Tropical Bryology 3: 45-57, 1990

A Key to the New World species of holostipous Lejeuneaceae

S. Rob Gradstein
Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands

(Studies on Lejeuneaceae subfam. Ptychanthoideae XVIII)

Abstract. A synopsis and key emphasizing vegetative characters are provided for the 967species (in 36 genera) of Lejeuneaceae with undivided underleaves recorded from the New World.

In practical Lejeuneaceae taxonomy traditionally two main groups of species are recognized: 'holostipous' Lejeuneaceae, characterized by the presence of undivided underleaves, and 'schizostipous' Lejeuneaceae, characterized by bifid underleaves (Spruce 1884). In addition, 'astipous' Lejeuneaceae may be recognized, which lack underleaves. Though unnatural, polyphyletic groups, the subdivision into holostipous, schizostipous and astipous Lejeuneaceae remains useful today for identification purposes.

The present Key to the New World species of holostipous Lejeuneaceae was prepared in the course of my monographic work on ptychanthoid Lejeuneaceae for FLORA NEOTROPICA and is a sequel to my generic key to the holostipous Lejeuneaceae of the World (Gradstein 1985a, 1987, in prep.). In all, 97 species in 36 genera are included. A few schizostipous taxa with shallowly bifid underleaves, resembling the holostipous condition, are also included: *Cheilolejeunea fragrantissima, Lepidolejeunea eluta, Cyrtolejeunea venezuelana, Omphalanthus jackii* and *Taxilejeunea sulphurea.*

The Key emphasizes vegetative characters to facilitate the identification of sterile material. Important sources for species descriptions and keys to individual genera are referred to in the Synopsis. The data on distribution and ecology are based on the literature as well as on the author's unpublished field observations. Life zone definitions for the neotropics follow Prance (1989) and Frahm & Gradstein (in press) and are as follows (the altitudes given are *approximations* for continental equatorial regions and may become lower with increasing latitude and on islands): *lowlands*, up to 300-500 m.; *submontane*, up to 1000-1400 m.; *lower montane*, up to 1800-2400 m.; *upper montane*, up to 3000-3400 m.; *subalpine*, up to the tree line; *alpine.* Species which occur throughout the lower and upper montane belts are *montane* species.

Synopsis of the New World species of holostipous Lejeuneaceae

PTYCHANTHOIDEAE

Acanthocoleus aberrans, juddii (Kruijt 1988)

Acrolejeunea emergens, heterophylla,

torulosa (Gradstein 1975)

Archilejeunea auberiana, crispistipula, fuscescens, parviflora, porelloides (Gradstein & Buskes 1985, Gradstein 1987)

Blepharolejeunea chimantaensis, fuegiana, incongrua, saccata, securifolia (van Slageren & Kruijt 1985)

Brachiolejeunea fernandeziana, laxifolia, leiboldiana, phyllorhiza, spruceana (van Slageren 1985, Kruijt & Gradstein 1986)

Bryopteris diffusa, filicina, flaccida (Stotler & Crandall-Stotler 1974, Gradstein in prep.)

Caudalejeunea lehmanniana (Schuster 1980)

Dicranolejeunea axillaris (Kruijt 1988)

Frullanoides bahamensis, corticalis, densifolia, laciniatiflora, liebmanniana, mexicana (van Slageren 1985, Gradstein in prep.)

Lindigianthus cipaconeus (Kruijt & Gradstein 1985)

Lopholejeunea eulopha, muelleriana, quelchii, subfusca (Schuster 1980, Gradstein in prep.)

Marchesinia brachiata, robusta (Geissler in prep.)

Mastigolejeunea auriculata, plicatiflora (Gradstein in prep.)

Neurolejeunea breutelii, catenulata, sastreana, seminervis (Gradstein in prep.)

Odontolejeunea decemdentata, lunulata, rhomalea (Teeuwen 1989)

Schiffneriolejeunea amazonica, polycarpa (Gradstein 1985a, in prep.)

Spruceanthus theobromae (Gradstein 1985a)

Stictolejeunea balfourii, squamata (Gradstein 1985b)

Symbiezidium barbiflorum, dentatum, transversale (Gradstein & van Beek 1985)

Thysananthus amazonica, evansii, pterobryoides (Fulford 1941, Gradstein in prep.)

Verdoornianthus griffinii, marsupiifolius (Gradstein 1978)

LEJEUNEOIDEAE

Amblyolejeunea fulfordiae (Jovet-Ast 1948)

Amphilejeunea catinulifera, patellifera, viridissima (Schuster 1986)

Anoplolejeunea conferta (Evans 1908)

Aureolejeunea aurifera, fulva, lumae, paramicola, quinquecarinata (Schuster 1986, 1987)

Ceratolejeunea (subgen. *Ceratophora*) *desciscens, globulifera, grandiloba, lechleriana* (Fulford 1945, Grolle 1987)

Cheilolejeunea fragrantissima (Spruce 1884)

Cyclolejeunea convexistipa (Evans 1904, Grolle 1984)

Cyrtolejeunea antillana, holostipa, inermis, saccatiloba, venezuelana (Schuster 1970, 1978, Gradstein & Buskes 1985)

Lejeunea reflexistipula (Spruce 1884)

Lepidolejeunea eluta, spongia (Piippo 1986)

Leucolejeunea clypeata, conchifolia, unciloba, xanthocarpa (Schuster 1980)

Luteolejeunea herzogii (Piippo 1986)

Omphalanthus filiformis, huanucensis, jackii, ovalis, platycoleus, wallisii (Gradstein et al. 1981, Gradstein & Buskes 1985)

Physantholejeunea portoricensis (Fulford 1945 sub *Ceratolej.*, Schuster 1978)

Taxilejeunea sulphurea

Key to the New World species of holostipous Lejeuneaceae

1. Leaf margin toothed, at least near apex.....2
1. Leaf margin entire.....19

2. Ventral stem surface only 2(-3) epidermis cells wide above or below the

underleaf insertion area.....3
2. Ventral stem surface 4 or more cells wide throughout 12

3. Underleaves toothed ..... **.....Odontolejeunea** (Spruce) Schiffn. 4
3. Underleaves entire.....5

4. Leaves revoluted when dry, the cells orientated in transverse rows extending from dorsal to ventral leaf margin; lobule with (3-)4-6 teeth. South and Central America, on living leaves or twigs in submontane and montane rain forest (rarely lowlands), uncommon..... .....**O. rhomalea** (Spruce) Steph.
4. Leaves irregularly crisped-convoluted or +/- plane when dry, not revoluted, the cells orientated in longitudinal rows (as usual in Lejeuneaceae) extending from leaf base to apex; lobule with 2-4 teeth. Throughout tropical America (also in Africa), on living leaves or bark in lowland and montane forest, very common.....**O. lunulata** (Web.) Schiffn.

5. Ocelli present: scattered, in a short row or 1-2 near leaf base.....6
5. Ocelli lacking.....9

6. Plants pale-green; discoid gemmae may be produced on leaf margins; perianth strongly toothed, without horns. Throughout tropical America, on living leaves, bark or rock in lowland and montane forest, common..... **.....Cyclolejeunea convexistipa** (Lehm. & Lindenb.) Evans
6. Plants brown; discoid gemmae lacking; perianth without teeth, the apex with four horn-like extensions..... **Ceratolejeunea** (Spruce) Schiffn. (subg. *Ceratophora)* 7

7. Plants blackish-brown, ca. 2 mm wide; underleaves 3-4x stem width; ocelli present in leaves and also in underleaves (R. Grolle, in litt.). Tropical Andes, montane and subalpine.....**C. grandiloba** Jack & Steph.
7. Plants lighter brown, smaller, 1-1.5 mm wide; underleaves 2x stem width.....8

8. Apex of female bracteole broadly rounded, undivided; branch base usually with a huge, inflated lobule ('utricle'). Tropical Andes, lower montane.....**C. globulifera** Herz.
8. Apex of female bracteole narrow, shallowly bifid; utricles lacking. Peru.....**C. lechleriana** Steph.

9. Underleaves very large, 6-10x stem width, at apex short bifid or notched; lobule minute; perianth smooth cylindrical. Throughout tropical America, submontane - montane, on bark in moist forest..... **Taxilejeunea sulphurea** (Lehm. & Lindenb.) Schiffn..

9. Underleaves smaller, apex undivided 9a

9a. Leaves with (5-)7-25 teeth; underleaves often producing a large, circular disc formed by coalesced rhizoids; plants usually epiphyllous..... **Odontolejeunea** (Spruce) Schiffn. 10
9a. Leaves with 1-7 teeth; rhizoid disc lacking; not epiphyllous.....11

10. Underleaf bases auriculate, with a sharp 'spur'; lobule with 2-4 teeth. Throughout tropical America, on living leaves or bark in lowland and montane forest, very common..... **.....O. lunulata** (Web.)

Schiffn.

10. Underleaf bases cuneate, spur lacking; lobule with 0-1(-2) teeth or reduced. Throughout tropical America, on living leaves or twigs in lowland and lower montane rain forest, uncommon...**O. decemdentata** (Spruce) Steph.

11. Lobule at least 1/2x leaf length; underleaf insertion straight; leaves strongly falcate; small (1-2 cm long) creeping plants. Cuba, Costa Rica, Ecuador, on bark at lower montane elevations, uncommon ..... **Blepharo-lejeunea saccata** (Steph.) van Slag. & Kruijt

11. Lobule up to 1/3x leaf length, sometimes reduced; underleaf insertion arched; leaves not or slightly falcate.....49

12. Leaf cells longer than wide, with small cordate trigones having 2 sides convex and 1 side concave.....13

12. Leaf cells isodiametric, the trigones various but not cordate.....16

13. Underleaves entire; perianth 8-10-keeled, on an elongated shoot with 2 innovations. High Andes of Peru .....**Frullanoides laciniatiflora** (Loitl.) van Slag.

13. Underleaves toothed; perianth 3-keeled, on a short lateral branch without innovations. Widespread in submontane and lower montane forests..... **Bryopteris** (Nees) Lindenb. 14

14. Branching dichotomous; lobule with several large teeth. Throughout tropical America, uncommon.....**B. diffusa** (Sw.) Nees

14. Branching +/- pinnate; lobule with 1 small tooth.....15

15. Leaves distinctly toothed, at least near apex. Throughout the neotropics, very common.....**B. filicina** (Sw.) Nees s.l.

(including *B. fruticulosa* Tayl., *B. liebmanniana* Lindenb. & Gott. and *B. trinitensis* (Lehm. & Lindenb.) Lehm. & Lindenb.)

15. Leaves entire or with a few small teeth. Central America, Brazil, uncommon..... **B. flaccida** Lindenb. & Hampe.

16. Underleaves toothed; leaf cells evenly thick-walled, trigones and intermediate thickenings lacking or obscure; leaves coarsely dentate. Northern Andes and Central America, in submontane rain forest ..... **Thysananthus pterobryoides** (Spruce) Schiffn.

(a form with finely dentate-denticulate leaves from Belize has been described as *T. evansii* Fulf.)

16. Underleaves entire; leaf cells with discrete trigones and intermediate thickenings 17

17. Leaf apex broadly recurved; cell walls colorless; epidermal cells thin-walled; lobule ca. 1/3x leaf length. Northern Andes and Costa Rica, above 2000 m., on shrubs, tree ferns and litter in humid environments .....**Lindigianthus cipaconeus** (Gott.) Kruijt & Gradst.

17. Leaf apex plane; cell walls often with blackish pigmentation; epidermal cells thickened; lobule smaller; usually below 2000 m.....18

18. Lobule plane, with 2-4 teeth spaced regularly along the free margin; epidermal cells not larger than inner stem cells. Throughout tropical America, on bark or rock at submontane and lower montane elevations, very common... .....**Marchesinia brachiata** (Sw.) Schiffn.

18. Lobule inflated-rounded, teeth lacking or obscure; epidermal cells larger than inner cells. Pacific coast of Colombia and northern Ecuador, on bark in lowland rain forest .....**Symbiezidium dentatum** Herz.

(= *S. transversale* subsp. *dentatum* (Herz.) Gradst. & van Beek)

19. Leaves with ocelli.....20
19. Ocelli lacking.....27

20. All ocelli of the leaf arranged in a row, forming a vitta (=nerve).....21
20. Ocelli scattered through the leaf.....23

21. Vitta up to 5 cells long; ventral stem surface only 2(3) cells wide; lobule tooth 1 cell long. Northern South America, in lowland forest.....**Ceratolejeunea desciscens** (Sande Lac.) Schiffn.
21. Vitta 7-22 cells; ventral stem surface 4-6 cells wide; lobule tooth 3-5 cells long . . . . . **.....Neurolejeunea** (Spruce) Schiffn. 22

22. Leaf apex (at least on younger, branch leaves) capped by a whitish border of thin-walled cells in 2-4 rows, border fragile and breaking off in older leaves (leaf apex then becoming irregularly crenate); leaves oblong, 1,5-2x longer than wide. West Indies..... .....**N. catenulata** (Nees) Schiffn.
22. Leaf apex entire, lacking a whitish border; leaves ovate, less than 1.5x longer than wide. Northern South America, Guatemala, in the canopy of lowland rain forest and on bushes .....**N. seminervis** (Spruce) Schiffn.

23. Ventral stem surface 4 or more cells wide; *Frullania*-type branching present or lacking .....**Stictolejeunea** (Spruce) Schiffn. 24
(*Lepidolejeunea eluta* (Nees) Schust. might also key out here. This species has underleaves shallowly bifid however, up to 0,1-0,2 of their length; furthermore, lobules are rather large, ca. 1/3x lobe length, the leaf apex is acute and the cells are very thin-walled).
23. Ventral stem surface 2 cells wide; *Frullania*-type branching lacking.....25

24. Underleaves wider than long, (3)4-10 x stem width; vegetative branches always of the *Frullania*-type; plants 1,2-2,5 mm wide, creeping or pendent, when pendent regularly (bi-)pinnate, when creeping irregulay branched. Common epiphyte in lowland and lower montane rain forests.....**S. squamata** (Willd. ex Web.) Schiffn.
24. Underleaves suborbicular, 2-3 x stem width; vegetative branches of the *Lejeunea*-type (rarely a *Frullania*-type branch present); plants smaller, 1-1,3 mm wide, creeping, irregularly branched. Peru, Colombia, Guianas, in the shaded understorey of lowland rain forest (on tree bases, roots), usually near running water, often overlooked.....**S. balfourii** (Mitt.) E.W. Jones

25. Underleaves orbicular, 2-3x stem width; leaf apex often with a whitish group of dead cells; plants small, ca. 1 mm wide. West Indies.....**Physantholejeunea portoricensis** (Hampe & Gott.) Schust.
25. Underleaves reniform, large, 6-10x stem width; leaf apex lacking a whitish group of dead cells; plants 1-2 mm wide..... 26

26. Stem fragile, the cell walls thin; lobule 'normal' in position (opening oriented toward leaf apex), the keel forming an angle of 50-90° with the stem; ocelli +/- equal in size to ordinary leaf cells or smaller, rather inconspicuous; trigones lacking. Northern Andes, Cuba, in the canopy of montane rain forest or on shrubs..... .....**Lepidolejeunea spongia** (Spruce) B. Thiers
26. Stem rigid, the walls thickened; lobule curved downwards, the keel forming an angle of 120-140° with the stem; ocelli mostly larger than leaf cells; trigones well-developed. Pacific side of northern South America and Panama, in lowland and lower montane forest.....**Luteolejeunea herzogii** (Buchloh) Piippo

27. Leaf cells more or less longer than wide, with cordate trigones having 2 side convex and 1 side concave; leaves when dry convoluted (weakly so in *Caudalejeunea*, couplet 50).....28
27. Leaf cells isodiametric (elongated in *Neurolejeunea*, couplet 54, and *Spruceanthus*, couplet 71), the trigones various but not cordate; leaves when dry spreading, curved down or folded but not convoluted.....52

28. Lobule with 3-10 teeth (teeth sometimes inflexed and inconspicuous).....29
28. Lobule with 1-2 teeth.....38

29. Epidermis cells +/- thick-walled, surrounding a thin-walled medulla; lobule with 3-4 teeth; perianth with 3 keels and 2 innovations; paroicous. In tropical America only above 1500 m., in southern South America reaching sea level.....**Brachiolejeunea** (Spruce) Schiffn. 30
(see also couplet 51 for species of *Brachiolejeunea* with predominantly 2 lobule teeth)
29. Epidermis cells +/- thin-walled (especially dorsally), surrounding a thicker-walled medulla; lobule with 3-10 teeth; perianth with 5-10 keels or plicae, with or without innovations. Throughout tropical America, lowlands or submontane, lacking in southern South America.....32

30. Dorsal stem surface with a 1-4 cells high lamellate paraphyllium. Common at high elevations (2000-3500 m.) in tropical America, on bark or rock.....**B. laxifolia** (Tayl.) Schiffn.
30. Paraphyllium lacking; temperate southern South America 31

31. Lobule with 4 teeth. Juan Fernandez islands.....**B. fernandeziana** S. Arn.
31. Lobule with 3 teeth. S. Argentina and Chile: Valdivia to Tierra del Fuego.....**B. spruceana** (Mass.) Schiffn.

32. Cell walls in older leaves usually with darkish pigmentation, the plants turning blackish; innovations present; flagelliform shoots lacking. Lowlands and montane .....**Frullanoides** Raddi 33
32 Cell walls lacking darkish pigmentation, the plants turning (yellowish-)brown; innovations lacking; caducous leaves may be produced on flagelliform shoots. Lowlands only, rather xerophytic.....**Acrolejeunea** (Spruce) Schiffn. 36

33. Leaf apex acute-apiculate or (narrowly) rounded; underleaves distinctly auriculate (auricles 0.1-0.3 mm long, appressed to the stem), the insertion line deeply arched. Tropical South America, Costa Rica, Mexico, on bark or rock, montane.....**F. densifolia** Raddi
33. Leaf apex broadly rounded; underleaves not or weakly auriculate (auricles less than 0.15 mm long), the insertion line straight or curved 34

34. Underleaves auriculate; plants 1.5-3 mm wide; lobule with 4-11 teeth. Submontane and montane.....34a
34. Underleaves not auriculate; plants smaller, 1-1.6 mm wide; lobule with 4-6 teeth. Lowlands and submontane, up to 600 m, mainly in coastal areas.....35

34a. Lobule with 4-8 teeth consisting of more than one cell. Widespread .....**F. liebmanniana** (Gott. & Lindenb.) van Slag. (= *F. tristis* (Steph.) van Slag.)
34a. Lobule with 8-11 teeth consisting of only one cell. Southern Mexico, Honduras.....**F. mexicana**

van Slag.

35. Lobule teeth 1-2 cells long, the first tooth situated in the sinus, at the junction with the ventral leaf margin; usually dioicous; male bracts hypostatic. Widespread.....**F. corticalis** (Lehm. & Lindenb.) van Slag.
35. Lobule teeth 3 cells long, the first tooth not situated in the sinus; monoicous; male bracts epistatic. Bahamas, Cuba, Florida ..... **F. bahamensis** (Evans) van Slag.

36. Lobule with 3-4 teeth, the first tooth erect. Mainly northern S. America, uncommon .....**A. emergens** (Mitt.) Steph.
36. Lobule with 5-8 teeth, the first tooth erect, inflexed or outwardly curved.....37

37. First tooth of the lobule longer than the other teeth, 2-4 cells long. Common in northern South America.....**A. torulosa** (Lehm. & Lindenb.) Schiffn.

(when vegetative, *A. torulosa* might be confused with unpigmented phases of *Frullanoides corticalis*. The latter species is recognized, however, by the presence of a small, 'extra' tooth beyond the apical tooth of the lobule, located in the sinus at the junction of the keel and the ventral leaf margin).

37. First tooth of the lobule not longer than the other teeth, consisting of only 1 rounded cell; Florida, Mexico, northern Central America, rare.....**A. heterophylla** (Evans) Grolle & Gradst.

38. Underleaves toothed. Central America, Brazil, uncommon .....**Bryopteris flaccida** Lindenb. & Hampe
38. Underleaves entire.....39

39. Ventral epidermal cells not larger than inner stem cells (cross section). Plants of lower elevations (below 1500 m.) 40
39. Ventral epidermis cells larger than inner cells. High or low elevations 43

40. Lobule with (1-)2 teeth; cell walls colorless, plants turning brown; innovations lacking.....**Schiffneriolejeunea** Verd. 41
40. Lobule with 0-1 teeth; cell walls of older leaves normally with darkish pigmentation, plants turning blackish; 1-2 innovations present.....42

41. Lobule ovate, 1/3-2/5x leaf length; perianth with 2 short, broadly rounded ventral keels; lobule of inner female bract shorter than lobe. Widespread but rare in humid equatorial regions, mainly in coastal areas..... .....**S. polycarpa** (Nees) Gradst.
41. Lobule narrow rectangular, 1/2-3/5 x lobe length; perianth with 2 long, sharp ventral keels; lobule of inner female bract as long as the lobe. Amazonia, Guianas, in lowland savannas, bushes and tree crowns, uncommon..... .....**S. amazonica** Gradst.

42. Underleaf apex rounded or truncate; dorsal epidermis cells larger than inner stem cells (cross section); plants creeping; female involucre and perianth lacking teeth; dioicous or autoicous. Widespread..... **Mastigolejeunea auriculata** (Wils.) Schiffn.

(a form from Amazonia with pluriplicate perianths has been described as *M. plicatiflora* (Spruce) Steph.)

42. Underleaf apex retuse; dorsal epidermis cells not larger than inner cells; plants creeping or pendent; female involucre and perianth ± toothed; paroicous. Northern South America, Cuba, in lowland rain forest... ..... **Thysananthus amazonicus** (Spruce) Schiffn.

43. Lobule never reduced, the apex

truncate, with 2 dissimilar teeth, the second tooth usually more conspicuous than the first one: first tooth situated in the sinus, incurved and blunt, second tooth situated at lobule angle, sharp, pointing outwards. In tropical America above 1500 m., in southern Chile at sea level.. .....**Blepharolejeunea** S. Arn. 44

43. Lobule reduced or well-developed, the apex rounded, oblique or subtruncate, the teeth equal or the first tooth more conspicuous. Lowland or montane.....47

44. Keel +/- straight; second lobule tooth very long (ca. 6-10 cells) and curved. Southern Chile.....**B. fuegiana** (Besch. & Mass.) Gradst.

44. Keel arched; second tooth shorter; tropical America.....45

45. First lobule tooth consisting of one enlarged margin cell; female bracteole as long as the bracts, strongly concave; leaves strongly concave, the apex broadly rounded. Guayana Highlands (Macizo del Chimantá)..... **B. chimantaensis** van Slag. & Kruijt

45. First lobule tooth 2-3 cells long, often incurved (when incurved seemingly consisting of only one cell!); female bracteole shorter than the bracts, plane or concave above; leaves plane or concave, the apex narrowly rounded, obtuse or apiculate.....46

46. Lobule bordered by enlarged margin cells; perianth up to 1 mm long, the lateral keels sharp, entire or ciliate; lobule of female bract small, less than 1/3x lobe length. Central and South America, 2000-4100 m., on bark in open vegetations.....**B. incongrua** (Lindenb. & Gott.) van Slag. & Kruijt

46. Lobule margin cells not enlarged; perianth over 1 mm long, the lateral keels broadly rounded, entire; lobule of female bract larger, 1/2-2/3x lobe length. Above 3000 m. in Central and South America, on bark or rock.. ....**B. securifolia** (Spruce) Schust.

47. Ventral stem surface 2 epidermis cells wide (outside leaf insertion area).....48

47. Ventral stem surface 4 epidermis cells wide (by exception 2 cells wide in *Brachiolejeunea phyllorhiza*, couplet 51).....50

48. Lobule 1/2-2/3x lobe length, the first tooth very large, 3-6 cells long. Greater Antilles, Mexico, ca. 1000-2500 m., on rock .....**Acanthocoleus juddii** Kruijt

48. Lobule smaller, the first tooth 0-2 cells long.....49

49. Branches predominantly *Frullania*-type; epidermis cells thin-walled, bulging outwards; female bracteole toothed. Common at submontane and montane elevations, on bark, rock or soil in open habitats, often weedy.... .....**Dicranolejeunea axillaris** (Nees & Mont.) Schiffn.

49. Branches predominantly *Lejeunea*-type; epidermis cells +/- thick-walled, not bulging outwards (stem surface smooth); female bracteole entire. Widespread, submontane and lower montane (300-2500 m), on bark or rock, in open habitats and tree crowns..... **Acanthocoleus aberrans** (Lindenb. & Gott.) Kruijt

50. Leaves not squarrose when moist; *Frullania*-type branches lacking; intermediate thickenings numerous, 1-3 per cell wall; innovations lack-ing; perianth with 4-5 keels. Widespread in lowland areas, on leaves or twigs ..... **Caudalejeunea lehmanniana** (Gott.) Evans

50. Leaves squarrose when moist, when dry strongly convoluted; *Frullania*-type branches usually present; cell walls with 0-1 intermediate thickenings; innovations

present; perianth with 3 keels.....**Brachiolejeunea** (Spruce) Schiffn..51

51. Stem dorsally with a 1 cell high lamellate paraphyllium; lateral perianth keels rounded, smooth; dioicous? (males unknown). Through-out tropical America at lower montane elevations (800-2000 m.), on bark or rock in sunny habitats, uncommon ..... **B. leiboldiana** (Gott. & Lindenb.) Schiffn.
51. Paraphyllium lacking; lateral perianth keels sharp, dentate-ciliate or (rarely) smooth; autoicous, male bracts on short-specialized *Lejeunea*-type branches. Throughout tropical America at submontane and lower montane elevations (300-2000 m.), on bark or rock in sunny habitats, rather common..... .....**B. phyllorhiza** (Nees) Kruijt & Gradst.

52. Ventral stem surface 4 or more cells wide (outside underleaf insertion area) 53
52. Ventral stem surface 2 cells wide.....83

53. Leaf cells small, ca. 10-20 µm, without or with obscure trigones; lobule usually conspicuously darker than lobe, flask-shaped; perianth keels at apex expanded into auricles; plants small, less than 1,5 mm wide, usually blackish....**Neurolejeunea** (Spruce) Schiffn. 54
53. Leaf cells larger, usually with distinct trigones; lobule not conspicuously darker than lobe; perianth keels not expanded into auricles.....55

54. Lobule apex with a long, sharp, curved tooth. Throughout tropical America, 0-2000(3000) m., on bark or rock..... .....**N. breutelii** (Gott.) Evans
54. Lobule apex with a very large, rounded, hyaline 'papilla-like' cell protruding upwards beyond the free margin. West Indies (mainly Puerto Rico), Venezuela, 0-1500 m., on bark.....**N. sastreana** Gradst.

55. Lobule with 2-4 teeth 56
55. Lobule with only one tooth or tooth lacking 60

56. Lobule well-developed, the apex truncate, with 2 dissimilar teeth, the second tooth more conspicuous than the first tooth: first tooth situated in the sinus, incurved and blunt, second tooth situated at lobule angle, sharp, pointed outwards 57
56. Lobule reduced or well-developed, the apex rounded, oblique or subtruncate, the teeth identical or the first tooth more conspicuous 58

57. Plants whitish to pale grayish-green; lobule about 2x longer than wide; *Frullania*-type branches lacking; autoicous; androecia on short, specialized branches. Lowland and lower montane..... **Leucolejeunea unciloba** (Lindenb.) Evans 63
57. Plants darker, greenish-brown to dark brown; lobule 1-1.5x longer than wide; *Frullania*-type branches present; paroicous; androecia on main stem or on long, unspecialized branches. Montane-alpine (above 1500 m.), in southern Chile at sea level..... .....**Blepharolejeunea** S. Arn. 44

58. Lobules sometimes reduced, when well-developed rectangular, with 2 teeth at apex; underleaves 3-4,5 x stem width, the insertion line straight; plants 1-2 mm

wide, greenish to yellowish-brown; perianth inflated, with 2 ventral keels. Lowland and submontane (0-1000 m) .....**Archilejeunea auberiana** (Mont.) Evans (= *A. parviflora* var. *florentissima* (Spruce) Gradst. & Buskes)
58. Lobules never reduced, ovate-trapezoidal, with 2-4 teeth regularly spaced along the free margin; underleaves 4-10 x stem width, the line of insertion deeply arched; plants rather robust, usually more than 2 mm wide, often blackish; perianth flattened, without ventral keels. Submontane and montane, lacking in lowlands.....**Marchesinia** S.Gray 59

59. Underleaf margin entire. Throughout tropical America, submontane and montane, on bark, rock or soil.....**M. brachiata** (Sw.) Schiffn.
59. Underleaf margin dentate. Tropical South and Central America, montane ....**M. robusta** (Mitt.) Schiffn.

60. Plants whitish, pale yellowish or grayish, growing appressed on bark or rock in rather exposed habitats.....**Leucolejeunea** Evans 61
60. Plants darker, green, brown or blackish, growing appressed or free from the substrate in sheltered or exposed habitats 64

61. Ventral leaf margin strongly involuted 62
61. Ventral leaf margin plane or slightly upcurved 63

62. Lobule tooth 4-6 cells long, clearly visible *in situ*; plants 0.7-1.2(1.5) mm wide. Southeastern U.S.A., 0-1000 m., on bark.....**L. conchifolia** (Evans) Evans
62. Lobule tooth 1-4 cells long, usually invisible *in situ* (because of the involuted leaf margin); plants larger, 1.1-2 mm wide. Throughout tropical America, also in southern Florida, lowlands and lower montane, on bark or rock..... **L. xanthocarpa** (Lehm. & Lindenb.) Evans

63. Lobule tooth 3-7 cells long; underleaves 3-5x stem width; plants 1.5-2.5 mm wide. Throughout tropical America, also in southeastern U.S.A., usually in coastal areas, lowland and lower montane, on bark or rock..... .....**L. unciloba** (Lindenb.) Evans
63. Lobule tooth 1-2 cells long; underleaves 2-2.5x stem width; plants 1-1.6 mm wide. Eastern U.S.A, on bark and often on rock ....**L. clypeata** (Schwein.) Evans

64. Epidermis cells larger than inner stem cells (cross section); plants often blackish; perianth keels dentate-laciniate.....65
64. Epidermis cells not larger than inner cells; plants not blackish (except sometimes *Archilej. parviflora*, couplet 71); perianth keels smooth or denticulate.....69

65. Plants (1.5-)2-5 mm wide; perianth on a very short shoot (appearing lateral on the stem), with one short innovation; lobule very small, 1/10-1/4x leaf length, strongly inflated-saccate; underleaves 5-10x stem width; leaves often different in length on opposite sides of the stem..... .....**Symbiezidium** Trevis. 66
65. Plants smaller, 1-2 mm wide; perianth on an elongated shoot, usually without innovations; lobule 1/3-1/2x leaf length or reduced, inflated or partly flattened, when reduced ± flattened; underleaves 2-5x stem width (sometimes broader, couplet 68!); leaves uniform in length.....**Lopholejeunea** (Spruce) Schiffn. 67

66. Plants 2-2.5(-3) mm wide; ventral surface of perianth rough due to spines or laciniae, which are distributed randomly

as well as (sometimes) in 1-2 rows. Throughout tropical America, 0-2000(2800) m., on bark in forests.. .....**S. barbiflorum** (Gott.) Evans

66. Plants 2.5-5 mm wide; ventral surface of perianth entirely smooth or with a few spines and laciniae arranged in 1-2 rows (never randomly distributed). Distribution as *S. barbiflorum* but usually at lower altitudes (not found above 1700 m.).....**S. transversale** (Sw.) Trevis.

(plants with 1-2 longitudinal rows of spines/laciniae on the ventral surface of the perianth have been described as *S. transversale* var. *hookerianum* (Gott.) Gradst. & van Beek)

67. Underleaves about 2x wider than long (length measured from rhizoid disc to apex), 5-10x stem width; female bracteole toothed.....67a

67. Underleaves 1-1.5x wider than long, 2-5x stem width; female bracteole entire 68

67a. Leaf apex recurved in all leaves; lobule of female bracts more than 1/2x lobe lenght, strongly toothed-laciniate. Guyana, on bark in lowland rain forest..... .....**L. eulopha** (Tayl.) Schiffn. (This widespread palaeotropical species is recorded here for the first time from the New World. Collections seen: Guyana, Mabura Hill, 0-50 m, in dry evergreen rain forest, on trunk base and lower canopy branch of *Eperua grandiflora*, H. Cornelissen & H. ter Steege C579, C807, det. S.R.Gradstein & B. Bleij, herb. U).

67a. Leaf apex plane or slightly recurved in a few leaves; lobule of female bracts 1/4-1/2x lobe length, entire or with 1-2 short teeth. West Indies, Guianas, on bark in lowland rain forest.....**L. quelchii** Steph. (= *L. howei* Evans)

68. Female bracteole very large, broader than long, entirely covering the immersed (rarely emergent), strongly laciniate perianth; plants always growing in dense, low mats; leaf apex rounded; small, recurved microphyllous branches usually originating from lower stem portions; dorsal epidermal cells as large as the ventral epidermal cells (stemcross section). Throughout tropical America, lowland-submontane, on bark or rock .....**L. subfusca** (Nees) Steph.

68. Female bracteole smaller, longer than broad or orbicular, perianth always emergent, weakly toothed-laciniate; plants growing in loose mats; leaf apex acute or rounded; microphyllous shoots lacking; stem usually with 1-2 dorsal epidermal cells smaller than the ventral epidermal cells. Throughout tropical America, sub-montane-lower montane, occasionally in lowlands, on bark or rock..... .....**L. muelleriana** (Gott.) Schiffn.

69. Leaf cells with frequent intermediate thickenings (1-3 per cell), trigones radiate; hyaline papilla proximal of the apical tooth of the lobule; male bracteoles present throughout the male spike. Plants of lowland (and submontane) forests.....70

69. Intermediate thickenings lacking or very few (0-1 per cell), trigones usually large and bulging, not radiate; 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. Plants of mountain forests and páramos.....76

70. All or at least some lobules reduced to a small fold (or +/- lacking); innovations *lejeuneoid* (first leafy appendage at base of the innovation is a lateral leaf) 71

70. Lobules well-developed, not showing a tendency for reduction; innovations *pycnolejeuneoid* (first leafy appendage is an underleaf) or lacking.....72

71. Leaf cells distinctly elongated, about 2x longer than wide; plants robust, ca. 3 mm wide; ventral stem surface ca. 12 cells wide. Pacific coast of Ecuador, on bark of cacao tree (only known from the type)..... **Sprucean-**

thus theobromae (Spruce) Gradst.
71. Leaf cells isodiametric; plants smaller, 1-2 mm wide; ventral stem surface 4-6 cells wide. Throughout tropical America (but rare in Amazonia), in moist lowland and submontane forests (0-1500 m.), on bark or rock.....**Archilejeunea parviflora** (Nees) Gradst.

72. Plants glossy brownish; leaves when moist widely spreading, not squarrose; free margin of the lobule plane; innovations 1-2; dioicous..... **Archilejeunea** (Spruce) Schiffn. (subg. *Archilej*.) 73
72. Plants dull brownish; leaves when moist suberect, not spreading widely, ± squarrose; free margin of the lobule at least in part involuted; innovations lacking; autoicous..... .....**Verdoornianthus** Gradst. 75

73. Underleaf margins undulate; ventral leaf margin auriculate at the junction with the keel. Epiphyte in periodically inundated forests of inner Amazonia ....**A. crispistipula** (Spruce) Steph.
73. Underleaf margins plane; ventral leaf margin not auriculate.....74

74. Plants robust, 2-3 mm wide; underleaves longer than wide to orbicular; lobule apex triangular, lacking a discrete tooth. Epiphyte in lowland rain forests of inner Amazonia..... .....**A. porelloides** (Spruce) Schiffn.
74. Plants smaller, 1-2 mm wide; underleaves wider than long or (in small plants) orbicular; lobule apex with 1 tooth. Common epiphyte in rain forests of northern South America..... **A. fuscescens** (Hampe) Fulf. (= *A. juliformis* (Nees) Gradst.)

75. Lobule ovate, ca. 1.2x longer than wide, the apex folded inwards and the tooth therefore invisible *in situ*. Northern Amazonia, on bark, uncommon.....**V. marsupiifolius** (Spruce) Gradst.
75. Lobule rectangular, ca. 2x longer than wide, the apex plane, the tooth clearly visible. Amazonia, Guianas, in tree crowns and on shrubs.....**V. griffinii** Gradst.

76. Lobules subquadrate-trapezioid, 1/4-1/3x lobe length; plants usually pendent, with simple or sparingly branched stems, green or pale yellowish-brown in color; perianth with 0-5 keels. Throughout the mountains of tropical America, common.....**Omphalanthus** Nees 77
76. Lobules oblong-rectangular, 2/5-1/2x lobe length; plants creeping or +/- ascending, with shorter, irregularly branched stems, brownish in color (golden green to light brown in *A. fulva*, couplet 82); perianth with 3-10 keels. Tropical Andes, Guayana Highlands, above 2000 m., also in southern Chile, on bark, uncommon.....**Aureolejeunea** Schust. 80

77. Leaf apex narrow, (sub)acute to acuminate; underleaves normally longer than wide; perianth with 5 keels and a long (8 cells) beak.....78
77. Leaf apex broader, rounded to subobtuse; underleaves wider than long (rarely longer than wide); perianth with or without keels, beak shorter or lacking.....79

78. Leaf apex (sub)acute; underleaves undivided. Widespread lower montane..... .....**O. ovalis** (Lindenb. & Gott.) Gradst.
78. Leaf apex acuminate; underleaves short bifid. Peru, Ecuador, Galapagos Is., uncommon.....**O. jackii** (Steph.) Gradst.

79. Underleaf apex widely recurved; free margin of the lobules inrolled near the

base. Peru (?), only known from the type..... .....**O. huanucensis** (Gott.) Gradst.

79. Underleaf apex ± plane, free margin of the lobule not inrolled. Very common throughout the mountains of tropical America..... .....**O. filiformis** (Sw.) Nees

(*O. filiformis* by its cylindrical, eplicate perianth differs from *O. platycoleus* Herz., which has a 3-4-keeled perianth, and from *O. wallisii* (Steph.) Gradst., which has a 5-keeled perianth. The status of the latter two species, which have been reported a few times from the northern Andes and Central America, has not yet been clarified).

80. Leaf cells strongly mamillose-papillose; leaf margins crenulate. Venezuela, Colombia (?), on bark in páramo, above 3500 m .....**A. aurifera** Schust.

(*A. lumae* (Herz.) van Slag. from southern Chile differs from *A. aurifera* in the 10-plicate perianth and less strongly papillose cells).

80. Leaf cells +/- smooth; leaf margins entire 81

81. Perianth pluriplicate, with 3-5 ventral keels; innovations 2; plants rather robust, ascending from the substrate. Colombia, Venezuela, Guyana, (2300)2800-3700 m..... .....**A. paramicola** (Herz.) Schust.

(this species has also been placed in the genus *Omphalanthus* [as *O. paramicola* (Herz.) Gradst.)] from which it differs, however, by the rectangular lobule and the reddish- to darkish-brown pigmentation).

81. Perianth with only 1-2 ventral keels; innovations 1-2; plants smaller, creeping 82

82. Perianth with 5 long, sharp keels, the perianth apex rounded (beak not recessed); plants reddish- to dark-brown. Venezuela, Colombia, on shrubs at the forest line and in the páramo..... **A. quinquecarinata** Schust.

82. Perianth near apex with 3-4 short, broadly rounded keels, the perianth apex emarginate, the beak recessed; plants golden green to light brown. Venezuela, Colombia, on canopy branches in montane rain forest ..... **A. fulva** Schust.

83. Lobules uniformily swollen and strongly involute, the free margin inrolled 2-3 times. Throughout tropical America, ca. 500-3500 m., on bark and rock in sunny habitats..... **Anoplolejeunea conferta** (Meissn.) Schiffn.

83. Lobule not or only weakly involute 84

84. *Frullania*-type branches present (though sometimes only few); lobule when well-developed with 2 teeth; male bracteoles present throughout the male spike; plants +/- brownish pigmented 48

84. *Frullania*-type branches entirely lacking; lobules with 1 tooth only; male bracteoles limited to the base of the spike; plants pale green, rarely brownish 85

85. Lobule large, 2/5-1/2x lobe length (or more) 86

85. Lobule small, less than 1/3x lobe length 93

86. Underleaves large, 4-5x stem width, imbricate; plants rather robust, ca. 1-2 mm wide. Above 1500 m (Andes only) 87

86. Underleaves smaller, 1-2.5x stem width; plants tiny and fragile, 0,5-1 mm wide. Mainly at lower elevations.....88

87. Plants brownish; leaf cells with large, bulging trigones, intermediate thickenings lacking; stems rigid, cells strongly thickened ....**Aureolejeunea** p.p. 82

87. Plants pale greenish; leaf cells with small trigones and intermediate thickenings; stem cells +/- thin-walled. Andes of Venezuela and Colombia, epiphyte in montane rain forest (canopy) and bushes ....**Amphilejeunea viridissima** Schust.

(two further species, *A. catinulifera* (Spruce) Schust. and *A. patellifera* (Spruce) Schust. from the Andes of Ecuador, have been placed in *Amphilejeunea* (Schuster 1986). The differences among the three species of *Amphilejeunea* are not clear, however, and need further study).