of *S. vincentinum* (G, W). *transversale:* Mt. St. Andrews, Hobson s.n., the type of *S. hobsonianum* (MANCH, NY, S).

TRINIDAD *barbiflorum:* s.l., Fendler s.n. (NY). *hookeriana:* Ortoire river, Britton 2573 (NY, YU). *transversale:* s.l., Thaxter s.n., 1912-13 (NY, YU); Ortoire river, Britton 2565a (NY, YU); Aripo road, Broadway 5418, 5867, IX.1924 (BM, NY, YU, hb. Fulford).

FRENCH GUIANA *barbiflorum:* s.l., Leprieur s.n., as *Lejeunea granulata* var. *minor* (PC-Mont, W). *hookeriana:* Saül, Cremers 4163 (hb Onraedt); Itany, Cremers 4805 (hb. Onraedt). *transversale:* s.l., Sagot s.n. (YU).

SURINAME *barbiflorum:* s.l., van Sypesteyn s.n. (L); Paramaribo, Kegel s.n., the type of *Lejeunea barbiflora* var. *depauperata* (GOET); Joden Savanna, Kegel s.n. (W); Brownsberg, Bekker 1063 & 1150, X.1981 (U); Kabalebo Dam area, Bekker 1635, 1638a, 1672, 1673 & 1717, XI.1981 (U). *hookeriana:* Groningen, McGillary s.n., 1971, ex hb. Luitingh (U); Brownsberg, van Slageren H401, VII.1981 (U); near Grote Zwiebelzwamp, Lanjouw & Lindeman 819, X.1948 (U). *hookeriana/transversale:* Lelie Mts., Lindeman et al., 746, X.1975 (U). *transversale:* s.l., Kegel s.n. (GOET); s.l., ex hb. Miquel (L).

GUYANA *hookeriana:* near Bartica, Richards 170, 341 (YU). *hookeriana/transversale:* near Bartica, Richards 120 (YU).

BRAZIL *barbiflorum:* Pará, Caripi, the lectotype of *Lej. pogonoptera* (G, MANCH); Amazonas, Maués, Nelson 13, IV.1974 (NY, U); ibid., Manaus, campus of the INPA, Griffin et al. I-61, I-69, 1974

(FLAS, U)); ibid., Rio Negro, Spruce s.n. (NY); Rio de Janeiro, s.c., the type of *Lej. transversalis* var. *fluminensis* (S); Sao Paulo State, Rio Branco, Schiffner 1915, 1967, 2126 & 2130, IX.1901 (S, W); ibid., Rio Comprido, Schiffner 251 (W); ibid., Brasso Grande near Icapecirica, Schiffner 1339 & 1428 (W); ibid., Raiz do Sierra, Schiffner 907 & 924 (S, W); ibid., Cardoso I., Yano 466, VIII. 1976 (SP, U); ibid., Cananeia, Vital 6682, XI.1976 (SP, U); St. Catarina, Krone s.n., the type of *S. kroneanum* (G, MANCH, YU). *hookeriana:* Parà, Spruce l 140, the lectotype of *S. taeniopsis* (MANCH, NY, W, YU); ibid., Belem, Reserva Mocambo, Lisboa 660 & 663a, VI.1983 (MG, U); "ad Tanau", Spruce s.n. (MANCH); Amazonas: Manaus to Itacoatiara, Griffin et al. 184, 480, 485, 493, 505 & 509, VII.1974 (FLAS, U). *hookeriana/transversale:* Amazonia, Maronayacu, Spruce s.n. (MANCH). *transversale:* Amazonia, Sellow s.n., the type of *S. granulatum* (STR, W); Manaus to Itacoatiara, Griffin et al. 516, 576, 1006, VII.1974 (FLAS); rio Bombonasa, Spruce l 109 (MANCH).

VENEZUELA *barbiflorum:* Sucre, Griffin & Bermudez 40, 46, IV.1974 (FLAS, U); Merida, Moritz s.n. (BM, L); Sierra de Perija, Griffin 40, 54, 271, 187 (FLAS, U); Casiquiare, Mägdefrau 205 (U). *hookeriana:* Casiquiare, Mägdefrau 220 & 228, I.1958 (hb. Mägdefrau, U). *transversale:* Falcon, Mirando, Sipman & van der Werff 10915, I.1979 (U); Amazonia, San Carlos del Rio Negro, Spruce s.n. (MANCH, NY, W, YU).

COLOMBIA *barbiflorum:* Santander, road Santander to San Pedro, Bischler 270, VII.1958 (COL, PC, U); Risaralda, near Marsella, Gradstein 3606 and Van Reenen et al. 1848 & 1881, VIII.1980 (COL, U); Huila, San Agustin, Bischler 609, VIII.1958 (COL, PC, U). *dentatum:* Chocó, road Quibdo to Tutunendo, Bischler 191, IV.1957 (COL, PC, U); El Valle, Dagua Valley, the type of *S. dentatum*, Killip 11545, IX.1922 (JE); ibid, near Buenaventura, Bischler 323 & 472, VIII.1958 (COL, PC, U). *transversale:* Chocó, Quibdo, Bischler 158, 163 & 193, IV.1957 (COL, PC, U). ssp. *transversale:* Ibague, Mt. Tolima, Humboldt s.n., 1800, the type of *S. subrotundum* (BM, MANCH, NY, S); Cauca, Tambito, Bischler 286, VII.1958 (COL, PC, U).

ECUADOR *barbiflorum:* Quito, Jameson s.n. (NY); Chimborazo, Spruce s.n. (MANCH). *dentatum:* Esmeraldas, Rio San Miguel, Harling 702 & 4670, 1959 (S). ssp. *transversale:* Amazonia, Canelos, Spruce s.n. (MANCH); Santiago-Zamora, Mendez, Harling 2221 & 2222, 1947 (S).

PERU *barbiflorum:* "hot country at the western base of the Andes", Jameson s.n. (NY); Rio Huallaga, Spruce l 531 (MANCH). *hookeriana:* S. Martin, road Moyabamba - Chachapoyas, mountain rainforest, Frahm et al. 451 & 1304, IX.1982 (B, U); ibid., road Yurimaguas - Tarapoto, submontane rainforest, Frahm et al. 1394, 1395, 1396, 1685, 1731 & 1799, IX.1982 (B, U). *transversale:* middle Rio Blanco, Tessmann 3, VII.1923 (B, S).

BOLIVIA ssp. *transversale:* Tumupasa, Williams 2184, I.1902 (NY, U).

Excludenda

1. *Symbiezidium aberrans* (Lindenb. et Gott.) Trevis.
   = *Dicranolejeunea aberrans* (Lindenb. et Gott.) Steph.
2. *Symbiezidium applanatum* (Reinw., Blume et Nees) Trevis.
   = *Lopholejeunea applanatum* (Reinw., Blume et Nees) Schiffn.
3. *Symbiezidium axillare* (Nees et Mont.) Trevis.
   = *Dicranolejeunea axillaris* (Nees et Mont.) Schiffn.
4. *Symbiezidium balfourii* (Mitt.) Steph.
   = *Stictolejeunea balfourii* (Mitt.) E. Jones.
5. *Symbiezidium brachiatum* (Sw.) Trevis.
   = *Marchesinia brachiata* (Sw.) Schiffn.

6. *Symbiezidium breutelii* (Gott.) Trevis.
   = *Neurolejeunea breutelii* (Gott.) Evans.
7. *Symbiezidium calyculatum* (Tayl.) Trevis.
   = *Leucolejeunea clypeata* (Schweinf.) Evans (cf. Torreya 7: 227 (1907)).
8. *Symbiezidium catenulatum* (Nees) Trevis.
   = *Neurolejeunea catenulata* (Nees) Schiffn.
9. *Symbiezidium cruegeri* (Lindenb.) Trevis.
   = *Archilejeunea cruegeri* (Lindenb.) Steph.
10. *Symbiezidium cyclostipum* (Tayl.) Trevis.
    = *Lopholejeunea subfusca* (Nees) Schiffn. (fide Gradstein & Buskes, this volume)
11. *Symbiezidium devexum* (Lindenb. et Gott.) Trevis.
    = *Neurolejeunea devexa* (Lindenb. et Gott.) Herz.
12. *Symbiezidium eulophum* (Tayl.) Trevis.
    = *Lopholejeunea eulopha* (Tayl.) Schiffn.
13. *Symbiezidium fischerianum* (Nees) Trevis.
    = *Archilejeunea fischeriana* (Nees) Steph.
14. *Symbiezidium floccosum* (Lehm. et Lindenb.) Trevis.
    = *Cololejeunea floccosa* (Lehm. et Lindenb.) Schiffn.
15. *Symbiezidium incongruum* (Lindenb. et Gott.) Trevis.
    = *Dicranolejeunea incongrua* (Lindenb. et Gott.) Steph.
16. *Symbiezidium integristipulum* (Jack et Steph.) Steph.
    = *Pycnolejeunea integristipula* (Jack et Steph.) Mizut.
17. *Symbiezidium intermedium* (Lindenb.) Trevis.
    = *Lopholejeunea nigricans* (Lindenb.) Schiffn. (fide Verdoorn 1934)
18. *Symbiezidium javanicum* (Nees) Trevis.
    = *Lopholejeunea javanica* (Nees) Schiffn.
19. *Symbiezidium languidum* (Nees et Mont.) Trevis.
    = *Marchesinia languida* (Nees et Mont.) Steph.
20. *Symbiezidium leprieurii* (Mont.) Trevis.
    = *Archilejeunea leprieurii* (Mont.) Steph.
21. *Symbiezidium lorianum* Steph.
    = *Leucolejeunea decurrens* (Steph.) Mizut. (fide Mizutani 1976)
22. *Symbiezidium nigricans* (Lindenb.) Trevis.
    = *Lopholejeunea nigricans* (Lindenb.) Schiffn.
23. *Symbiezidium parviflorum* (Nees) Trevis.
    = *Archilejeunea parviflora* (Nees) Schiffn.
24. *Symbiezidium phyllorhizum* (Nees) Trevis.
    = *Dicranolejeunea phyllorhiza* (Nees) Schiffn.

25. *Symbiezidium plicatiscyphum* (Tayl.) Trevis.
= *Thysananthus anguiformis* (Tayl.) Tayl. ex Gottsche, Lindenb. et Nees (fide Mitten 1855)

26. *Symbiezidium polyphyllum* (Tayl.) Trevis.
= *Acrolejeunea torulosa* (Lehm. et Lindenb.) Schiffn. (fide Gradstein 1975)

27. *Symbiezidium rotale* (Tayl.) Trevis.
= *Leucolejeunea rotalis* (Tayl.) S. Arnell

28. *Symbiezidium sagraeanum* (Mont.) Trevis.
= *Lopholejeunea subfusca* (Nees) Schiffn. (fide Vanden Berghen 1950).

29. *Symbiezidium samoanum* (Steph.) Steph.
= *Pycnolejeunea graeffii* (Jack & Steph.) Mizut., J. Hattori Bot. Lab. 33: 257 (1970) "Verd. 1934". The combination has been ascribed to Verdoorn (1934: 46) who, however, did not validly publish it (ICBN art. 33).

30. *Symbiezidium squamatum* (Willd. ex Web.) Trevis.
= *Stictolejeunea squamata* (Willd. ex Web.) Schiffn.

31. *Symbiezidium subfuscum* (Nees) Trevis.
= *Lopholejeunea subfusca* (Nees) Schiffn.

32. *Symbiezidium tenuifolium* (Tayl.) Trevis.
= *Omphalanthus filiformis* (Sw.) Nees (fide Stephani 1911).

33. *Symbiezidium viridissimum* (Lindenb.) Trevis.
= *Archilejeunea viridissima* (Lindenb.) Evans.

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We wish to acknowledge the help of the curators of the herbaria cited for the loan of specimens. We express our gratitude to Dr. E.P. Geissler for critically reading the manuscript, to M.W. van Slageren for providing the SEM pictures of the sporophyte of *Symbiezidium*, and to T. Schipper for his usual inking of the pencil drawings.

References

BISCHLER, H. 1965. Recherches sur l'anatomie de la tige chez les Lejeuneaceae II. Les sous-familles Lejeuneoideae, tribu Ptychantheae, Nipponolejeuneoideae et Myriocoleoideae. Revue Bryol. Lichénol. 33: 399-458.

EVANS, A.W. 1900. Hawaiian Hepaticae of the tribe Jubuloideae. Trans. Conn. Acad. 10: 387-462.

EVANS, A.W. 1907. Hepaticae of Puerto Rico VIII. *Symbiezidium, Marchesinia, Mastigolejeunea, Caudalejeunea* and *Bryopteris*. Bull. Torrey Bot. Club 34: 533-568.

FULFORD, M. 1942. Studies on American Hepaticae IV. A revision of the genus *Symbiezidium*. Lloydia 5: 293-304.

GEISSLER, P. & GRADSTEIN, R. 1981. On a small collection of living Lejeuneaceae from Peru. Candollea 36: 119-130.

GEISSLER, P. & GRADSTEIN, S.R. 1982. SEM-studies on sporophyte characters in Lejeuneaceae (Ptychanthoideae), a preliminary report. J. Hattori Bot. Lab. 53: 127-131.

GOTTSCHE, C.M., LINDENBERG, J.B.G. & NEES VON ESENBECK, C.G. 1844-47. Synopsis Hepaticarum. Hamburg.

GRADSTEIN, S.R. 1975. A taxonomic monograph of the genus *Acrolejeunea*. Bryophyt. Bibl. 4: 1-162.

GRADSTEIN, S.R. & HEKKING, W.H. 1979. A catalogue of the Hepaticae of Colombia. J. Hattori Bot. Lab. 45: 93-144.

GRADSTEIN, S.R., MATSUDA, R. & ASAKAWA, Y. 1981. Oil bodies and terpenoids in Lejeuneaceae and other selected Hepaticae. J. Hattori Bot. Lab. 50: 231-248.

GRADSTEIN, S.R. & WEBER, W.A. 1982. Bryogeography of the Galapagos Islands. J. Hattori Bot. Lab. 52: 127-152.

GRADSTEIN, S.R., PÓCS, T. & VÁNA, J. 1983. Disjunct Hepaticae in tropical America and Africa. Acta Bot. Hung. 29: 127-171.

KUNTH, C.S. 1822. Synopsis Plantarum, quas....collegerunt Al. de Humboldt et Am. Bonpland. 1. Paris.

NEES VON ESENBECK, C.G. 1833. Hepaticae. In: C.F.Ph. de Martius, Flora Brasiliensis I: 295-390. Stuttgart & Tübingen.

SCHUSTER, R.M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae I. Introduction; annotated keys to subfamilies and genera. Nova Hedwigia Beih. 9: 1-203.

SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Jubuleae. Trans. Proc. Bot. Soc. Edinburgh 15: i-ix, 1-308.

STEARN, W.T. 1971. A survey of the tropical genera *Oplonia* and *Psilanthele* (Acanthaceae). Bull. Brit. Mus. Hist. Nat. 4: 259-323.

STEPHANI, F. 1890. Die Gattung *Lejeunea* im Herbarium Lindenberg. Hedwigia 29: 1-23, 68-99, 133-142.

STEPHANI, F. 1912. *Symbiezidium*. Spec. Hep. 5: 97-108. Geneva.

STOTLER, R.E. & CRANDALL—STOTLER, B. 1974. A monograph of the genus *Bryopteris* (Swartz) Nees von Esenbeck. Bryophyt. Bibl. 3: 1-159.

SWARTZ, O. 1788. Nova genera & species plantarum...Stockholm.

WEBER, F. 1815. Historia Muscorum Hepaticorum Prodromus. Kiel.

WINKLER, S. 1970. Zur Anatomie der Rhizoidplatten neotropischer Lejeuneaceen. Revue Bryol. Lichénol. 37: 47-55.

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Accepted names are set in roman type, synonyms in *italics;* names of taxa above the rank of genus are omitted. New names and combinations as well as the pages on which detailed treatments of accepted taxa begin are in **bold** type.