BRACHIOLEJEUNEA FRULLANOIDES SEM PTYCHANTHOIDEAE

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A taxonomic monograph of the genera Brachiolejeunea and Frullanoides



I A taxonomic monograph of the genera Brachiolejeunea and Frullanoides

HISTORY AND NOMENCLATURE

1. Brachiolejeunea (Spruce) Schiffn.

SPRUCE (1884) published *Brachiolejeunea* as one of his 37 subgenera of *Le-jeunea*, a genus which was then more or less equivalent to the present family Lejeuneaceae. Similar to several others of his subgenera, *Brachiolejeunea* was established to include a number of species previously placed in the very hete-rogeneous (not to say artificial) genus *Phragmicoma* Dum. The subgenus *Bra-chiolejeunea*, which belongs to the Holostipae Spruce (possessing undivided underleaves), was essentially characterised by the dichotomous branching from below the perianth, and by the more or less compressed perianth with 3-10 plicae, positioned on and between 3-4 keels. Three species were included in this subgenus, which were distinguished by perianth characters. According to SPRUCE, species of the subg. *Brachiolejeunea*, especially *L. laxifolia*, resembled those of subg. *Homalolejeunea* Spruce (nowadays synonymous with the genus *Marchesinia* S.F. Gray) in general habit, but differed in the shape of the perianth: triplicate in *Brachiolejeunea*, dorsoventrally compressed in *Homalolejeunea*.

Between 1884 and 1893 several taxonomic studies on tropical liverworts, mainly by STEPHANI (1889, 1890), contributed to a rapid increase in the size of the group, which was elevated to generic rank under the name *Brachiolejeunea* (Spruce) Schiffn. by SCHIFFNER (1893). Summarizing previous treatments he assigned 23 species to the genus. Thus, within ten years the number of species had increased almost tenfold. SPRUCE (1884) listed three South American species, but in 1893 African and Asiatic species were also ascribed to the genus, so that *Brachiolejeunea* had become pantropical in distribution. The number of species increased to 65 in 1912, when the treatment of *Brachiolejeunea* was published in the Species Hepaticarum of STEPHANI. The increase was again mainly due to STEPHANI (1895a-b, 1896a-b, 1897, 1910, 1910-1911), but also to SCHIFFNER's (1894) revision of GOTTSCHE's material in Berlin. In the Species Hepaticarum the 65 species of *Brachiolejeunea* were divided between Africa, tropical America, Asia and Oceania. Between 1912 and 1934 a few more species were assigned to the genus by STEPHANI (1923) and by some authors dealing with regional floristics (PEARSON 1922, SIM 1926, HERZOG 1939). Between 1934 and the present day the total number of species assigned to *Brachiolejeunea* rose to 104. In addition nine varieties and formae were described.

An important publication on the genus was EVANS' (1908a) treatment in his classical series Hepaticae of Puerto Rico. Two major issues were dealt with: 1) a lectotype was chosen (B. laxifolia (Tayl.) Schiffn.), which has been accepted ever since, 2) the genus was more solidly delimited and taxonomic affinities, especially with Acrolejeunea (Spruce) Schiffn., were reviewed (see below). VERDOORN's (1934a-c) revisions of the Asian and Australasian species of the genus were the first large scale attempt to apply EVANS' generic circumscription to the species, included for that region in the Species Hepaticarum. Of 31 species VERDOORN left only B. sandvicensis (Gott.) Evans and B. recondita (Steph.) Steph.; they were removed by MIZUTANI in 1962 and 1969 respectively (MIZUTANI 1962, 1969b). By redefining species and providing lists of synonyms VERDOORN presented an important contribution to the revision of the genus. The smaller number of African species was revised by VANDEN BERGHEN (1951), JONES (1957) and ARNELL (1963a), resulting in a reduction to only two species. After these revisions the total number of accepted or unrevised binomials in Brachiolejeunea became c. 50.

EVANS (1908a) defined the genus by its: 1) squarrose leaves, 2) large leaf lobule with teeth along the margin, 3) usually paired subfloral innovations, and 4) plicate perianth with unarmed keels. This circumscription has remained unchallenged but the considerable, infrageneric variation has been dealt with by MIZUTANI (1961, 1962), SCHUSTER (1961, 1963) and BISCHLER (1965). MIZUTANI (1961) accurately described the variation of B. sandvicensis and in 1962 transferred the species with its seven heterotypic synonyms to Trochole*jeunea* Schiffn., because of its single, *Frullania*-type innovation, its dimorphic female bracts, and its diverging seta, not found in other species of Brachiolejeuneg. SCHUSTER (1961, 1963) included Trocholejeuneg as a subgenus of Brachiolejeunea, based mainly on T. pluriplicata (Steph.) Verd., which has a pluriplicate perianth similar to other members of Brachiolejeunea. His main contribution was the creation of two further subgenera, Brachiolejeunea and Plicolejeuneg Schust., based on stem anatomy, leaf lobule teeth and perianth outline. The variation in stem anatomy was studied in detail by BISCHLER (1965), who confirmed this subgeneric classification. The transfer of Trocholejeunea pluriplicata to Spruceanthus Verd. (Gradstein in: HIEPKO 3 SCHULTZE-MOTEL 1981) added to the circumscription of Trocholejeunea. Widely accepted as a separate genus by that time, Trocholejeunea consisted only of T. infuscata (Mitt.) Verd. and a T. sandvicensis. A third fossil species, T. contorta (Göppert & Berendt) Gradst. & Grolle, was added recently (GROLLE 1982). The establisment of Trocholejeunea and the revisionary work of VERDOORN, MIZUTANI and others has lead to the "extinction" of Brachiolejeunea in Asia and Australia. A "true" Brachiolejeunea was described only recently for this area, B. poeltii Grolle & Mizut. from Nepal (GROLLE 1966).

GRADSTEIN (1975) estimated the genus *Brachiolejeunea* to be much smaller than ever before: only 1-4 species in subg. *Brachiolejeunea* and 5-10 in subg. *Plicolejeunea*. The present revision shows that these estimates are correct. Moreover it is shown that only 36 out of 104 binomials in *Brachiolejeunea* are correctly assigned, whereas 68 binomials should be excluded.

2. Frullanoides Raddi

RADDI (1822) established the genus Frullanoides for two new species from Brazil: F. riojaneirensis and F. densifolia. The different affinities of these species were realized by GOTTSCHE, LINDENBERG & NEES (1845) who transferred them to Frullania Raddi and Phragmicoma Dum. respectively. TREVISAN (1877), in his classification of the Hepaticae, treated Frullanoides as follows: 1) the generic name Ptychocoleus Trev. was proposed as a substitute for Frullanoides, and 2) Frullanoides was lectotypified by F, densifolia and F. riojaneirensis was excluded. According to the I.C.B.N. Art. 63.1 (ed. 1983) Ptychocoleus is illegitimate since it was nomenclaturally superfluous when published. The synonymy of these names was already realized by SCHIFFNER (1893: 128). SCHUSTER (1966: 89) designated F. riojaneirensis as the type of Frullanoides, overlooking, however, the older lectotypification by TREVISAN. F. densifolia was transferred to Brachiolejeunea by EVANS (1908a). Thus, Frullanoides Raddi, Ptychocoleus Trev. and Brachiolejeunea (Spruce) Schiffn. became synonymous. GRADSTEIN (1974a, 1975) drew attention to these nomenclatural and taxonomical problems in his study on the nomenclature of and synonymized **Ptychocoleus** Brachiolejeunea suba. Since in present with Frullanoides. the publication Plicoleieunea Brachiolejeunea subg. Plicolejeunea is raised to generic rank, Frullanoides Raddi is reinstated for that group and nomenclatural changes are made accordingly.

With Brachiolejeunea restricted to SCHUSTER's (1963) subg. Brachiolejeuneg and Frullanoides replacing the subg. Plicolejeunea, the need for conservation of Brachiolejeunea (Spruce) Schiffn. 1893 against Frullanoides Raddi 1822, advocated by GRADSTEIN (1974a) and GROLLE (1983), is no longer necessary. However, the conservation of another name, is still necessary: Brgchiolejeunea (Spruce) Schiffn. 1893, lectotypified by B. laxifolia (EVANS 1908a), against Brachioleieuneg Steph. & Spruce (STEPHANI 1889) with B. plagiochiloides Steph. & Spruce as the lectotype. BONNER et al. (1961) were the first to realize that, according to Art. 42 of the I.C.B.N., Brachiolejeunea was formally established as a monotypic new genus through the publication of B. plagiochiloides. According to VERDOORN (1934a) and plagiochiloides is synonymous with BISCHLER (1965) Β. Archileieunea scutellata (Tayl.) Steph., but I consider it a synonym of Spruceanthus semirepandus (Nees) Verd. (see Excludenda). If Brachiolejeunea Steph. & Spruce 1889 is not rejected, this generic name will fall into the synonymy of Spruceanthus and a new generic name is needed for Brachioleieunea (Spruce) Schiffn. as no other legitimate name is available for that genus, as it is

currently circumscribed. As in 1889, STEPHANI refered to *Brachiolejeunea* as a genus also in 1890 (p. 9), but according to the I.C.B.N. Art. 34.1(a) the name is invalid at the generic level because in the introduction (p. 1), conclusion (p. 98), and index (p. 133) of the same paper STEPHANI treated "*Brachio-Lejeunea*" (hyphenated Sprucean spelling) as a subgenus (ZIJLSTRA 1982, GROLLE 1983). The conservation of *Brachiolejeunea* (Spruce) Schiffn. 1893 will be formally proposed in TAXON in due course.

MATERIALS AND METHODS

1. Materials

For the present study I have examined about 1000 specimens of *Brachiolejeunea*, which were obtained on Ioan from the following herbaria (abbrevations according to the Index Herbariorum ed. 7): B, BM, BR, C, COL, EGR, FH (including FH-Taylor and FH-Schiffner), FLAS, G, GRO, JE, L, MANCH, PC (including PC-Montagne), PRE, S, U, WTU, YU, and the private herbaria of Dr. M.H. Fulford (Cincinnatti), Dr. E.W. Jones (Kirtlington), Fr. M.H. Onraedt (Malonne), and Dr. C. Vanden Berghen (Brussels).

Besides herbarium material, living specimens of *Brachiolejeunea* and some related genera from Colombia and Peru have kindly been sent to me for examination by Dr. S.R. Gradstein. This material has been cultured for some time in a microphytotron (see under 2.).

2. Description, cultivation and drawings

Descriptions and discussions of diagnostic and differentiating characters of each taxon are based upon examination of herbarium material from as many different geographical areas as possible. Specimens were examined in the dry state for determining the habit of the leaves, while they were moistened for the description of all other aspects. When available, data obtained from living populations were added.

Bracketed measurements, e.g. in stem cortex and medulla, leaf lobule teeth and series of male bracts, indicate that these are rare for that taxon when taken as the sum of the component populations, and <u>not</u> that these numbers are uncommon in individual populations.

There appears to be a lack of uniformity in terminology concerning the size of the individual plants. In *Lopholejeunea*, for instance, MIZUTANI (1961) describes plants with stems 10-30 mm long as "medium", and 10-20 mm as "small"; VANDEN BERGHEN (1951), however, describes plants with stems 10-40 mm long as "robust"; and ARNELL (1963) describes two *Brachiolejeunea* species with lengths 10-25 mm as "large". In this publication I have arbitrarily chosen the following definitions for plant sizes: 1) species with an average length of one centimeter or less are small, 2) species with an average length of more than five centimeters are large.

In order to obtain standardisation, leaf length and width are measured similar as has been done for *Acrolejeunea* (GRADSTEIN 1975). Leaf length is measured as the distance from the basal insertion of the leaf on the stem to the apex of the leaf lobe; leaf width is measured parallel to the stem and is the distance from the apical insertion of the free margin of the lobule on the ventral lobe margin to the dorsal margin of the lobe. Leaf length and width are thus not necessarily perpendicularly orientated.

The leaf lobule length is the distance from the basal insertion on the stem to the apex of the lobule, i.e. where the free margin meets the ventral leaf lobe margin. The leaf lobule width is arbitrarily chosen as the widest distance of the lobule that can be measured parallel to the stem. The length of the cells is arbitrarily defined as the longest distance between the trigones, present in the angles; the width is measured perpendicularly to length.

Length of the underleaf attachment is measured as follows. In a longitudinal section the outer surfaces of the ventral cortical cells are connected by an imaginary line through the underleaf attachment. One end of the attachment is located in the midst of where this line intersects the superior central cell. The other end is located centrally on the margin of the first underleaf lamina cell (PI. II, fig. 2: u) with its adjacent cell. In nearly adjacent cell is the superior species this central cell, all but in Brachiolejeunea leiboldiana (Pl. 11, figs. 10, 13; Pl. XII, figs. 6-7) and Blepharolejeunea securifolia (Pl. 11, fig. 5) intermediate cells are found between the underleaf lamina cell and the superior central cell.

Oil bodies have been examined in living material of several species, cultivated in an Uni-Matic microphytotron, where plants were grown on a mixture of sand and peat-dust in plastic boxes. Temperature in the phytotron varied between $12-15^{\circ}$ C; a day/night shift of 12 hours was maintained.

Sporeling development was followed by cultivating spores on standard agar plates, kept in an Uni-Matic microphytotron at $20-22^{\circ}$ C and a day/night shift of 12 hours.

Line drawings of plant habits are from specimens soaked in water and placed on a slide. Drawings of the different parts of the plants are from specimens preserved in Hoyer's solution. All light microscopic drawings are made with the aid of a Wild drawing tube.

3. Scanning Electron Micrographs

Scanning Electron Microscopical (SEM) examination has been applied to study the structure of the sporophyte generation, which in Lejeuneaceae is sometimes difficult to analyse with light microscopy. Moreover, it is shown that submicroscopical examination of the sporophyte may reveal new characters that are of taxonomic importance. Two preparation methods have been used here, each for different parts of the sporophyte:

- direct mounting and coating (elater morphology, spore shape and sporoderm ornamentation as well as the storage of the spores inside the capsule): 1) cleavage of dry capsules, taken from herbarium material, by means of length and transverse sections, and 2) mounting of the cleaved capsules on aluminium stubs;
- fixation and critical point drying, prior to direct mounting and coating (seta morphology, inner, outer and lateral surface of the capsule valves and the elater arrangement on the valves). This was studied after application of the following preparation: 1) hydration after isolation of setae and valves, 2) fixation in 2.5% glutaric aldehyde, buffered in 0.1 M K-Na-phosphate buffer, for 2.5 hours, 3) rinsing in the same buffer, 4) post fixation in 1% Os04, buffered in 0.1 M K-Na-phosphate buffer for 45 minutes, 5) rinsing in the same buffer, 6) dehydration through a graded series of ethanol, up to 100%, 7) critical point drying (c.p.d.), and 8) mounting on aluminium stubs.

The procedure is described in more detail in Chapter III.

4. Nomenclature and bibliography

Nomenclature is in accordance with the latest edition of the International Code of Botanical Nomenclature (VOSS et al. 1983). The present circumscription of the *Brachiolejeunea* group necessitates the nomenclatural conservation of *Brachiolejeunea* (Spruce) Schiffn. 1893 against *Brachiolejeunea* Steph. & Spruce 1889. According to current rules, this proposal is published separately in TAXON.

The citation of nomenclature and types follows the Code and the recommendations of FRAHM & GRADSTEIN (1984), in order to obtain uniformity in these matters.

Citation of journals is according to the Botanico-Periodicum-Huntianum (LAWRENCE et al. 1968). Herbarium abbreviations are according to the Index Herbariorum ed. 7 (HOLMGREN et al. 1981). Authority names are abbreviated according to SAYRE et al. (1964). Names of recent authors which are not listed in the latter index are, in accordance with current usage, written in full.

MORPHOLOGY AND ANATOMY

1. Introduction

In recent decades our knowledge of the morphology, anatomy and cytology of liverworts has greatly expanded due to the introduction and application of new ideas and techniques. An excellent review of the current knowledge is given in the New Manual of Bryology (SCHUSTER 1983-1984). Progress in the understanding of the complex family of the Lejeuneaceae has recently been compiled by GRADSTEIN (1979) and SCHUSTER (1980b). Besides data presented in monographic treatments of genera in the Lejeuneaceae, comparative studies have been executed, dealing with single or sets of characters (e.g. BISCHLER 1961, 1965, 1966; WINKLER 1968, 1970; GRADSTEIN et al. 1977, 1981, 1985; THIERS 1984, 1985).

Finally, much more has recently become known of the sporophyte generation (e.g. STOTLER & CRANDALL 1969; GEISSLER & GRADSTEIN 1982; CRANDALL-STOTLER & GEISSLER 1983; UDAR & AWASHTI 1982, 1983). Especially in the examination of the sporophytes, the application of scanning electron microscopy (SEM) and transmission electron microscopy (TEM) has revealed new characters, leading to a better understanding of the structure and ontogeny of sporophyte characters and their systematic relevance.

In this treatment the morphology and anatomy of *Brachiolejeunea* and *Frullanoides* are discussed against the background of the developing new concepts. The morphology and anatomy of the sporophyte generation and taxonomic significance are discussed in a broader, subfamilial perspective in a separate chapter (Chapter III).

2. Leaves

The mature leaves in Brachiolejeunea and Frullanoides are inserted incubously and are complicate-bilobed with a large dorsal lobe, that is (broadly) ovate to ovate-falcate or ovate-oblong, and a small, inflated ventral lobule that is ovate-triangular in outline in *Brachiolejeunea* and (broadly) ovate to ovate-triangular in Frullanoides. The leaf is attached to the axis along an Sshaped line of insertion. The insertion-line of the lobe is c. 1.5 x the length of the insertion-line of the lobule and covers $\frac{1}{2}$ to the entire length of the merophyte (DOUIN 1925) in Brachiolejeunea and 2/3 to the entire length of the merophyte in Frullanoides. Similar to the sect. Acrolejeunea of the genus Acrolejeunea (GRADSTEIN 1975) the lateral merophytes in Frullanoides meet dorsally in an oblique zig-zag line; in Brachiolejeunea they meet in a straight line. The interlocking patterns thus present a generic difference. The juvenile leaf in both Brachiolejeunea and Frullanoides has three hyaline papillae, two of them located on the outer ends of the insertion line of the leaf, the third one located on the apex of the leaf lobule. These positions are usual for hyaline papillae in the Leieuneaceae. In a mature leaf the first two papillae are usually deteriorate, but they are more easily observed in the juvenile leaves and the first cycles of adult leaves of a sporeling (PI. VI, fig. 4: pa). STOTLER (1969) and STOTLER & CRANDALL-STOTLER (1974) have reported a fourth hyaline papilla at the apex of the leaf lobe in *Frullania* and *Bryopteris* respectively. This papilla is lacking in *Brachiolejeunea* and *Frullanoides*.

A marked difference in appearance between the dry and moist state of the leaves in *Brachiolejeunea* and *Frullanoides* is observed. In the dry state, the leaves are suberect-convoluted and more or less wrapped around the stem; when moistened, the leaves are spreading widely and assume a convex and erecto-patent to squarrose position. The leaves are less strongly squarrose than in *Acrolejeunea*, and never become subvertical as in the latter genus. This difference serves to separate sterile plants of *Frullanoides corticalis* and *Acrolejeunea torulosa*.

The lobule in *Brachiolejeunea* is $0.3-0.6 \times the length of the lobe; in$ *Frullanoides* $<math>0.3-0.7 \times the length of the lobe. In both genera the lobule consists of an inflated, convex portion along the keel, serving as a "water-sac", and is gradually narrowing towards a flattened portion along the free margin. Thus$ *in situ*the lobule free margin is folded against the lobe, leaving only a very narrow opening of the water-sac between the insertion on the stem and the apex of the lobule.

In Brachiolejeunea the keel, which connects the lobule with the lobe, is gradually curved, but in *B. fernandeziana* straight to even weakly concave. The surface of the keel is always smooth. When the leaf is dissected from the stem and spread out, the angle between keel and ventral leaf margin is $90-150^{\circ}$, but up to $160-180^{\circ}$ in *B. fernandeziana* (PI. VII, fig. 7). The free margin of the lobule is plane and weakly curved when observed from the stem onwards (PI. VII, fig. 7; PI. IX, fig. 4; PI. XII, fig. 1). In *B. leiboldiana* the outline is somewhat different, showing a distinct angle of $\pm 150^{\circ}$ at the location of the second tooth. In this species the apical part of the free margin is thus not strongly curved but \pm straight (PI. XI, figs. 5-6). The teeth on the free margin are always inflexed and their number varies between two and four. At the apex of the lobule the free margin and the keel meet in an oblique angle, but the free margin is not continuing into the ventral margin of the lobe.

In Frullanoides the keel of the leaf lobule is smooth and varies in shape from weakly curved to \pm straight to weakly convex. When the leaf is dissected from the stem and spread out, the angle between keel and ventral leaf margin is 150-180°, thus forming an almost straight line. The free margin is plane and straight to weakly curved towards the apex, except in *F. liebmanniana* where a different shape is present: irregularly arched with triangular segments (PI. XXIII, fig. 4). The number of teeth in *Frullanoides* is variable: (3-)5-9(-11). The lobules of *F. liebmanniana* present only 3-5 teeth; the lobule of *F. mexicana* presents, on the contrary, 8-11 teeth (PI. XXVI, fig. 5). The lobule of the other five species of *Frullanoides* shows more or less regularly arranged, inflexed teeth on a weakly curved margin. At the apex of the lobule the free margin meets the keel in an oblique angle and, unlike *Brachiolejeunea*, the free margin continues over a short distance into the ventral margin of the lobe. A small club-shaped, hyaline papilla is present 1-2 cells below the proximal base of the apical tooth in all species of *Brachiolejeunea* and *Frullanoides*; except *F. liebmanniana* where it is at the base of one of the triangular segments, about six cells below the tooth (PI. XXIII, fig. 5). As in *Acrolejeunea pycnoclada* (GRADSTEIN 1975), the first tooth in *Frullanoides corticalis* is situated at the extreme end of the free margin of the lobule (PI. XVIII, fig. 3) and the hyaline papilla is inserted at the proximal base of the second tooth. I therefore agree with GRADSTEIN (1975: 18) in using "first tooth", "second tooth" etc. only numerical and not in connection with the location of the hyaline papilla. Consequently, the apical tooth with its hyaline papilla is the first tooth in all species of *Frullanoides* and *Brachiolejeunea*, except in *F. corticalis*.

3. Cells

The cells in the leaf lobe of *Brachiolejeunea* and *Frullanoides* are elongatehexagonal and are arranged in more or less diverging rows. Median leaf cells are 21-54 x 13-33 μ m, slightly larger at the leaf base and smaller at the margins where the cells are rectangular to subquadrate. A vitta of considerably longer cells, as is present in e.g. *Thysananthus* sect. *Vittatae*, is never observed; ocelli are entirely lacking.

The cell walls are smooth and yellowish in all species of *Brachiolejeunea*, but darkish-brown in the species of *Frullanoides* due to secondary pigmentation. This pigmentation is responsible for the characteristic darkish-brown to black colour of dry plants of *Frullanoides*; an ink-black colour may be found in *F. bahamensis* and *F. corticalis*.

The cell wall consists of a thin lamella with collenchymatous thickenings in angles of the cells (trigones) and elliptic-rounded to elongated the thickenings, which may be present singly on the longer, intermediate walls. The intermediate thickenings are scarce to frequent in leaf cells. The trigones are always heart-shaped ("cordate"), possessing two convex sides and one concave side. Semicordate trigones, with two concave sides and only one convex side, as reported for Acrolejeunea (GRADSTEIN 1975), are not observed in Brachiolejeunea and Frullanoides. The cordate shape is already present in very young leaves and is apparently initiated at an early stage of development. The occurrence of cordate trigones leaf in the Brachiolejeunea-Frullanoides group was noted earlier in descriptions by EVANS (1908a), VANDEN BERGHEN (1948) and SCHUSTER (1980b).

Oil bodies are present in all cells of leaves, underleaves, involucrum, perianth and stem cortex. In *Brachiolejeunea* and *Frullanoides* 15-30 *Massula*-type oil bodies per cell are present (PI. XXXV, figs. 1-2). They are small, only $(2.5-)3-6(-8) \times 1.5-2.5 \mu m$ and narrow ellipsoid to fusiform in outline. The oil bodies appear spherical when seen from the side. Upon degeneration (which occurs rapidly when the plant dries up!) they disintegrate into minute granulae. Great attention should therefore be paid to the fresh condition of the plant material when observing the oil bodies. Homogeneous oil bodies tend to appear segmented when degenerating and segmented oil bodies tend to

appear like homogeneous oil bodies when falling apart (GRADSTEIN 1975). This phenomenon has frequently lead to misinterpretations, e.g. in *Blepharolejeunea* where *B. incongrua* (GRADSTEIN et al. 1977, sub *Brachio-lejeunea* hans-meyeri) and *B. securifolia* (GRADSTEIN et al. 1981, doubtful record) are reported to possess *Massula*-type oil bodies. Recent comparison of fresh material of *Brachiolejeunea* laxifolia and *Blepharolejeunea* incongrua in the field by Dr. S.R. Gradstein showed finely granulose, *Jungermannia*-type oil bodies (PI. XXXV, fig. 3) rather than *Massula*-type in the latter species (VAN SLAGEREN & KRUIJT 1985).

4. Stem structure (Plates I-II)

Stem structure is important in distinguishing taxa in the Lejeuneaceae, predominantly at the generic and subfamilial level. EVANS (1935) postulated major lines of evolution, considering complex types of stem structure primitive, preceding more advanced types which would develop through differentiation and reduction.

For the present study, transverse and longitudinal sections (PI. II) of the stems have been made of all species of *Brachiolejeunea* and *Frullanoides* as well as for selected species of related genera. Both *Brachiolejeunea* and *Frullanoides* possess an advanced type of stem structure, as defined by EVANS, characterised by a distinctive differentiation into a (one-layered) cortex and medulla.

4.1 Brachiolejeunea (Plate I, figs. 9, 10)

The stem in *Brachiolejeunea* measures 0.10-0.25 mm in diameter, which is $0.05-0.20 \times the$ width of the leafy plant. In transverse section the stem is suborbicular in outline. All four species show a distinct cortex, consisting of one layer of thick-walled cells, surrounding a medulla of thin-walled cells. The wall of the cells of the stem are yellowish and without secondary pigmentation. The total number of cortical cells in stem cross section varies between 11 and 23, but may be up to 30 in *B. laxifolia*. The number of medullary cells varies between 16 and 55, but may be up to 82 in *B. laxifolia*. Transverse sections of the stem show that the dorsal cortical cells are c. 1.5 x as high as both the ventral cortical cells and the medullary cells, which are \pm similar in size. Since the dorsal cortical cells are not only higher but also larger, i.e. height and width combined, than the ventral cortical cells, the stem in *Brachiolejeunea* may be designated <u>asymmetric</u> in the sense of GRADSTEIN (1975: 20).

Transverse sectioning of the axis in *Brachiolejeunea* reveals one of the most characteristic features of two species of the genus: the dorsal lamellate paraphyllium (Pl. I, fig. 10; Pl. IX, figs. 1a, 2; Pl. XI, figs. 2-3). They have been described for *B. laxifolia* (VAN SLAGEREN & GRADSTEIN 1981) and are also present in *B. leiboldiana*. In *Brachiolejeunea laxifolia* they are instantly observed after removal of the leaves under a dissecting microscope. In both species, these unistratose, lamellate outgrowths are located at the

dorsal interlocking border of the lateral merophytes and separated only by the dorsal leaf insertions (PI. VIII, figs. 3, 7). The paraphyllia are present throughout the axis except at the base of *Frullania*-type branches, below the second leafy appendage (PI. VIII, fig. 4). Their function is still unclear; enhancement of water storage or photosynthetical activity are rather unlikely due to their relatively small size and concealed position. In *B. fernandeziana* and *B. spruceana*, paraphyllia are lacking or rudimentary (PI. VII, fig. 3; PI. XIII, figs. 2-3).

Longitudinal sectioning of the stems reveals the presence of a thick-walled cortex and thin-walled medulla in all four species of *Brachiolejeunea* (PI. II, figs. 8, 10, 13; PI. VIII, figs. 2-3; PI. XII, figs. 6-7; PI. XIII, fig. 5). Length sections show, in addition, long medullary cells, tapering towards truncate ends, and short-elongated dorsal and ventral cortical cells. The dorsal leaf insertion cells are visible as irregular trapezoid or V- to U-shaped cells. In a few well developed specimens of *B. laxifolia* stem transverse sections show the presence of several thickened outer cell layers instead of only one (PI. IX, figs. 1a-b, 2). Based on the difference in shape between the cortex and medulla cells, as shown by longitudinal sections, it appears that these layers represent medullary tissue (except for the outermost layer). Longitudinal section also shows the difference in height between the antical and postical ends of the paraphyllia in *B. laxifolia*: (2-)3-4(-5) cells versus 1-2 cells (PI. VIII, fig. 3).

On the ventral outer surface the width of the ventral merophyte is defined as the number of cells outside the base of the underleaf insertion, since the ventral merophyte has reached its defitive width there. The number of cells in *Brachiolejeunea* varies: 4-6(-8), caused entirely by luxuriant growth of *B*. *laxifolia* (e.g. in Pl. X, fig. 1).

4.2 Frullanoides (Plate I, figs. 7-8)

The stem in *Frullanoides* measures 0.10-0.35 mm in diameter, which is 0.1-0.2 x the width of the leafy plant. In transverse section the stem is suborbicular in outline. Transverse sections furthermore show a thin-walled dorsal and lateral cortex in all species. The ventral cortical cells are also thin-walled, except in *F. densifolia* and *F. laciniatiflora* where thick-walled ventral cortical cells are present (PI. XVIII, fig. 5; PI. XIX, fig. 8; PI. XXII, fig. 3). The medullary cells are always thick-walled. The walls of the cells of the stem are darkish brown due to secondary pigmentation. The total number of cortex and medulla cells varies widely: 11-36 rows of cortical cells surround 17-115 rows of medullary cells. The dorsal cortical cells are c. 1.5 x as high as both the ventral cortical cells are not only higher but also larger than the ventral cortical cells, all stems in *Frullanoides* are asymmetric (e.g. Pl. 1, fig. 8).

Longitudinal sectioning shows narrowly elongated medullary cells, tapering towards truncate ends. They are much longer than the shortly elongated cortical cells, even when compared with the elongated ventral cortical cells of *F*. *densifolia* and *F*. *laciniatiflora* (PI. XVIII, fig 4; PI. XIX, fig. 6; PI. XXII, fig. 4). Contrary to the thickened ventral cortical cells in these two species, the thickenings of the medullary cells in other species are unevenly distributed over the cell walls (e.g. P. XVIII, fig. 1). The dorsal leaf insertion cells are irregular trapezoid to V-shaped. The width of the ventral merophyte surface varies widely in the genus: only four cells wide in the small *F. bahamensis* and *F. corticalis*; 4-8 cells wide in *F. liebmanniana*, *F. mexicana* and *F. tristis*, and (6-)8-10(-14) cells wide in *F. densifolia* and *F. laciniatiflora*. Except in *F. densifolia* and *F. laciniatiflora*, the ventral cortical cells in surface view are subquadrate to shortly rectangular. Well developed specimens of *F. densifolia* and *F. laciniatiflora* show narrow rectangular ventral cortical cells with conspicuous, irregular wall thickenings (PI. XVIII, fig. 6).

5. Underleaves and primary rhizoid disc (Plate II)

The underleaves in *Brachiolejeunea* and *Frullanoides* are always undivided and suborbicular in shape. In *Brachiolejeunea* the apex is widely rounded and the bases of the underleaves are rounded and short decurrent. Due to the recurved apical margin, in combination with the incurved (parts of the) lateral margins, the outline in situ is rather variable: suborbicular to \pm rectangular to obtriangular (PI. VIII, figs. 5-6; PI. X, fig. 10; PI. XIII, fig. 6). On the shoots the underleaves are distant to only slightly imbricate (PI. VII, fig. 1a; PI. XI, fig. 1). The line of insertion on the stem is always cuneate. There are no auricles developed at the bases.

The underleaves in *Frullanoides* vary from suborbicular to elliptic to obtrapezoid (*F. mexicana*, PI. XXV, fig. 5). The apex is always undivided, rounded to truncate, and plane or recurved (in *F. densifolia*, *F. laciniatiflora* and *F. mexicana*). The lateral margins are entire and plane or recurved. Auricles are developed at the bases, and vary greatly in size between the several species. In *F. bahamensis* and *F. corticalis* auricles are absent or minute, consisting of a few cells only (PI. XV, fig. 4). Auricles are small in *F. liebmanniana* (PI. XXIV, figs. 1, 5), *F. mexicana* (PI. XXV, figs. 5-6) and *F. densifolia* ssp. grandidentata (PI. XX, figs. 7, 10); they vary from small to distinct in *F. tristis* (PI. XXI, fig. 4) and *F. densifolia* where, in addition, a considerable variation in the outline of the underleaves is observed (PI. XIX, fig. 7; PI. XX, figs. 3-4). In the latter two species the underleaves are appressed to the ventral-lateral side of the stem. The line of insertion of the underleaves is arched to subtransverse.

In both genera the rhizoid initial cells are restricted to discs, located at the base of the underleaves. These initial cells give rise to a short bundle of unicellular rhizoids (PI. II, figs. 4, 10, 13), which firmly attach the plant to the substrate. Often the rhizoid apex develops a hand-shaped proliferation, which is environmentally induced (PI. II, fig. 4; ODU & RICHARDS 1976).

WINKLER (1968, 1970), BISCHLER (1968) and GRADSTEIN (1975) have called attention to the taxonomic importance of the anatomy of the underleaf

base. This structure has been studied through longitudinal sectioning in all species of *Brachiolejeunea* and *Frullanoides* and in selected species of related genera as well (PI. II, figs. 1-14). Attachment of the underleaf to the stem is by large U-shaped cells: the superior central cells (PI. II, figs. 2, 5, 10, 13: s). These cells also support the primary rhizoid disc (PI. II, fig. 2: r). The primary rhizoid disc, in its turn, is not only supported by the superior central cells, but also by various other cells:

- by the "inferior central cell", connecting the rhizoid disc with the adjacent cortex cells (Pl. II, fig. 2: i);
- by a modified cortical cell, which is located between the inferior central cell, the superior central cell and the medulla (Pl. II, fig. 2: mc);
- by an intermediate cell layer, which may be present between the superior central cell and the primary rhizoid disc in some genera of Ptychanthoideae (Pl. II, figs. 3, 11: i.l.).

The type of attachment, lacking an intermediate cell layer, is bistratose and has been designated the Stictolejeunea-type (WINKLER 1970); when the intermediate cell layer is developed, the type of attachment is tristratose and is called Symbiezidium-type. I have observed the tristratose attachment in Brachiolejeunea (Pl. II, figs. 10, 11, 13) and, amongst others, in several species of Blepharolejeunea (Pl. 11, fig. 2; Chapter п). The Stictolejeunea-type is present in Frullanoides and, amongst others, in Trocholejeunea, Acrolejeunea and Mastigolejeunea (Pl. II, figs. 1-2, 4, 7, 9). The underleaf attachment thus provides a generic difference between Brachiolejeunea and Frullanoides. In F. liebmanniana, however, a kind of intermediate cell layer is sometimes observed (PI. XIII, fig. 8), but the resultina configuration is nevertheless guite different from that in Brachiolejeunea.

In Brachiolejeunea the underleaf attachment is elongated like a stalk, most distinctly so in *B. leiboldiana*, and $(35-)60-200 \ \mu m$ in length (in the small *B. spruceana* only 30-60 μm). In *Frullanoides* the attachment is shorter, only 35-60(-90) um long. According to WINKLER (1970), the underleaf attachment type may serve as a generic character, but GRADSTEIN (1974b) showed the presence of both tristratose as well as unique polystratose underleaf attachments in *Caudalejeunea*, and in *Blepharolejeunea* both bi- and tristratose attachments occur (VAN SLAGEREN & KRUIJT 1985), even within a single species (*B. securifolia*, PI. II, figs. 5, 8).

In *Brachiolejeunea* the number of superior central cells is always four, but the number of cell rows constituting the ventral merophyte varies from 4-6(-8). In *Frullanoides* the number of superior central cells varies from 4-8; the number of ventral merophyte cell rows varies to an even greater extent: (4-)6-8(-14). The number of cells of the ventral merophyte is thus not a stable character, but the same holds to a lesser extent for the number of superior central cells.

6. Branching

The morphology and taxonomic significance of branches in the Lejeuneaceae

and more specifically in the subfam. Ptychanthoideae have recently been treated in detail by THIERS (1982, 1984, 1985). In her 1985 study of the Ptychanthoideae she enumerates a number of characters which are excellent tools in describing the various aspects of growth and branching.

6.1 Growth habit and ramification pattern

The growth habit of *Brachiolejeunea* and *Frullanoides* is deliquescent, i.e. the secondary branches are as strongly developed as the primary ones. Moreover, branching is irregular pinnate, i.e. the secondary branches are not evenly and regularly spaced along the stem (as e.g. in *Bryopteris fruticulosa*, STOTLER ε CRANDALL-STOTLER 1974: fig. 96). Although species of both genera have been reported to grow in loose mats, partly ascending from the substrate (S.R. Gradstein, pers. obs.), I found that this feature was not reflected in the ramification pattern.

6.2 Lateral branch type (Plate III)

In all species of *Brachiolejeunea* and *Frullanoides* two types of lateral branches are found: the *Frullania*-type branch and the *Lejeunea*-type branch. These lateral branches subtend vegetative leaves as opposed to innovations, which subtend gynoecial bracts. The majority of the branches are of the *Frullania*-type. *Lejeunea*-type branches are less frequently present, except in *Frullanoides bahamensis* and *F. corticalis*, where the majority of the branches are of the *Lejeunea*-type. *Frullania*-type branches are few in *F. corticalis* and very rare (but present! - see Pl. III, figs. 15, 18-19) in *F. bahamensis*. Absence of *Frullania*-type branches in *F. bahamensis*, as stated by SCHUSTER (1980b) and THIERS (1985), thus cannot serve as a distinction between the two species.

When both *Frullania*-type and *Lejeunea*-type branches are developed, the *Frullania*-type branches are restricted to long, robust and vegetative axes, often loosely creeping over the substrate (EVANS 1908a, GRADSTEIN 1975). The development of this branch type may result from luxuriant growth of the plants (JONES 1970, GRADSTEIN 1975). On the relation between growth and branching-type I made some observations in specimens of *Brachiolejeunea laxifolia* and *B. leiboldiana*, cultivated in a phytotron. Newly grown stems of these species, which under natural conditions produce *Lejeunea*-type branches only occasionally, develop almost solely *Lejeunea*-type branches under the different climatic conditions of the phytotron. Gametoecia in *Brachiolejeunea* and *Frullanoides* are almost exclusively produced on *Frullania*-type branches, with the exception of *F. bahamensis* and *F. corticalis* where they are found on *Lejeunea*-type branches only (PI. XIV, fig. 5; PI. XVII, fig. 1a).

The development and morphology of the branching types in the Lejeuneaceae was studied in considerable detail by EVANS (1912a) and, more recently, by CRANDALL (1969). CRANDALL (I.c.) showed fundamental differences in the origin of the *Frullania*-type and *Lejeunea*-type branches. The *Frullania* branches lack a collar at the base and are called "athecal", whereas the collared *Lejeunea* branches are called "gyrothecal". The modified dorsal stem half-leaf of a *Frullania*-type branch is closely associated with the

developing branch and is partly inserted on it (PI. VIII, fig. 4). Its insertion line thus becomes \pm widely cuneate (PI. III). The outline of the dorsal stem half-leaf in *Brachiolejeunea* and *Frullanoides* is ovate to broadly ovate with the apex rounded to blunt to \pm acute (PI. III, figs. 17, 22).

In addition the first underleaf and first acroscopic leaf of a *Frullania*-type branch are also modified (Pl. III). The form of the first branch underleaf differs from the other stem and branch underleaves and its position is on the lateral side of the main stem at the ultimate base of the branch rather than on the ventral side of the branch itself. The first branch acroscopic leaf is inserted on the ventral-lateral side of the branch, rather than lateral. *In situ* both first branch appendages are canaliculate and more or less wrapped around the branch. The outline of the first underleaf and first lateral leaf is depicted in the plates of all species of *Brachiolejeunea* and *Frullanoides*. They are described in Table 1.

Table	1.	Form	of	Frullania-Ble	pharole	<i>jeunea</i> -type	branch	appendages.
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	Brachiolejeunea	Frullanoides
First branch underleaf	suborbicular-emarginate to	suborbicular-bilobed with blunt
	symmetrically bilobed to	but distinct lobes (F. bahamen-
	strongly asymmetrically	sis, F. corticalis) to a more
	bilobed.	or less rectangular fold with
		an irregular sinuate apical
		margin, vaguely to distinctly
		divided into two (a)symmetric
		lobes. More or less auriculate
		in the large species (F. densi-
		folia, F. laciniatiflora).
First branch acroscopic	similar to first under-	similar to first underleaf.
leaf	leaf.	

Several authors have recently paid attention to the taxonomic interpretation of the various types of Frullania branch appendages (MIZUTANI 1970, GRADSTEIN 1975, VAN SLAGEREN & KRUIJT 1985, THIERS 1985). MIZUTANI (1970) recognised three different subtypes of the Frullania branch, of which the Frullania-Ptychanthus-subtype and the Frullania-Jubula-subtype are present in Brachiolejeunea, Frullanoides and their related genera. A third Frullania-Blepharolejeunea-subtype, characterised the by the type, combination of a first underleaf, similar to the Frullania-Ptychanthus-subtype and a first acroscopic leaf, similar to the Frullania-Jubula-subtype, was recently described by VAN SLAGEREN & KRUIJT (1985). This subtype is also found in Frullanoides and Brachiolejeunea.

In the Lejeunea-type branch the cells of the associated leaf base (brace-cells) develop into a distinct "collar" at the base of the branch, which, at maturity, breaks into several lobes. This process has been described and illustrated in detail for *Brachiolejeunea laxifolia* by FULFORD & CRANDALL (1967). As the Lejeunea-type branch developes, the leaves and underleaves become gradually larger until the typical mature size is reached (see e.g. the Lejeunea-type branches in the habit illustrations of *F. bahamensis*, Pl. XIV, fig. 1).

6.3 Gynoecial pattern and innovation types

With the exception of the genera Trocholejeunea and Plagiolejeunea (MIZUTANI 1984), which have Frullania-Ptychanthus-type innovations, all innovations in the Ptychanthoideae are of the Radula-type. Two types of Radula innovations have been described: Radula-Jubula-type and Radula-Lejeunea-type (MIZUTANI 1970, GRADSTEIN 1979), "pycnolejeuneoid" and "lejeuneoid" respectively (GROLLE 1980; THIERS 1984, 1985). I have chosen to follow the terminology of MIZUTANI (1970) for convenience. In Brachiolejeunea and Frullanoides Radula-Jubula-type innovation are present. The dichotomous appearance of parts of the shoots due to the presence of two, repeatedly floriferous, Radula-Jubula-type innovations below a gynoecium, has always been considered a main characteristic of Brachiolejeunea and Frullanoides (EVANS 1908a, SCHUSTER 1980b), distinguishing the two genera at once from the related genera Trocholejeunea and Acrolejeunea (GRADSTEIN 1975: 145). Detailed research has, however, somewhat obscured this view. GRADSTEIN (1975: 25) reports the occasional presence of a single Radula-type innovation in several species of Acrolejeunea. THIERS (1985) reports the occasional presence of paired innovations in Trocholejeunea, the second innovation being of the Radula-type. Single instead of paired innovations sometimes occur in Brachiolejeunea as well as in Frullanoides, for instance in B. laxifolia (Pl. IX, fig. 7: arrow), B. leiboldiana (Pl. XI, fig. 1), in the type collection of F. bahamensis (EVANS 1908b), in F. tristis (colls. Grossman s.n., Düll 4/A52a), and in F. corticalis (coll. Reyes 719). The occurrence of a single innovation in Brachiolejeunea and Frullanoides is anomalous, since it occurs comparatively rarely (but rather frequently in B. leiboldiana). When only one innovation is present, the bracts are anisomorphous in outline. The bract where the innovation is lacking is essentially a vegetative leaf with a somewhat more swollen lobule (PI. X, fig. 7) and an oblique insertion on the stem. In addition a wing is not developed.

The spatial arrangement of the gynoecia concerns: 1) the gynoecial branch length, 2) the presence or absence of innovations, 3) the number and length of innovations, and 4) the ability of innovations to become floriferous again (THIERS 1985). The patterns observed in the Ptychanthoideae are simple, diffuse, monochasial and dichasial. *Brachiolejeunea*, *Frullanoides* (and *Blepharolejeunea*) are distinguished by their dichasial inflorescences. The genera *Trocholejeunea* (diffuse to monochasial), *Mastigolejeunea* (diffuse, monochasial or dichasial) and *Dicranolejeunea* (diffuse, monochasial or dichasial) are more variable.

7. Gametoecia (Plates IV-V)

Gametoecia are known in all species of Brachiolejeunea and Frullanoides, except B. leiboldiana where only gynoecia are known. Brachiolejeunea fernandeziana, B. laxifolia and B. spruceana as well as Frullanoides tristis and F. densifolia ssp. grandidentata are paroecious with the male bracts located just below the gynoecium. Frullanoides densifolia ssp. densifolia, F. laciniatiflora, F. liebmanniana and F. mexicang are dioecious species. Frullanoides corticalis is normally dioecious, but one monoecious specimen has also been found (coll. Ule 94). Brachiolejeunea leiboldiana has been designated dioecious, but male bracts have not (yet) been found. F. bahamensis is the only autoecious species of the Brachiolejeunea-Frullanoides group, but several paroecious specimens have also been found. It is often difficult to ascertain whether a taxon is autoecious or dioecious, because the male bracts closely resemble the leaves (F. densifolia and F. laciniatiflora excepted) and seasonal differences in the development of androecia and gynoecia are likely to occur. The dioecious species have their male bracts in spikes, which become intercalary due to proliferated vegetative growth of the stems and branches on which they are located. In the paroecious species the male bracts are located mainly on Frullania-type stems and branches, but also on the less frequent Lejeunea-type branches. In addition the Radula-type innovations are often again floriferous, locating androecial spikes also on Radula-type branches. The longest male spikes in Frullanoides, made up of 3-15(-23) series, are produced in the dioecious species. Somewhat shorter male spikes are present in the autoecious F. bahamensis: 4-9(-12) series. In paroecious species the male spikes are even shorter, consisting of only 1-4 series in total and located below the gynoecium after 1-3 series of vegetative leaves. Branching of the Frullania-type and of the Lejeunea-type has been observed in a male spike of F. densifolia ssp. densifolia. When of the Frullania-type, the first fully grown lateral (basiscopic) leaf may again be the first male bract of a developing new spike (coll, Hegewald 6556).

The androecium consists of a slightly to considerably modified leaf ("bract") enveloping one or two antheridia (Pl. IV, fig. 5). The lobe of the bract is similar to the lobe of a vegetative leaf, but somewhat smaller in size. The lobule is more strongly inflated and the teeth are generally fewer than in the vegetative leaves or virtually lacking (e.g. only two small teeth in *F. bahamensis*, Pl. XIV, fig. 9).

In Brachiolejeunea and Frullanoides (F. corticalis excepted, see below) the male bracts are epistatic, i.e. the free margin of the lobules – in ventral view – curves behind the lobule of the younger bract, whereas in <u>hypostatic</u> lobules the free margin distinctly overlaps the younger bract. In F. corticalis the male bracts are hypostatic except of a few series at the basal and apical end of a spike, giving the male spike a very compact appearance (PI. XVII, figs. 1b, 8). Although epistatic and hypostatic male bracts are considered characters at the generic level (GRADSTEIN 1975), Frullanoides apparently is

an exception to this rule. I have observed two antheridia per bract in the dioecious species of *Frullanoides*. Only one antheridium per bract was observed in the paroecious species of *Brachiolejeunea* and in the paroecious *Frullanoides tristis*. The statement of EVANS (1908a: 158) that paroecious species have one antheridium, and that autoecious (*F. bahamensis*!) and dioecious species have two antheridia per bract, is thus confirmed in *Brachiolejeunea* and *Frullanoides*. One to two antheridia are observed in *F. liebmanniana* and *F. bahamensis*. This variation may be due to the abortion of one of the two antheridia in a bract.

The mature antheridium is uniform in all species and globose to ovoid and 120-200 um in diameter (Pl. IV, fig. 4). It consists of a single outer layer of thin-walled and colourless cells, 27-45 x 14-22 μ m in size, quadrate to irregular rectangular in outline and 18-20 μ m thick. The cells contain chloroplasts but oil bodies are lacking. The sphere is filled with a mass of antherozoids, which are emerald-green in colour. The antheridium is subtended by a curved, uniseriate stalk of c. 20 μ m in diam., which is attached to the lateral side of the stem. The stalk is about as long as the diameter of the antheridium.

The gynoecium in *Brachiolejeunea* and *Frullanoides* terminates stems and long or short *Frullania*-type and *Lejeunea*-type branches. The gynoecial axis in both genera is slightly swollen (Pl. V, fig. 2). The gynoecium consists of a single archegonium surrounded by a perianth and one series of bracts and bracteole. The bracts tend to become complicate-bilobed when large lobules are present: up to $2/3 \times the$ length of the lobe in *Brachiolejeunea*, up to 3/4 of the length in *Frullanoides*.

In *Brachiolejeunea* the ovate-falcate bract lobes are plane with a concave apical region. They partially envelop the perianth. The margins are entire in all species. The lobule varies from rectangular to rectangular-rhomboid, in the latter case elongated beyond the keel. A narrow linear to elliptic wing runs along the keel to the dorsal-lateral side of the main stem. The obovate to obovate-spathulate bracteole is larger and more elongated than the underleaves, but smaller in size than the bracts. The apical region is slightly recurved, the apex is widely rounded to emarginate and the base of the bracteole is inserted on the main stem only. The subgynoecial leaves and underleaves are similar to the other vegetative leaves and underleaves.

The bract lobes in *Frullanoides* are obovate-elliptic to obovate-oblong. They are plane to concave and partially enveloping the perianth in *F*. bahamensis and *F*. corticalis; in the other species of the genus they are squarrose, especially in the upper half. The margins of the bract lobe are entire in all species except *F*. laciniatiflora where they are dentate-ciliate in the apical region (PI. XXI, figs. 7, 9). The lobule varies from rectangular to rectangular-rhomboid, in the latter case elongated beyond the keel. In *F*. bahamensis and *F*. tristis a different insertion of the lobule is observed in several specimens due to an outgrowth of the apex of the bract wing, resulting in an entally displaced lobule (PI. XV, figs. 2, 14). This is also observed in *Blepharolejeunea incongrua* (Chapter II, PI. V, fig. 3). A wing, varying in outline from small linear (*Frullanoides bahamensis*) to large elliptic-rounded (e.g. *F. densifolia*, *F. laciniatiflora*), runs along the entire keel and is also inserted on the innovation, hence is curved *in situ* (PI. XVII, fig. 2). In *Brachiolejeunea* the wing is restricted to the keel and not inserted on the innovation, hence presenting a generic difference. The outline of the bracteole varies from rectangular to rectangular-spathulate with the apex widely rounded to emarginate (bifid to deeply bifid in *F. laciniatiflora*; PI. XXI, figs. 5-6). In most species the insertion line of the bracteole extends laterally to the innovations.

The subgynoecial leaves are similar to the vegetative leaves, except in *Frullanoides corticalis*, which has subgynoecial leaves with narrow linear and hypostatic lobules, possessing only one (apical) tooth of 2-6 cells (PI. XVII, fig. 2). The subgynoecial underleaf is somewhat larger than the vegetative underleaves, and in *F. laciniatiflora* it is further characterised by the ciliate apical margin (PI. XXI, fig. 8a-b).

The archegonium is flask-shaped and has a very long neck of cells in c. 5 longitudinal rows, long extending beyond the beak of the juvenile perianth (Pl. IV, figs. 1-3). After fertilisation and during the entire development of the sporophyte, the archegonial neck does not undergo any further cellular divisions and remains uniform in shape, finally becoming located at the upper extremity of the mature calyptra (Pl. V, figs. 1, 4: a). The juvenile perianth consists of: 1) a basal portion, surrounding the venter of the archegonium, 2) a central portion which is \pm trigonous in outline (soon becoming pluriplicate in *Frullanoides*; Pl. IV, figs. 2-3), and 3) a beak, which has apparently completed its development and measures about half the length of the juvenile perianth (Pl. IV, fig. 3). The base of the archegonial neck is surrounded by the beak.

After fertilisation, the expanding venter develops into the calyptra, which remains the surrounding outer layer of the archegonium until the developing sporophyte has matured. A longitudinal section of a mature sporophyte shows a calyptral base, surrounding the sporophyte seta and foot, of 3-7 cell layers, gradually decreasing to 1(-2) layers in the upper part, surrounding the sporophyte capsule (PI. V, figs. 2-3: ca). The calyptra has large outer cells, similar to the calyptral stalk cells, and many inner cells, which are \pm isodiametric and much smaller (PI. V, fig. 2: ca). It remains intact until, through elongation of the seta, the sporophyte capsule tears it apart. The mature calyptra is shortly stalked: 50-125 µm (PI. VI, figs. 1-2: cs). The stalk is free from the perianth and is easily discerned, contrary to the border between the calyptral stalk and the calyptral base, which is marked only by an abrupt constriction.

The rapidly growing, trigonous perianth encloses the archegonium and the archegonial neck (Pl. V, fig. 1). In *Brachiolejeunea* the trigonous outline of the juvenile perianth is preserved in the mature stage (Pl. IX, fig. 6; Pl. XI, fig. 4), but in *Frullanoides* (5-)8-11 rounded plicae differentiate on the three keels. The basically trigonous condition of pluriplicate perianths as in *Frullanoides* has lead to the assumption that this condition is to be regarded as primitive (MIZUTANI 1961, SCHUSTER 1961, 1963). Mature pluriplicate

perianths in *Frullanoides* are terete and isoplicate, except in *F. liebmanniana* and *F. mexicana*, where the trigonous condition is sometimes still to be observed (PI. XXIV, fig. 4; PI. XXVI, figs. 2, 9).

All plicae of the perianths of Brachiolejeunea and Frullanoides are smooth along their backs, even in the early stages of development. In Brachiolejeunea the mature perianth exceeds the bracts for 1/2-2/3 of its length; in *Frullanoides* only for 1/5-1/3(-1/2) of its length. When emerging, the basal portion of the perianth is often elongated and forms a short stalk (GRADSTEIN 1975). The mature perianth is obovoid to obovoid-oblong in Brachiolejeunea and (ob)ovoid-cylindrical to obovoid-oblong in Frullanoides. The perianth is one cell layer thick, except at the base where it is 3-4 cell layers thick (PI. V, figs. 1-2). The beak is 4-6(-18) cells long. The cell wall thickenings are similar to those in the leaves. Small trigones are found in the large cells of the lower part of the perianth, gradually increasing in size in the smaller cells of the upper part.

8. Sporophyte and sporeling development (Plates IV-VI, XXX-XXXIV)

8.1 Introduction

The sporophyte generation provides the most important set of characters which have lead to my decision to elevate the two generally accepted subgenera of Brachiolejeunea, subg. Brachiolejeunea and subg. Plicolejeunea, to separate generic status. Fundamental differences are observed concerning: 1) capsule valve morphology, 2) spore shape and ornamentation, 3) elater morphology and arrangement, and 4) the mechanism of capsule opening and spore dispersal. Examination of the sporophytes has been carried out with light microscopy (hereafter LM) and scanning electron microscopy (hereafter SEM). Two types of sporophytes are distinguished: the "nodular-type", Brachiolejeunea, "fenestrate-type", present in and the present in Frullanoides. The development of the sporophyte and the shoot-sporophyte relationship are identical for each type and these aspects are therefore not treated separately.

8.2 Shoot-sporophyte relationship (Plate V)

The shoot-sporophyte relationship in Brachiolejeunea and Frullanoides is of the Lejeunea-type (SCHUSTER 1966: 563) and is similarly described for other members of the Ptychanthoideae and for Bryopteris (FULFORD 1961, STOTLER SCHUSTER 1966, CRANDALL 1967, 3 CRANDALL 1969, STOTLER 3 CRANDALL-STOTLER 1974, GRADSTEIN 1975). The sporophyte is short-stalked, and the foot is reduced and not penetrating into the axis. The structure of the young sporophyte is studied through longitudinal sections of the apex of an axis (PI. V, figs. 1-3). The sporophytes are mature but prior to seta elongation.

8.3 Sporophyte foot and seta (Plates IV-V)

The foot is the only part of the sporophyte that remains in contact with the gametophyte during its entire life. At a young stage the basal part of the

seta may also be in direct contact with the surrounding calyptral tissue, as is illustrated for *Brachiolejeunea laxifolia* (FULFORD 1961). During maturation, a small air space develops between the seta and calyptra (Pl. V, fig. 1: black area). The sporophyte foot is composed of a small number of large cells, each c. 60 μ m in diameter. In longitudinal section the foot is inverted-conical in shape (Pl. V, fig. 2: f), and appears to be arranged in tiers. Contrary to *Acrolejeunea* (GRADSTEIN 1975: Pl. 5, fig. 1) the transition foot-seta is very distinct in both *Brachiolejeunea* and *Frullanoides*. The seta cells at this stage are much smaller and are strictly arranged in straight vertical rows.

In Brachiolejeunea and Frullanoides the seta consists of 16 rows of outer cells, surrounding 4 rows of inner cells. SCHUSTER (1980b) reports slight irregularities in the number of both inner and outer cell rows in F. densifolia. The configuration of 16+4 seta cells unites all genera in the Ptychanthoideae, Trocholejeunea excepted, which has 16-32 rows of outer cells and 6-12 rows of inner cells (PI. IV, figs. 8-11; GROLLE 1982). As opposed to non-articulate, the seta in Brachiolejeunea and Frullanoides is articulate, i.e. after elongation all cells of both inner and outer rows are levelled vertically (GRADSTEIN 1975). In longitudinal section the articulate seta in Frullanoides and Brachiolejeunea is composed of c. 13-17 tiers (Pl. V, fig. 2: se). The outer cells in Brachiolejeunea are 144-200 x 50 µm, elevating the capsule to 1.2 mm above the perianth; the outer cells in Frullanoides are somewhat shorter: 95-130 x 35-50 µm, elevating the capsule up to 0.8 mm above the perianth. The two capsule types in the Ptychanthoideae, the "fenestrate-type" and the "nodular-type", are not strictly correlated to seta types. Fenestrate capsules are correlated with articulate and non-articulate setae; in species with nodular-type capsules, however, only articulate setae are present (see Chapter III).

8.5 Sporophyte capsule (Plates XXX-XXXIV)

The mature capsule in *Brachiolejeunea* and *Frullanoides* is dark brown, globose and 0.45-0.60 mm in diameter. Upon dehiscence the capsule splits over 4/5 of its length into four valves. In both genera the valves are 0.5-0.6 mm long and 0.3-0.4 mm wide. The capsules present a set of characters, which show mayor differences between *Brachiolejeunea* and *Frullanoides*, including: 1) the morphology of the valves, 2) the morphology and arrangement of the elaters, 3) the spore morphology and ultrastructure of the exine layer, and 4) the arrangement of spores and elaters in a closed capsule.

8.5.1 Nodular-type capsule (*Brachiolejeunea*; Plates XXX-XXXI)

In this capsule-type the valves remain suberect after dehiscence: the central part remains concave and the lateral parts become \pm plane (Pl. XXX, fig 1), allowing the spores to disperse through relatively narrow slits. The valves are two cell layers thick in the upper half, and 3-4 layers thick in the lower half (Pl. IV, fig. 7; Pl. XXX, fig. 4). Lateral view shows the outer and inner valve layers to be \pm equally thick (Pl. XXX, fig. 5).

The outer cells of the valves are arranged radially, rather small (30-45 x

15-35 μ m) and elongate-hexagonal in the centro-basal part of the valve; much larger (35-65 x 30-55 μ m) and quadrate to rhombic in the apical part. The valves are bordered by a single row of small, quadrate-rectangular cells. In the extreme basal-lateral part of the valve, at the lateral end of the valve dehiscence line, a few cells with ± equally thickened walls are present (PI. XXX, fig. 1: arrow).

Cells of the outer valve layer possess yellowish, sinuose-nodulose thickenings in the angles but not on the intermediate walls. The trigones tend to become confluent in the basal and central part (PI. XXX, fig. 2). The centro-basal part of the valve is characterised by the presence of small cells with thickenings that are more strongly developed than elsewhere. This valve portion is therefore rather inflexible. The valve border cells have enlarged trigones along the valve margin, where they form a continuous line of more or less triangular elements. The trigones in the opposite angles are smaller and confluent with the trigones of the adjacent cells (PI. XXX, fig. 2).

SEM examination shows that the inner valve layer and the capsule base have a smooth surface (PI. XXX, figs. 3-4). LM analysis shows roundish, nodular thickenings present in the angles and on the intermediate, radiate walls of all cells except those in the base of the capsule (above the seta attachment). Where they are present, the yellowish, nodular thickenings are uniformly developed throughout.

In lateral view the cells of the outer valve layer appear to be covered with a wrinkled surface and have a narrow linear pit. The cells of the inner layer show a smooth radial wall with, in addition, a large, rounded to elliptic pit. Frequently the whole cell wall has disappeared and the nodules inside the cells of this layer are indistinctly visible (PI. XXX, fig. 5). The elaters are attached only to the surface of the inner tangential wall.

Two types of elaters are distinguished in *Brachiolejeunea*: marginal elaters, which are attached to the apical part of the valve margin and to the capsule base, and "additional" elaters, which are attached with both ends to the inner valve surface (PI. XXX, figs. 3-4: m.e. and a.e.).

Opposite valves have five marginal elaters (one apical and four lateral), or six marginal elaters. The length of the elaters is correlated with the place of attachment: the apical ones are $325-470 \mu m$ long, the lowermost lateral ones only 220-340 um. The apical end of the marginal elaters is only slightly dilated, but the basal end is dilated into a wide, suborbicular plane. The "additional" elaters are located on the central and lateral parts of the valve. These elaters differ from the marginal elaters in their narrowly tapered ends. Unlike the marginal elaters the "additional" elaters remain attached by both ends to the valve at capsule dehiscence. One central elater, $280-400 \mu m$ long, and two lateral elaters, $145-270 \mu m$ long, are present on each valve. The total number of elaters in a nodular-type capsule is 2x(1+4) + 2x6 + 4x3 = 34. Both marginal and additional elaters are c. $16-20 \mu m$ wide. They are monospiralled by a c. 4 um wide thickening band. The thickenings are pale yellow to almost colourless and often incompletely developed, consisting of wall thickenings only (Pl. XXX, fig. 6).

The mature spores undergo precocious germination; consequently they are

green and relatively large, 45-75(-105) µm in length. Within the capsule the shape of the spores is variable. In a longitudinal section the spores are quadrate to rectangular (PI. XXXI, fig. 2), becoming somewhat irregular near the valves, whereas in a transverse section they are ± rectangular to trapezoid (PI. XXXI, fig. 4). The ornamentation of the spores is described in detail in Chapter III (under 4.7).

A transverse section of the spore capsule shows the marginal elaters to be concentrated along two axes, meeting at right angles in the centre of the capsule and dividing the capsule into four compartments. The alternate location of the elaters on adjacent valves causes the oblique zig-zag pattern in the axes (PI. XXXI, fig. 4: m.e.). Each compartment in the capsule contains a mass of spores, arranged in tetrads. In each compartment this spore mass is intersected only by the three additional elaters (PI. XXXI, fig. 4: a.e.). In longitudinal section the spores are piled up like paired bricks, each spore pair alternating with the pairs above and below (PI. XXX, fig. 6; PI. XXXI, fig. 2). The attachment of the four spores in a tetrad becomes visible when one or two spores are removed.

In the sporeling, which is of the Lejeunea-type (sensu NEHIRA 1983), endogenous germination leads to an increase in size of the spores which is accommodated by stretching of the wall. An eight-celled protonema is formed (two rows of four cells; FULFORD 1956) before the development of the leafy shoot starts. Germination is precocious, i.e. taking place inside the capsule. The shape of the spore changes from rectangular-trapezoid to more roundish-rectangular (PI. VI, figs. 1-2). The ornamentation of the exine is still visible but less dense. The sporeling is initiated on one of the ends of the enlarged spore and three plane, ovate and increasingly large primary leaves are formed, followed by the first juvenile leaf and its accompanying underleaf. Though the first juvenile leaf is characterised by the accompanying underleaf, as well as by its large, saccate-inflated appearance, the third primary leaf may also be more or less saccate-inflated (Pl. VI, figs, 3-4). The first underleaf is ovate-lanceolate in outline and the ventral merophyte is only two cell rows wide here.

8.5.2 Fenestrate-type capsule (Frullanoides; Pl. XXXII-XXXIV)

In this capsule type the upper half of the valves curves outward after capsule dehiscence (PI. XXXII, fig. 1), while the basal half remains more or less convex. The whole capsule thus opens widely, allowing the spores to disperse (the spores are actually hurled out by the movement of the elaters). The valves are two cell layers thick in the upper half, 3-5 layers in the lower half (PI. IV, fig. 6). The outer cell layer of the valve is considerably wider (up to about three times) than the inner layer(s) (PI. XXXIII, fig. 5).

The outer cells of the valves are arranged radially. In the basal-central part of the valve the cells are rather small (20-35 x 15-25 μ m) and elongate-hexagonal, whereas in the apical part they are larger (35-70 x 30-40 μ m) and hexagonal to rhombic to rectangular (PI. XXXII, figs. 1-2). Each valve is bordered by a single row of small, narrow rectangular cells. At the extreme basal-lateral part of the valve, at the lateral end of the capsule

dehiscence lines, a few cells with \pm equally thickened walls are present (PI. XXXII, fig. 1: arrow).

Cells of the outer valve layer possess sinuose-nodulose thickenings in the angles as well as on the intermediate walls (PI. XXXII, fig. 2). Contrary to the nodular-type capsules, the thickenings are uniformily developed throughout and do not become confluent in the central part of the valve.

The cells of the inner valve layer are smaller than those of the outer layer. In the central part the areolation is longitudinal, in the apical part it is radial. Cells in the central part are subquadrate to rectangular, in the apical part rectangular to rhombic (PI. XXXII, figs. 3-5). Except for the smooth base of the capsule (PI. XXXII, fig. 6) the inner tangential walls of the cells are covered with yellow-brown, sheet-like thickenings, except for 4-12 pitted regions ("fenestrae"), which appear as depressed areas in SEM micrographs (PI. XXXII, figs. 3-4; PI. XXXIII, fig. 5). The fenestrae are circular to oblong in shape. The thickened cells are normally plurifenestrate, but in the apical part the number of fenestrae is usually lower (4-6 versus 6-12) and occasionally reduced to only one ("monofenestrate").

In the central part of the valve 5-7 ridges are present, consisting of narrow-rectangular cells which protrude from the valve surface (PI. XXXII, fig. 5). Five ridges are present in *F. bahamensis* and *F. corticalis* (characterised by the presence of 30 elaters). Seven ridges are present in the other species (with 56-68(=72?) elaters). Both apical and basal ends of the ridges are formed by tapering cells. In the capsule base they are short and blunt and protrude shortly into the smooth capsule base (PI. XXXII, fig. 6); in the apical part of the valve they are long and narrow and protrude into the radially arranged cells (PI. XXXII, fig. 4). In a closed capsule the ridges separate the vertically arranged piles of spores that are adjacent to the inner surface of the valve.

In lateral view the cells of the outer valve layer appear to be covered with a wrinkled surface and have a narrow linear pit. The inner valve layer is very thin and SEM examination shows hardly more than the margin of the plurifenestrate thickenings of the inner tangential wall (PI. XXXIII, fig. 5). Elater attachment is seemingly only on to the surface of the thickening layer.

All elaters are regularly distributed over the inner surface of the apical region of the valves. In a closed capsule they are in a vertical position and attached by their broadly dilated bases to the smooth inner capsule base (PI. XXXIII, fig. 4). The elaters, at equal distances from each other, are arranged regularly as is clearly reflected in the attachment pattern on the capsule base. As to the number of elaters per capsule, two types exist.

In type "1" the valves have alternately 16 (1+3+5+7) elaters or 20 (2+4+6+8) elaters, totalling 72 elaters per capsule. This capsule type is found in most genera of Ptychanthoideae, but in *Frullanoides* only 68 elaters (valves with 16 (1+3+5+7) or 18 (2+4+6+6) elaters) and 56 elaters (valves with (1+3+5+7) or (2+4+6) elaters) have been found. We assume that these lower numbers are due to the loss of elaters during capsule dehiscence and spore dispersal.

In type "2" the valves have alternately 9 (1+3+5) or 6 (2+4) elaters,

totalling 30 elaters per capsule. This arrangement is present in *Frullanoides* bahamensis and *F. corticalis* (Pl. XXXII, fig. 3).

The length of the elaters is correlated with the place of attachment, hence а considerable_ variation observed: 260-550 μm. The elaters are (15-)18-20(-25) µm wide, and monospiralled by a well developed, yellow-brown thickening band, which is c. 4 um wide. The thickening band encircles the free, flattened, suborbicular basis of the elater and extends to just below the apical attachment at the valve (PI. XXXIII, fig. 5). Close examination of elaters shows ornamentation with very small, randomly scattered punctae on the spiral band and small, pit-like depressions in the elater wall just adjacent to the spiral (PI. XXXIII, fig. 6). These punctae are, besides for Frullanoides densifolia, reported for Spruceanthus marianus (CRANDALL-STOTLER 3 GEISSLER 1983) and Marchesinia brachiata (GEISSLER & GRADSTEIN 1982).

The mature spores undergo precocious germination; consequently they are green and relatively large, $38-65 \mu m$ in diam. Within the capsule the spores are isodiametric and possess a \pm regular, polyhedral shape with eight pentagonal or hexagonal facets (PI. XXXIII, figs. 2-3). Upon sporeling development spores turn globose. The distal facet of the spore is always somewhat larger than the proximal facets (PI. XXXIII, fig. 2). The spore surface is ornamented in various ways (Chapter III: 4.7.2) and includes one "rosette" per facet, hence a total of eight rosettes per spore. The regular shape of the spores of *Frullanoides* greatly contrasts with the irregular spore shape in *Brachiolejeunea*.

Spore ornamentation is developed prior to tetrad separation, as has been shown for *Spruceanthus marianus* by CRANDALL-STOTLER & GEISSLER (1983). The ornamentation is described in detail in Chapter III (under 4.7).

Spore storage and elater arrangement have been studied by means of longitudinal and transverse sections of a closed capsule. Both sections show a very regular arrangement of the elaters, which intersect the spore mass at equal distances from each other. The spore mass is made up of square vertical columns, with an elater on each corner, in which the individual spores are piled in tetrads. Tetrads are made up of two perpendicularly arranged pairs of spores (PI. XXXIII, fig. 3). The spores of each pair are parallel to one another. The attachment of the spores in the tetrads is located in the centre of each column. Spores of adjacent columns have their distal facets facing each other.

In the sporeling, which is of the *Lopholejeunea*-type (*sensu* NEHIRA 1966, 1974, 1983), endogenous germination leads to an increase in size of the spores, the spore wall stretching to accommodate this increase. In this sporeling type the number of cells in the enlarged spore varies from 4 to 20 before the development of the leafy shoot starts. Germination is precocious, i.e. it takes place inside the capsule. The shape of the spore changes from isodiametric with eight facets to more or less spherical. The ornamentation of the exine is still visible during this enlargement and forms an even covering (FULFORD 1942b) although the rosettes become less clear (Pl. VI, figs. 6-7).

After emergence of the mature protonema 3(-5) primary leaves are formed,

which are small, plane and ovate (FULFORD 1942a-c). Each new primary leaf is larger than its predecessor. The sporeling at this stage is rather compact (PI. VI, fig. 6-7). Usually the third primary leaf is followed by the juvenile leaves, which are much larger in size and saccate-inflated with the lobule nearly as large as the lobe. The first, narrow lanceolate underleaf is formed at the same time as the first juvenile leaf.

PHYLOGENY OF FRULLANOIDES AND BRACHIOLEJEUNEA

In this chapter, an attempt is made to analyse the phylogeny of *Frullanoides* and *Brachiolejeunea* using the cladistic approach (e.g. WILEY 1981). As the genera are now considered to belong to different tribes, it can be assumed that their evolutionary histories occurred along very different lines. No attempt has therefore been made to integrate the results.

I have considered WAGNER's "groundplan/divergence" method for the phylogentic analysis of *Frullanoides* and *Brachiolejeunea* an approapriate method. The method is considered phylogenetic *sensu* Hennig (WILEY 1981) and aims at linking subtaxa (here: species) within a taxon (here: genus) by means of their relative degree of apotypy. Both the assignment of an ancestral bodyplan of the group, i.e. a set of characters present in the hypothetical ancester of the group, or an out-group comparison can be used to determine the polarity of the involved characters. Calculation of a Wagner tree can be done by hand for a small data set, and several methods have been described (e.g. WHIFFIN & BIERNER 1972, WILEY 1981). For a computer analysis of large data sets algorithms, based on the parsimony criterium have been developed by KLUGE & FARRIS (see WILEY 1981: 180-192). This algorithm is used here; my data set allowed hand application for both genera.

I have assigned an ancestral bodyplan, using the principle of "common equals primitive" to determine the polarity of character states. However, as pointed out by WATROUS & WHEELER (1981), out-group comparison is needed to differentiate those cases where common equals primitive from those where it does not. Future analysis using the out-group rule may deal with this disadvantage of *a priori* statements, used in the application of the commonality principle.

Following the assignment of the ancestor or of an out-group, a matrix of characters is drawn. Plesiotypic character states score 0, apotypic states 1. When the transformation series contains more than two homologues, so called intermediate apotypies may be scaled between 0 and 1. As to graphic presentation, results of Wagner analyses are normally plotted on concentric semicircles, presenting degrees of divergence. The algorithm procedure applied here leads to the construction of cladistic trees.

Frullanoides

A cladistic reconstruction of the phylogeny of the taxa in *Frullanoides*, based on three-taxon statements and using out-group comparison, is presently difficult to execute. Some of the potential out-groups are in strong need of revision (*Mastigolejeunea*), others show variation in relevant characters to an extent that the direction in evolutionary development can hardly be determined (e.g. stem anatomy, location of hyaline papilla, and leaf lobule structure in *Acrolejeunea*; seta-type, innovation-type and stem structure in *Trocholejeunea*. The assignment of polarity to the character states should therefore be considered speculative, and is in part based on current phylogenetic thinking (e.g. SCHUSTER 1980b). General overviews of the Lejeuneaceae have demonstrated that the general tendency in the family is one of reduction and differentiation (e.g. EVANS 1935, SCHUSTER 1980b). I have therefore assumed that the ancestor of *Frullanoides* featured the following characters: 1) large plants with heavy, asymmetric stems that had no clearly differentiated cortex and medulla, 2) leaf lobule with many teeth, 3) underleaves with large auricles, 4) dioecious sex distribution, and 5) sporophyte with many (72) elaters. These assumptions have lead to the designation of *F. densifolia* ssp. *densifolia* as the species with the largest number of plesiotypic character states (Table 2). Table 2 shows the matrix for 14 characters; table 3 the computed differences between the taxa.

Table 2.	Character matrix of the taxa in <i>Frullanoides</i> ; 0 = plesiotypic state,
	0.5 = intermediate apotypic state, 1 = apotypic state; A = F.
	densifolia ssp. densifolia, B = F. densifolia ssp. grandidentata, C =
	F. laciniatiflora, $D = F$. tristis, $E = F$. liebanniana, $F = F$.
	mexicana, $G = F$. corticalis, $H = F$. bahamensis.

TAXON		CHARACTER												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0
В	0	0	0	0	0	0	0.5	0	0	0.5	1	0	0	0
с	0	0	0	0	0.	1 ·	0.5	0	0	0	.0	0		0
D	0.5	0	1	0	1	0	0.5	0	0	0.5	1	0	0	0
Е	0.5	0	1	0	ı	0	1	0	0	0.5	0	0	0	0
F	0.5	0	1	0	0	0	÷ 0	1	0	0.5	0	0	0	0.
G	1	1	1	1	1	0	0.5	0	1	1	0	1 .	1	1
н	1	1	1	1	1	0	0.5	0	. 0	1	1	0	0	0

TAXON	A	В	С	D	E	F	G	Н
A	0	1.5	1	4	3.5	3.5	10	8
В		0	2.5	2.5	4	4	10.5	6.5
С			0	5	4.5	4.5	11	9
D				0	1.5	3.5	8	4
E					0	3	7.5	5.5
F						0	9.5	7.5
G							0	4
H								0

Table 3. Computed differences between the taxa of *Frullanoides*. A-H similar to Table 2.

1 <u>Size of plants</u>: plants large (0), medium (0.5), or small (1). Large, loosely spreading plants are considered more primitive, whereas small, compact plants are considered more advanced.

- 2 Branching: mainlyFrullania -type (0), or mainly Lejeunea-type (1). Surveys of branching types in the Lejeuneaceae show Frullania-type branches to be mainly present in groups that are considered more primitive and Lejeunea-type branches in groups that are more advanced (EVANS 1935; THIERS 1982, 1984, 1985).
- 3 Ventral cortex: thickened and similar to the medulla (0), or clearly differentiated (1). I follow EVANS (1935) who postulated that primitive stems in the Lejeuneaceae are large and uniform in structure, and that development points towards reduction and differentiation between cortex and medulla.
- 4 <u>Ventral merophyte</u>: more than four cell rows wide (0), or only four cell rows wide (1). Advancement coincides with a reduction of the width of the ventral merophyte.
- 5 Dorsal leaf insertion: auriculate (0), or straight (1). The designation of *F*. *densifolia* as species with the most plesiotypic character states points the direction of advancement.
- 6 <u>Leaf apex/female bracts and bracteole/subgynoecial under</u>leaf: entire (0), or serrulate/ciliate (1). Teeth and ciliae are confined to *F. laciniatiflora* and therefore considered autapotypic.
- 7 Lobule teeth: 8-11 (0), (3-)5-9 (0.5), or 3-5 (1). A development towards reduction of the number of teeth follows the assumption of the character state in the hypothetical ancestor.
- 8 Lobule teeth size: of more than one cell (0), or only one cell (1). One-celled teeth are only found in F. mexicana and estimated an autapotypy.
- 9 Hyaline papilla: situated at the base of the first tooth of the leaf lobule (0), or at the second tooth (1). The phylogenetic direction of this character is difficult to determine. In *Frullanoides* a location at the second tooth is present only in *F. corticalis*, and is therefore considered

autapotypic.

- 10 Underleaf auricles: large (0), medium-sized (0.5), or small (1). The character states follow the assumption of large auricles in the hypothetical ancestor.
- 11 <u>Sex distribution</u>: dioecious (0), or autoecious (1). Both in mosses (VITT 1971) and in hepatics (SCHUSTER 1966) the dieocious condition is considered to be more primitive, and has accordingly been hypothesised in the common ancestor of the group.
- 12 <u>Subgynoecial leaf</u>: similar to other vegetative leaves (0), or divergent (1). In \overline{F} . corticalis the lobule of the subgynoecial leaf is of consistently different outline (PI. XXVII, fig. 2) from that of the other vegetative leaves. The apotypy is based on the commonality principle.
- 13 <u>Male bracts</u>: always epistatic (0), or (partially) hypostatic (1). A direction of this character is difficult to determine, and designation of the states only follows the commonality principle.
- 14 <u>Sporophyte</u>: with 56-68 (72) elaters (0), or with 30 elaters (1). As is shown in Chapter III, the distribution of the character states in the primitive subfamilies of the Lejeuneaceae indicates that the presence of 72 elaters (or almost that number) is regarded as the more primitive state and that advancement towards reduction has occurred in a few genera. *Frullanoides* is the only genus of the Ptychanthoideae where both states are present.

Fig. 1 shows the computed Wagner tree for *Frullanoides*. The tree shows the species with large plants to be the least different from *F*. *densifolia*, and the small and compact species to be the most different. The taxa A and C are computed as the least different from each other (Table 3: 1); therefore they are the first to be connected with each other in the construction of the phylogenetic tree. The next least different taxon, B (= *F*. *densifolia* ssp. *grandidentata*) is now connected to A and C through the assumption of a hypothetical common ancestor, and so on. This method of construction, based on the application of the parsimony criterium, leads to an estimated tree of minimum evolutionary steps. After calculating the tree, I assigned a hypothetical common ancestor ANC in order to normalise its appearance.

Brachiolejeunea

In order to establish the relative apotypy of the taxa in *Brachiolejeunea*, out-group comparison has been applied instead of the designation of an ancestral bodyplan. The out-group of *Brachiolejeunea* is to be found in the group of genera of Ptychanthoideae with nodular-type sporophytes (= tribe Brachiolejeuneae, see Chapter III). In this group the genera *Blepharolejeunea* and *Lindigianthus* are the most closely related genera that have been revised (therefore *Dicranolejeunea* and *Odontolejeunea* cannot serve as such). Most closely related is interpreted here as having the greatest number of morphological, anatomical and geographical similarities. In view of the characters in the data matrix the species of *Blepharolejeunea* with mainly *Frullania*-type branches (*B. chimantaensis*, *B. incongrua*, *B. securifolia*) now pro-

ved to serve best as out-group. The out-group features by definition the plesiotypic character state when compared with the in-group. Table 4 shows the matrix for the six characters involved; table 5 the computed differences.

Table 4. Character matrix for the taxa in Brachiolejeunea; O = plesiotypic state, 1 = apotypic state; Blep. = Blepharolejeunea, A = B. fernandeziana, B = B. spruceana, C = B. leiboldiana, D = B. laxifolia.

TAXON	CHARACTERS							
	1	2	3	4	5	6		
Blep.	0	0	0	0	0	0		
A	0	0	1	1	0	1		
В	0	0	1	1	0	0		
С	0	1	0	0	0	0		
D	1	1	1	1	1	0		

Table 5. Computed differences between the taxa of *Brachiolejeunea*. Blep. and A-D are similar to Table 4.

TAXON	Blep.	A	В	С	D
Blep.	0	3	2	1	5
A		0	1	4	5
В			0	• 3	3
с				0	4
D					0

- 1. Ventral cortex: cells short rectangular (0), or long and narrow rectangular (1).
- 2. Paraphyllium: absent (0), or present (1).
- 3. Lobule teeth: two teeth (0), or more than two teeth (1). Note that the direction of this character is reverse to the direction in *Frullanoides*.
- 4. Leaf lobule free margin: distinct angle present (0), or absent and then with gradually curved margin (1).
- 5. Ventral merophyte: four cell rows wide (0), or 4-8 cell rows wide (1).
- 6. Branching: always mainl&rullania -type (0), or Frullania -type and Lejeunea-type evenly present (1).

When the tree is constructed, it is shown in Fig. 2 that taxon C (= B. *leiboldiana*) is the least different from the out-group, and then the taxa B (= B. *spruceana*) and A (= B. *fernandeziana*) respectively. However, the attachment to the tree of taxon D (= B. *laxifolia*) remains unresolved since
the total of apotypic character states of D when compared with A, B, or with the hypothetically assumed ancestor of A and B, is equal in all three cases. Therefore the phylogenetic tree for *Brachiolejeunea* shows a polytome on this location.

It must be noted that a precise, cladistic analysis of the taxonomic entities (genera, species) within the well delimited, next higher taxon (i.e. the tribe Brachiolejeuneae, see Chapter III) may throw more light on the matter of phylogenetic reconstruction.



Figure 1. Wagner tree of Frullanoides.



Figure 2. Wagner tree of Brachiolejeunea.

DISTRIBUTION (Plates XXVII-XXIX)

The genus *Brachiolejeunea* is distributed in the tropical and southern temperate regions of Latin America, ranging in altitude from sea-level to 3500 m. The highest records are from Colombia and Ecuador. The genus is primarily distributed in the Andes, with its northernmost limit in Mexico (at \pm 30° N. Lat.), and the southernmost limit as far down as Tierra del Fuego at 56° S. Lat. The major gap in its distribution corresponds with the arid regions of the Atacama desert in Northern Chile. Besides in the Andes, the genus is present in Southeastern Brazil, where comparable heights are reached in the Sierra Itatiaia, and in the mountainous areas of some Caribbean islands. The genus is still unknown in most parts of Central America and the Caribbean. This is most probably due to insufficient collecting since suitable habitats are likely to be found in these regions.

GRADSTEIN et al. (1983) use the following altitudinal zonation to characterise (neo)tropical species: lowland = 0-800 m; submontane = 800-1600 m; montane = 1600-3000 m; subalpine = 3000-3600 m; alpine = above 3600 m. The altitudinal characterization of the species of Brachiolejeunea is shown in Table 6. *B. fernandeziana* and *B. spruceana* in brackets because they occur outside the tropical belt.

Species	Altitude (m)	Zone
(B. fernandeziana	600-915	lowland to submontane)
B. laxifolia	(1500-)2000-3500	montane to subalpine
B. leiboldiana	800-1650	submontane
(B. spruceana	0-400	lowland)
F. bahamensis	0-350	lowland
F. corticalis	0-200(-650)	lowland
F. densifolia	0-1000/600-2500(-3650)	lowland to montane
		(to subalpine)
ssp. grandidentata	450-750	lowland
F. laciniatiflora	2000-3200	montane to subalpine
F. liebmanniana	200–1000	lowland to submontane
F. mexicana	20–600	lowland
F. tristis	0-1000(-3000)	lowland to montane

Table 6. Altitude and altitudinal zonation of Brachiolejeunea and Frullanoides.

It must be emphasised that the altitudinal values of the zones are much lower on oceanic islands (*B. fernandeziana*, *F. densifolia* ssp. grandidentata) and at

higher latitudes (*B. spruceana*) (GRADSTEIN et al. 1983: 131). Therefore the genus *Brachiolejeunea* may be characterised as a Neotropical-montane element with extensions into the submontane and subalpine zones.

Except for *F. tristis*, *Frullanoides* is distributed only in the tropical regions of Latin America (with a few locations in southern temperate areas). *F. tristis* is pantropical and is present, besides tropical Latin America, in tropical and southern temperate Africa and in tropical and northern temperate Asia (PI. XXIX). The genus ranges in altitude from sea-level up to 3650 m. The highest records are from Mexico, Colombia, Peru and Nepal. The northernmost limits in America are in southern Florida and the Bahamas (\pm 25° N. Lat.) while below the equator the genus extends south to the province of Valdivia in Chile at \pm 40° S. Lat. In Africa the limits are N. Nigeria and Ethiopia in the north and the Cape Province in South Africa in the south. In Asia the northernmost location is at 27° N. Lat. The main centre of distribution of the genus is Central and South America with four species in Mexico, Brazil and Peru, and three in Colombia.

As to altitudinal zonation several species of *Frullanoides* show a considerable range (*F. densifolia*, *F. tristis*), while others are present in a rather narrow range only (*F. bahamensis*, *F. mexicana*). The altitudinal range of *F. densifolia* ssp. grandidentata is probably low due to the compression of altitudinal zonation on islands.

It is difficult to characterise the distribution of *Frullanoides* on a generic level since it contains both Caribbean elements ("coastal oceanic-Neotropical", cf. GRADSTEIN & WEBER 1982) as well as Neotropical-montane and "wide-tropical" elements. Nevertheless, most species of *Frullanoides* occur in mountainous areas, so the genus may be considered in general to be Neotropical-submontane with *F. bahamensis*, *F. corticalis* and *F. mexicana* as typical lowland elements.

PHYTOGEOGRAPHICAL CONSIDERATIONS

The geographical distribution of *Brachiolejeunea* and *Frullanoides* strongly suggests a Gondwana origin for each of the genera. Regarding the mezozoic development of this continent, SCHUSTER (1983) argues that: 1) after its fragmentation (between 80-50 milj, years ago) the southern and western parts of South America became increasingly isolated and that these parts remained isolated from the Guiana sector until the mid-Tertiary, and 2) that the time interval between 80-50 milj, years ago and the present has been adequate for evolution and endemism in these areas.

view of this argumentation the distribution of the species of ln. Brachiolejeunea indicates a development of the genus that has been restricted to the southern and western parts of Gondwanaland. The spores of B. spruceana may have spread to Antarctica but southward migration and subsequent cooling of this continent, already starting in the mid-Cretaceous, probably lead to the extinction of the species in that area. The distribution of B. fernandeziana indicates endemism. Phylogenetic reconstruction of the Brachiolejeunea point rather genus at а advanced position of Β. fernandeziana, so a possible relict origin of this distribution seems less likely.

Brachiolejeunea laxifolia and B. leiboldiana also originated on the western fringe of Gondwanaland and their strict adaptation to wet, mountainous areas may be reason that they did not (yet) invade the Guiana sector after the mid-Tertiary. Both species have spread into Central America and the Caribbean. This may have been possible via short-range dispersal since the late Cretaceous (± 70 milj. years before present) since scattered islands existed in this region until the uplift of the Central American region started in the Miocene (RAVEN & AXELROD 1974). This uplift coincided with the uplift of Jamaica, where both species are also found. Especially the spores of the paroecious B. laxifolia may have been suitable for further invasion of the Antillian Arc, where it is presently found only on Hispaniola. The presence on Jamaica suggests the capacity for long-distance dispersal (RAVEN & AXELROD 1974: 548), which seems presently sustained in B. laxifolia. Dessication experiments with spores of this species indicate a resistance that may enable transport in dry or wet air currents at relatively low altitudes during a longer period of time (\pm 10-20 days, cf. van Zanten & Gradstein, in mss). Experimental data furthermore illustrate the difference in resistance capacity of *B. laxifolia* when compared with two species of the related genus Blepharolejeunea (B. incongrua and B. securifolia). These species are confined to the very wet, higher parts of the Andes chains (VAN SLAGEREN & KRUIJT 1985) and accordingly have shown a virtual lack of drought resistance (a few hours only, cf. van Zanten & Gradstein, in mss).

SCHUSTER (1966) postulated that in liverworts monoecious taxa tend to be distributed more widely than dioecious taxa. Assuming that *B. leiboldiana* is dioecious (males have not yet been found) this does not hold for *Brachiolejeunea* (see PI. XXVIII). It does hold, however, for *Frullanoides*, where only *F. bahamensis* may be an exception (see below).

Frullanoides most likely also originated in the western part of Gondwanaland. One species (the paroecious *F. tristis*) may have spread to the eastern part of Gondwana (India) before it began to rift apart from the central part (Africa) about 100 million years ago (RAVEN & AXELROD 1974). Presumably its capacity for drought tolerance and preference for mountainous habitats contributed to the survival of this species during the migration of India since the climate on this continent changed from humid to more seasonally arid. After reaching Laurasia 35-40 million years ago, the species could spread northward onto the Himalayas. The present occurrence of *F. tristis* at high altitudes (\pm 3000 m) in the northern temperate Himalayas is nevertheless remarkable since the mainly tropical distribution of the species would indicate a restriction to lower altitudes in the temperate zones. Unfortunately data on the spore resistance to drought and low temperatures are still lacking.

The centre of diversification of Frullanoides remained western Gondwanaland. Here most dioecious species assumedly developed and, despite a less effective dispersal, migrated northward into the Central American and Carribean regions; one species migrated also into southern temperate regions (F. densifolia; Pl. XXIX). As in Brachiolejeunea, migration into southern Central America may have been possible via the "stepping stones" formed by scattered islands, present in that area. The Guiana sector was also colonised since three species are now present in that area. During this diversification the taxa of Frullanoides remained in general restricted to mountainous areas although several of them became to lower altitudes (F. liebmanniana, F. densifolia, F. tristis). It is assumed that several species developed from an already present stock (e.g. F. laciniatiflora, F. mexicana). The development of F. mexicana is perhaps more recent than that of F. laciniatiflora since the species is confined to Central America, whereas its altitude may reflect its increasing adaptation to lower altitudes.

Two distributional features of *Frullanoides* deserve further attention: 1) the presence on the Galapagos, and 2) the distribution of *F*. *bahamensis* and *F*. *corticalis*.

The Galapagos islands are of recent age (late Pliocene) and there seems to be no evidence that they were ever connected to the mainland (GRADSTEIN & WEBER 1982). Consequently the flora consists of recent colonists. Though at present the direction of the wind varies from northeast to southeast, enabling immigration from the mainland, this may not always have been so in the past. I nevertheless assume that the widespread F. tristis has been succesful in long-distance dispersal from the mainland to the archipelago. F. densifolia ssp. grandidentata, which is confined to the islands, is to be regarded as a recent endemic taxon. The presence of the Neotropical-Carribean element F. bahamensis on the Galapagos (GRADSTEIN & WEBER 1982: 138) has been tentatively suggested and proved to be misidentified F. tristis.

The distribution of F. corticalis and, especially, F. bahamensis is different from the other species of the genus in the following ways: 1) they are restricted in their occurrence to low altitudes, 2) their main presence is in the Caribbean, and 3) they are present in Florida, U.S.A. Since several other species of the genus are also present in the Caribbean (F. *liebmanniana*, *F. tristis*), each of which did not migrate into Florida, the origin of *F. corticalis* and *F. bahamensis* might have been in the Caribbean area or at least in the northern part of West Gondwanaland. Short-range dispersal would then have enhanced their succesful migration through the Antillean Arc and to Central America. The presence of *F. corticalis* in Southeastern Brazil, however, suggests a capacity for long-range dispersal as well. It is assumed finally, that a possible adaptation of *F. bahamensis* and *F. corticalis* to low altitudes, together with a tolerance for seasonal drought and for brackish and maritime conditions (mangrove!), explains their succesful distribution in the Caribbean.

In summary, the following, hypothetical picture of the evolutionary history of *Frullanoides* arises. In the lower Cretaceous *Frullanoides*-like taxa existed on Western Gondwana. A dioecious stock slowly migrated over this western part in northern direction. A paroecious stock migrated much faster in both northern and eastern directions and reached the Indian part of Gondwana before this began to migrate towards Laurasia. Since the late Cretaceous migration into Central America and the Caribbean occurred; since the mid-Tertiary also into the Guiana sector. After invasion of the Caribbean new taxa arose, probably by adaptation to local conditions. Distribution patterns of several species indicate a potential for long-range dispersal, hence the presence of one of them on oceanic islands.

The phylogenetic tree of *Frullanoides* (Fig. 1) helps to explain the distribution patterns only to a limited extent. The autoecious species *F*. bahamensis and *F*. tristis appear greatly divergent from the ancestor, so probably the change in sex distribution may have occurred relatively late. The bisexual spores, however, warrant a rapid distribution, especially when coinciding with adaptation to a great variety of habitats. One may now hypothesise that one of the areas to which *F*. tristis has spread has been the Caribbean, and that the two most "modern" species of the genus, *F*. bahamensis and *F*. corticalis, evolved there out of a *F*. tristis-like ancestor. How the dioecious *F*. corticalis spread more widely than the monoecious *F*. bahamensis remains a matter of dispute.

It is noteworthy that the distribution pattern of Acrolejeunea subg. Acrolejeunea is fundamentally similar to that of Frullanoides (GRADSTEIN 1975). This may indicate, besides similarities in several morphological characters, a close taxonomic relationship. On the contrary the genus Trocholejeunea, which is considered to be closely related to both Acrolejeunea and Frullanoides, is distinctly Laurasian in distribution. The two present species of this genus occur in Southeastern Asia and the Pacific, and RAVEN & AXELROD (1974) argue that it is unlikely that any part of S.E. Asia was once a part of Gondwana. The gametophytic characters of Trocholejeunea, which indicate a close taxonomic relationship to Frullanoides, are therefore apparently the result of parallel development. PHENETIC GENERIC CONCEPTS AND RELATIONSHIPS (Tables 7-8; Plates 1-IV)

In the past, taxonomic characters in the Lejeuneaceae have been derived at the generic level from the gametophyte generation, e.g. general growth and branching patterns, leaf lobule structure, perianth morphology and presence or absence of vegetative propagation (SPRUCE 1884, EVANS 1908a). More recently characters have been derived from stem anatomy (EVANS 1935, BISCHLER 1965), merophyte topography (MIZUTANI 1969a), oil body type (SCHUSTER 1961, 1963; GRADSTEIN 1975), male bracts (GRADSTEIN 1975), branch- and innovation morphology (MIZUTANI 1970), trigones (GRADSTEIN 1975), and underleaf base anatomy (WINKLER 1970).

Sporophyte characters in the Lejeuneaceae have so far been employed mainly at the subfamilial level (MIZUTANI 1961, 1979a), but GEISSLER & GRADSTEIN (1982) have recently called attention to the existence of different types of sporophytes in the subfam. Ptychanthoideae. In the present work special attention has been paid to the neglected sporophyte characters, which has lead to a revised generic concept for *Brachiolejeunea* s.l.

Several authors have called attention to the close relationship between Brachiolejeunea s.l., Trocholejeunea and Acrolejeunea (e.g. EVANS 1908a, VERDOORN 1934c, SCHUSTER 1963, GRADSTEIN 1975). The three genera were united in the "Brachiolejeunea-complex" by GRADSTEIN (1975), based on the presence of homogeneous oil bodies, epistatic male bracts, a non-articulate seta and on similar stem anatomy. Relationships were also postulated between Brachioleieunea and Dicranolejeunea and between Frullanoides and Mostigolejeunea. The relationships among these genera are shown in Table 7. Two further genera are added: Blepharolejeunea, which was recently emended to accommodate several species formerly placed in Brachiolejeunea and Dicranolejeunea (VAN SLAGEREN & KRUIJT 1985), and the monotypic genus Lindigianthus, which was recently erected as a segregate of Dicranolejeunea (KRUIJT & GRADSTEIN 1985). MIZUTANI (1979b) also placed his genus Cephalolejeunea in the Brachiolejeunea-complex, but in my opinion this genus does not belong here and is therefore not included in Table 7.

The characters in Table 7 are arranged as follows: characters 1-11 illustrate differences between *Brachiolejeunea* and *Frullanoides* (except 4!), 12-17 illustrate GRADSTEIN's (1975) *Brachiolejeunea*-complex, 14-17 and 18-22 illustrate various diagnostic characters of individual (or groups of) genera, and 23 has been added for comparison.

Annotations to Table 7.

Sporophyte (1-6). The sporophytes of *Frullanoides* and *Brachiolejeunea* are of the fenestrate-type and the nodular-type respectively (see Morphology and Anatomy and Chapter III) and furnish the most fundamental differences between these two genera. The seta, however, is articulate in both genera. The sporophyte is discussed in detail in Chapter III.

Perianth (7). The bluntly trigonous perianth of Brachiolejeunea and the

GE	NUS	Mastigolejeunea	Acrolejeunea	Trocholejeunea	Frullanoides	Brachiolejeunea	Blepharolejeunea	Dioranolejeunea	Lindigianthus
	\rightarrow			<u> </u>		r			
1. Theca inner layer fenestrate (+) or		¦ +	+	+	+i	į -	-	-	-
nodular (-)	.	1	+	+	1	!_	-	-	_ }
2. Spores isociametric (+) or irregulari	,	1	*	*	1	1	-	-	
 elongated (-) Value at debiacence curving outwardly 		+	+	+	+	i -	-	-	_
(+) or staving subsect (-)		1	•	•	·	į			1
4. Seta not articulate (+) or articulate		+	+	+	- 1	-	_	-	-
(-)					į	1			
5. Sporeling Lopholejeunea-type (+) or		i+	+	+	+ İ	!_	-	-	-
Lejeunea-type (-)					į	1			1
6. Elaters with well developed spiral (+	·)	+	+	+	+ !	! -	-	-	- į
or wall thickenings only (-)						į			
7. Perianth with 2-5 ventral plicae (+)	or	¦±	+	+	+	-	-	-	-
0-1(-2) ventral plicae		-				1			i
8. Stem with massive, thick-walled medua	.1a	+	+	(x)	+	-	-	-	(x)
(+) or thickened cortex/outer medulls	(-)	{				ł			i
9. Underleaf attachment bistratose (+) o	r	+	+	+	+	į -	±	-	-
tristratose (-)									
10. Dorsal merophytes zig-zag (+) or in		-	±	-	+	i - I	÷	-	-
straight lines (-)									
11. Plants with secondary pigment (+) or		+	-	-	11	LE	-	-	-
not (-)			r			7			
12. Dorsal cortical cells larger than		+	±	+	+	+ i	-	-	-
ventral (+) or equal in size (-)						. 1			
13. Ventral merophyte at least 4 cell row	/5	+	+	+	+	+	-	-	-
wide (+) or 2-4 cell rows wide (-)		<u>r</u> -1					ŗ	7	רבי
14. Uil bodies homogeneous (+) or segment	ed		1 +	+	+	- + I	17	-	
(-); Massula-type (M), Jungermannia-	ype	L <u>-</u>]	^m	M	M	m		ا د ا	
(J) or Catypogeta-type (C)		*	1	-	-		1	- I	
13. Leaves superect-convoluted (+) of with	Tera	Ŧ	! *	Ŧ	. •	Ť	ļI	Ξį	1
be leaf cells elongeted (+) or feediame	tric	+	+	+	+	+ !	+	+	-
(-)		•	ļ.	•	•	•	<u>-</u>	÷	
17. Trigones cordate (+) or triangular to	,	+	+	+	+	+	+	+	-
radiate (-)			L			l	- <i>ت</i> ا	=J	· ـ ـ ـ ـ
18. Seta 16+4 cells (+) or (16-32)+(8-16)	,	+	+	[]]	+	+	+	+	+
cells in cross section (-)						_			
19. Innovations present (F, J, L) or		[1]	[]]	F	[]	J	J	J,L	J
absent (-)					L	J			
20. Branching predominantly Frullania-ty	pe	-	±	±	±	+	+	±	±
(+) or Lejeunea-type (-)									
21. Male bracts epistatic (+) or		-	+	+	+	+	+	+	+
hypostatic (-)									
22. Shoots not dimorphic (+) or dimorphic	-		+	+	+	+	+	+	+
(-)									
23. Number of teeth on leaf lobule		1-3	1-10	2-4	3-11	L 2-4	2	2	2

Table 7. A comparison of Brachiolejeunea, Frullanoides and related genera.

pluriplicate perianth of *Frullanoides* have constituted a diagnostic difference since both taxa were established as subgenera

(SCHUSTER 1963). The perianths of *Frullanoides* and *Trocholejeunea* differ to a certain extent since the plicae of the latter are frequently alate (HERZOG 1951). The perianth of *Brachiolejeunea* differs from the related genera in its rounded keels, which are sharp and often toothed in the other genera (*Blepharolejeunea securifolia* excepted, see Chapter II).

- Stem anatomy (8; Plate 1). Comparative stem anatomy shows that the type of stem is different in Brachiolejeunea and Frullanoides. In Acrolejeunea, Mastigolejeunea and Frullanoides a thick-walled medulla is present (Pl. 1, figs. 1-2, 7-8, 11-12, in Acrolejeunea and Frullanoides this is surrounded by a distinct hyalodermis. In Mastigolejeunea the cortex is also thick-walled. The uniformly thick-walled medulla is opposed to the uniformly thin-walled medulla, surrounded by a thick-walled cortex, found in Brachiolejeunea, Blepharolejeunea and Dicranolejeunea (Pl. 1, figs. 3, 5, 9-10). In Dicranolejeunea axillaris the thickenings are located in the outer rows of the medulla rather than in the cortex (Pl. 1, fig. 6). The stems of Trocholejeunea and Lindigianthus show a ± equally thick-walled cortex and medulla (Pl. 1, figs. 4, 13).
- Underleaf attachment (9; Plate II). The bistratose, Stictolejeunea-type attachment (WINKLER 1970) is present in Frullanoides and related genera, whereas the tristratose, Symbiezidium-type is present in Brachiolejeunea and related genera. In Blepharolejeunea, however, both types are present (VAN SLAGEREN & KRUIJT 1985; Pl. II, figs. 5, 8). The tristratose attachment frequently becomes elongated like a stalk. When very short, as in Dicranolejeunea axillaris (Pl. II, fig. 6), it becomes difficult to distinguish the tristratose type from the bistratose type. The occurence of extra cells between the superior central cell and the lowermost underleaf lamina cell is reported for both types (Pl. II, figs. 5, 10).
- <u>Dorsal merophyte</u> (10); secondary pigmentation (11). These characters differentiate between *Brachiolejeunea* and *Frullanoides* but their presence in the considered genera is rather casual.
- Stem cortical cells (12; Plate I). Stems are asymmetric when the dorsal cortical cells are larger than the ventral cortical cells; when equal in size the stems are symmetric. This character differentiates between Brachiolejeunea and Blepharolejeunea/Dicranolejeunea, whereas Brachiolejeunea and Frullanoides are similar in this respect.
- <u>Ventral merophyte</u> (13); <u>oil body type</u> (14; Plate XXXV). Like 12, these characters do not differentiate between *Brachiolejeunea* and *Frullanoides* and confirm the close relationship between *Blepharolejeunea* and *Dicranolejeunea*.
- Dry leaf position (15); cell shape (16); trigone shape (17). These characters have been used by GRADSTEIN (1975) to distinguish two tribes in the Ptychanthoideae. The presence of transitions in *Blepharolejeunea* and *Dicranolejeunea* somewhat obscures this distinction.
- Seta (18; Plate IV, figs. 8-11). The unique, enlarged seta of *Trocholejeunea* immediately distinguishes this genus from the other genera. The presence

of a deviant seta has been known for a long time in *T*. sandvicensis but is reported here in *T*. infuscata for the first time (PI. IV, figs. 10-11).

Branching type (20; Table 8; Plate III); innovations (19; F = Frullania-type, J = Radula-Jubula-type, L = Radula-Lejeuneatype). Table 8 shows that a different subtype of the Frullania-type branching distinguishes Trocholejeunea from Frullanoides (compare Pl. III, figs. 7-13 with figs. 14-24). Frullania-type branching fails to separate Brachiolejeunea from Blepharolejeunea and also from Dicranolejeunea, since in D. axillaris all three subtypes are found (Pl. III, fig. 26-28, 30-32). Mastigolejeunea is most clearly distinguished since only Lejeunea-type branches are present here (THIERS 1985; Table 8).

Table 8. A comparison of branching types of *Brachiolejeunea*, *Frullanoides* and related genera. + = branch type present; - = branch type absent. See also Plate III.

Branch type	Frullania-			Lejeunea	Radula-		
Genus	Ptychant	. Bleph.	Jubula		Jubula	Lejeunea	
Mastigolejeunea	-	-	-	+	-	+	
Acrolejeunea	+	+	-	+	-	-	
Trocholejeunea	+	-	-	+	-	-	
Frullanoides	-	+	-	+	+	-	
Brachiolejeunea	-	+	-	+	+	-	
Blepharolejeunea	+	+	-	+	· +	-	
Dicranolejeunea	+	+	+	+	+	+	
Lindigianthus	+	+	-	+ ·	-	+	

- <u>Male bracts</u> (21); <u>shoots</u> (22). Both characters contribute to the delimitation of <u>Mastigolejeunea</u>. Species of this genus often show shoots with a prostrate part of initial stems and a simple to subsimple part of ascending stems (SCHUSTER 1980b).
- Leaf lobule teeth (23). Although there is some overlap, the number of teeth on the leaf lobule presents a difference between *Frullanoides* and *Brachiolejeunea*.

Conclusions

1. Frullanoides and Brachiolejeunea

These two genera have previously been considered a single genus, based on the presence of paired and repeatedly floriferous innovations (EVANS 1908a, SCHUSTER 1963, 1980b) and a wing on the keel of the female bract. As is shown in Table 7, the two groups due not differ from *Blepharolejeunea* and *Dicranolejeunea* in these respects. The outline and insertion of the female bract wings, however, are different in *Brachiolejeunea* and *Frullanoides* (see Morphology and Anatomy).

To summarize, the genus *Frullanoides* is phenetically characterized by its: 1) fenestrate-type sporophyte, 2) pluriplicate perianth with smooth plicae, 3) thick-walled medulla, 4) bistratose underleaf attachment, 5) zig-zag dorsal interlocking border of the lateral merophytes, and 6) presence of secondary, blackish pigmentation (Tab. 7: 1-11). *Frullanoides* differs furthermore from *Brachiolejeunea* in: 1) the insertion of the female bract wings, and 2) the number of teeth on the leaf lobule (Tab. 7: 23), and from the other related genera in: 1) the articulate seta, 2) paired *Radula-Jubula*-type innovations, 3) winged female bract keels, and 4) to a lesser extent in the *Frullania-Blepharolejeunea*-type branches (Tab. 7: 4, 19, 20).

The genus Brachiolejeunea is phenetically characterized by its: 1) with three sporophyte, 2) perianth smooth nodular-type plicae, 3) cortex, 4) tristratose underleaf attachment, thick-walled 5) straight interlocking border of the lateral merophytes, and 6} lack of secondary pigmentation (Tab. 7: 1-11). Brachiolejeunea differs from related genera in asymmetric stem, 2) size of the ventral merophyte, and 3) its: 1) homogeneous oil bodies (Lindigianthus excepted).

2. Trocholejeunea

Ever since its erection (SCHIFFNER 1932), *Trocholejeunea* has been considered a well defined genus (GROLLE 1982) and its proposed, subgeneric status under *Brachiolejeunea* (SCHUSTER 1963, 1980b) has not been accepted. *Trocholejeunea* is most closely related to *Acrolejeunea* and *Frullanoides*, differing from the latter in seta structure, stem anatomy and type of vegetative branching (Tab. 7: 4, 8, 20; Pl. III, figs. 7-13). GROLLE (l.c.) also observed a difference in the direction of the leaf spiral between the main stem and the innovation: not changing in *Trocholejeunea*, changing in *Frullanoides* (innovations lacking in *Acrolejeunea*). In addition the chromosome number (n = 16, GROLLE 1982) is unique in Lejeuneaceae, but unfortunately I have been unable to determine chromosome numbers for *Frullanoides*.

3. Mastigolejeunea

This genus is similar to *Frullanoides* in many respects but differs in a number of diagnostic characters, including the oil body type (PI. XXXV, fig. 6) and the hypostatic male bracts, which characterise the *Ptychanthus*-complex to which *Mastigolejeunea* belongs (GRADSTEIN 1975). Further differences are branch type and innovation type and the dimorphic shoots (Tab. 7: 19, 20, 22). The stem anatomy is also characterised by its medullary cells, which are very strongly and irregularly thickened, and which are surrounded by a thick-walled cortex (PI. I, figs. 11-12; PI. II, fig. 7). The stem anatomy of *Frullanoides densifolia* and *F. laciniatiflora* is reminisent of that of *Mastigolejeunea*, but the thickenings are less strongly developed and are restricted to the ventral side of the cortex.

At the ultrastructural level, the two genera differ in spore ornamentation (PI. XXXIV, figs. 3, 7; see also Chapter III).

4. Blepharolejeunea/Dicranolejeunea/Lindigianthus

These three genera are similar to *Brachiolejeunea* in their sporophyte, in the number of ventral plicae of the perianth and in underleaf attachment (Tab. 7: 1-7, 9). With the exception of *Lindigianthus* the genera also agree in stem anatomy (Tab. 7: 8). The main differences with *Brachiolejeunea* are: the symmetric stem, the width of the ventral merophyte and the oil body type (except *Lindigianthus*; Tab. 7: 12-14).

5. Cephalolejeunea

This monotypic genus has been ascribed to the *Brachiolejeunea*-complex by MIZUTANI (1979b). Relevant generic characters are: 1) the vegetative branches, which are of the *Lejeunea*-type only, 2) the triangular trigones, 3) the leaf lobule with only one marginal tooth, 4) the presence of single *Radula-Lejeunea*-type innovations, 5) the perianth plicae, which are crenulate and restricted to the upper 1/3 of the perianth (1979b: figs. 2q-s), and 6) the plurifenestrate capsule valves. Characters 1, 3 and 4 are suggestive of *Mastigolejeunea* but the triangular trigones and the apparently isodiametric leaf cells (22-32 x 22-28 μ m) locate *Cephalolejeunea* in the tribe Archilejeuneae (*sensu* GRADSTEIN 1975). In this tribe it is, in my opinion, most closely allied to the members of the *Archilejeunea*-complex (GRADSTEIN 1975) due to: 1) lack of blackish pigmentation, 2) trigones triangular with short and wide rays, and 3) perianth with 2-5 plicae. The genus definitely does not have a close relationship with either *Brachiolejeunea* or *Frullanoides*.

TAXONOMIC TREATMENT

CONSPECTUAL KEY TO BRACHIOLEJEUNEA, FRULLANOIDES AND RELATED GENERA

1.	Inner layer of the sporophyte capsule valves with fenestrate cell wall
	thickenings; elaters regularly distributed over the inner surface of the
	apical part of the valve; sporeling of the Lopholejeunea-type; leaf cells
	elongate, length more than 1½ times width, trigones clearly cordate (to
	confluent)
1.	Inner layer of the sporophyte capsule valves with nodular cell wall
	thickenings; elaters located on the margin of the apical part of the valve;
	sporeling of the Lejeunea-type; leaf cells isodiametric to somewhat
	elongated, length up to $1\frac{1}{2}$ times width, trigones cordate to simple triangu-
	lar or radiate
	2. Seta not articulate; walls of the leaf cells without secondary blackish
	pigmentation; male bracts epistatic; innovations absent or 1 of the Frul-
	lania-Ptychanthus-type
	2. Seta articulate or not articulate; walls of the leaf cells with secondary
	blackish pigmentation; male bracts epistatic or hypostatic; 1-2
_	innovations of the Radula-Jubula-type
3.	Innovations absent; seta cross section with 16 outer and 4 inner cells; fe-
	male bracts and bracteoles in (1-)2-6 series; stem cortex thin-walled, me-
~	dulla with variable wall thickenings
3.	One innovation of the <i>rruliania-Ptychanthus</i> -type present; seta cross sec-
	tion with 16-32 outer and 8-16 inner cells; temale bracts and bracteole in 1
	series only; stem cortex and medulia equally thickened
	Wale bracks existential collection welled densel continue collection
	4. Male bracks episialic; contical cens thin-walled, dorsal contical cens in stem cross section larger than the modullary collet loaf lobule with 3-11
	teeth: branching at least in part <i>Frullania</i> -type: oil bodies
	homogeneous Massula-type: seta articulate Frullanoides
	4. Male bracts hypostatic: cortical cells thick-walled, dorsal cortical cells
	in stem cross section smaller than the medullary cells or equal in size:
	leaf lobule with $1-2(-3)$ teeth: branching solely Lejeunea- type; oil
	bodies segmented, Calypogeia-type; seta not articulate
5.	Lobule free margin gradually curved; all teeth on leaf lobule similar in
	shape and inflexed; dorsal cortical cells in stem cross section larger in
	size than the medullary cells
5.	Lobule free margin with a rectangular angle: teeth on leaf lobule dissimilar

in shape: apical tooth inflexed and blunt, second tooth straight and sharp

and located at the rectangular angle of the free margin; dorsal cortical cells in stem cross section equal or larger than the medullary cells . .

- 6. Dorsal cortical cells in stem cross section larger than the ventral cortical cells; leaf cells elongate with cordate trigones; perianth with 3

- 7. Trigones triangular to cordate; perianth with clearly swollen ventral plica(e); oil bodies Jungermannia-type Dicranolejeunea

BRACHIOLEJEUNEA (Spruce) Schiffn.

in Engl. & Prantl, Nat. Pfl.-fam. 1, 3(1): 128 (1893); Evans (1908a: 155); Stephani (1912: 110), (1923): 381); Verdoorn (1934c: 52); Vanden Berghen (1948: 42); Mizutani (1961: 165); Bischler (1965: 406); Bonner (1963: 445), (1977: 818); Schuster (1961: 157), (1963: 104), (1980b: 757); Farr et al. (1979: 228); Grolle (1982: 178), (1983: 7).

Lejeunea subg. Brachiolejeunea Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 129 (1884); Stephani (1889: 167).

Lectotype (Evans 1908a): Brachiolejeunea laxifolia (Tayl.) Schiffn.

Plants paroecious, growing ramicolous in loosely and ascending, or in densely appressed mats on corticolous, occasionally saxicolous or terrestric substrates, rarely pendulous, small to medium-sized to large, up to 5.5 cm long, green to olive-green, when dry becoming light to dark brown, branches of the of irregularly branched; Frullania-type and the Lejeunea-type; the Frullania-type branches long, vegetative or sexual, with the dorsal stem half-leaf partially inserted on the branch, the first branch underleaf (un)equally bilobed and the first branch acroscopic leaf (un)equally bilobed, the Lejeunea-type branches short, vegetative or sexual; the gynoecia with (1-)2 innovations of the Radula-type that may be repeatedly floriferous, giving parts of the shoots a dichotomous appearance.

Stem c. 0.05-0.20 x the width of the leafy plant, rigid or flaccid, 0.10-0.25 mm in diam., ventral merophyte 4-6(-8) cell rows wide; dorsal cortical cells arranged in straight longitudinal rows, a lamellate paraphyllium present along the dorsally interlocking border of the lateral merophytes (in *B. laxifolia* and *B. leiboldiana*); stem in transverse section with 11-23(-30) thick-walled cortical cells surrounding 16-55(-82) thin-walled medullary cells, the dorsal cortical cells larger than both the ventral cortical cells and the medullary cells, the medullary cells and the ventral cortical cells ± similar in size, the cell walls without secondary pigmentation; medullary cells in longitudinal section tapering towards relatively wide, truncate ends.

Leaves incubous, with a large dorsal lobe and a smaller ventral lobule, imbricated, suberect-convoluted when dry, when moist widely spreading to squarrose. Lobe broadly (ob)ovate to suborbicular or ovate-falcate, inserted along 1/2 to 1/1 of the length of the lateral merophyte, the dorsal base straight and not auriculate, not to slightly arching beyond the stem, the margins entire, the apex rounded to blunt to minutely apiculate, never acute, the apical region plane to incurved, the ventral margin plane, when spread out forming an angle of 90-150° with the keel (in B. leiboldiana rarely up to 170°; in B. fernandeziana 160-180°!), the keel smooth, curved or straight to weakly concave (B. fernandeziana), not decurrent (shortly so in B. fernandeziana); cells arranged in ± diverging rows, elongate-hexagonal, the median cells 22-47 x 13-33 µm, slightly larger at the leaf base, towards the gradually smaller, at the margins margin becoming rectangular to subquadrate, 9-20 um high; vitta and ocelli absent; trigones and intermediate thickenings present, the trigones small to medium-sized, <u>cordate</u>, the intermediate thickenings elliptic-rounded to elongated, one per each larger cell wall; cuticula smooth; oil bodies present in all cells of leaves, underleaves, involucrum, perianth and stem cortex, <u>Massula-type</u>, in the lobe 16-30 per cell, homogeneous, narrowly ellipsoid to fusiform, sphaerical when seen from the side, up to 7.5 um long, glistening, upon degeneration becoming septate and subsequently desintegrating into minute granulae.

Lobule 0.3-0.6 x the length of the lobe, <u>never</u> reduced, broadly ovate-triangular to ovate-rectangular (*B. fernandeziana* ε *B. leiboldiana*), inflated along the keel and with a plane to weakly concave distal part, the free margin plane, weakly curved or with a wide angle (*B. leiboldiana*), abruptly curved near the apex, with 2-4 inflexed teeth, beyond the apex <u>not</u> <u>continuing into the ventral margin of the lobe</u>; 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 distant to (barely) imbricated, 2-5 x the width of the stem, suborbicular, in situ varying from suborbicular to rectangular to obtriangular, the apex undivided, plane or recurved, the margins entire, plane or incurved, the bases rounded and shortly decurrent, the line of insertion cuneate; underleaf base with four superior central cells, the underleaf base at the rhizoid disc in longitudinal section tristratose and elongated (in B. leiboldiana often an extra cell row between the superior central cell and the rhizoid disc), the stalk of attachment (30-)60-200 um long; the primary rhizoid disc consisting of up to 62 thin-walled cells, giving rise to bundles of pale rhizoids.

Androecia located 1-3 series of vegetative leaves below the gynoecium on stems and *Frullania*-type branches, bracts and bracteoles in 1-4 series, the bracts strongly resembling leaves but usually smaller in size, the lobules with a more strongly inflated basal part and a concave distal part, <u>epistatic</u>, the free margin with 1-3(-4) reduced teeth, enveloping <u>one</u> globose antheridium subtended by a curved, uniseriate stalk; the bracteoles similar to underleaves, present throughout the male spike.

Gynoecium terminating stems and long or short Frullania-type or Lejeunea-type branches, bracts and bracteole in one series; bract lobe plane, the apical region concave, obovate or ovate-falcate, the margins entire, the apex rounded to blunt to minutely apiculate, the keel rounded to \pm 90°; with a narrow linear to ± elliptic wing, running along the keel to the dorsal-lateral side of the stem and not inserted on the innovation (wing reduced to frequently absent in B. fernandeziana and B. spruceana); bract lobule 1/3-2/3 x the length of the lobe, rectangular or rhomboid-rectangular, 3-4-celled apical tooth; bracteole obovate without or with а to obovate-spathulate, smaller in size than the bract lobe, weakly concave, the apex widely rounded-truncate to emarginate, slightly recurved, the basal part not inserted on the innovations.

Perianth emergent to 1/2-2/3 of its length when mature, obovoid to obovoid-oblong, frequently stalked, with three rounded plicae in the upper

1/5-3/4, two lateral and one, sometimes sulcate, ventral, the plicae smooth on their backs; beak 5-6 cells long; basal perianth cells large and thin-walled with small trigones, apical cells smaller with larger trigones and intermediate thickenings.

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

Mature sporophyte exserted up to 1.2 mm above the perianth, the foot consisting of a few bulging cells in c. three layers, the seta articulate, with 16 evenly tiered longitudinal rows of outer cells and 4 longitudinal rows of inner cells, the capsule globose, dark brown, splitting to near base into four valves; valves suberect, the central part concave, the lateral and apical parts plane and not recurved, alternatively with five - one apical and four lateral or with six elaters along the margins, thus six elaters along the interlocking of two adjacent valves, each valve in addition bearing three elaters on its inner surface, connected with their apical and basal ends to the valve surface, the capsule valves bistratose in the apical part, the outer cells with asymmetrically-nodulose trigones and (occasionally) intermediate thickenings, the thickenings weaker at the extreme base, the cells of the inner valve layer smooth on their outside surface and bearing irregular nodulose thickenings on the inner cell walls and angles, the capsule base 3-4 stratose, consisting of thin-walled cells; elaters 2x5 + 2x6 + 4x3 = 34 per capsule, the marginal elaters 220-470 µm long (the apical one 325-470 µm, the lowermost lateral ones 220-340 µm), the "surface" elaters 145-400 µm long: the central elater 280-400 um, the two lateral elaters 145-270 µm, all elaters 16-20 µm wide, with one colourless to yellowish, c. 4 µm wide spiral that is often incompletely developed (wall thickenings only); spores with precocious germination, the outline inside the capsule varying from more or less rectangular to trapezoid, 45-105 µm long, irregular angular when dry, the outer surface covered with numerous, irregularly arranged, compound verrucae (showing a tendency towards rosette formation in B. spruceana).

Sporelings of the Lejeunea-type (sensu NEHIRA 1983).

Chromosome number unknown.

<u>Distribution</u>: tropical and southern temperate LATIN AMERICA, ranging in altitude from sealevel up to 3500 m; highest records from the Andes of Colombia and Ecuador.

Ecology: mostly epiphytic, drought tolerant. Growing in loose to rather dense patches, which are usually ascending and only rarely pendulous on stems, trunks or branches of living trees and shrubs in a variety of habitats: Andean forests, (sub-)páramos and evergreen *Nothofagus* forests as well as xerophytic woodlands, along roadsides etc. Less frequently (mainly at higher altitudes) on decaying wood, rocks or peaty soils; not recorded epiphyllous. Frequently growing together with species of *Blepharolejeunea*, *Frullanoides*, or *Frullania*. Joint occurrence of more than one species of *Brachiolejeunea* rare..

Differentiation: important diagnostic characters are underlined in the description.

KEY TO THE SPECIES OF BRACHIOLEJEUNEA

1.	Dorsal stem surface with a 1-4 cells high lamellate paraphyllium; plants
	from tropical Central and South America
1.	Lamellate paraphyllium lacking; plants from the temperate region of
	southern South America
	2. Plants paroecious; leaves ovate-falcate; leaf lobule ovate, with (2-)3(-4)
	teeth, the free margin gradually curved, without a distinct angle;
	paraphyllium 3-4 cells high on the antical side, 1-2 cells high on the postical side
	2. Plants dioecious; leaves broadly obovate to suborbicular; leaf lobule
	broadly ovate-rectangular, with $2(-3)$ teeth; the free margin with an angle of ± 150° at the 2nd tooth; paraphyllium 1 cell high throughout
3.	Keel of leaf lobule straight to weakly curved; angle between keel and ven-
	tral leaf margin 160-180°; free margin of leaf lobule with 4 teeth
3.	Keel of leaf lobule distinctly curved; angle between keel and ventral leaf
	margin 120-145°; free margin of leaf lobule with 3 teeth

1. BRACHIOLEJEUNEA FERNANDEZIANA S. Arnell (Plates VII-VIII)

Ark. Bot. II, 4(1): 18 (1959); Solari (1983: 536).

<u>Type</u>: Chile, Juan Fernandez Islands, Masatierra, El Yunque, on fronds of *Blechnum schottii*, Kunkel H298, 6.111.1955 (S holo).

Plants paroecious, medium-sized, up to 2.6 cm long, 1.3-1.8 mm wide, green, becoming light brown when dry, irregularly branched, parts of the plants with a dichotomous appearance due to floriferous innovations; branches of the *Frullania*-type and the *Lejeunea*-type; shoots without a lamellate paraphyllium on the dorsal interlocking border of the lateral merophytes, but a tendency to form a one cell high paraphyllium sometimes present (PI. VII, fig. 3).

Stem rather flaccid, 0.12-0.15 mm in diam.; ventral merophyte four cellrows wide, the ventral cortical cells rectangular, $32-63 \times 18-36$ um, the dorsal cortical cells short rectangular, $30-54 \times 21-40$ um; stem in transverse section with 13-16 thick-walled cortical cells, surrounding 24-28 thin-walled medullary cells, the dorsal cortical cells 21-29 um high, the ventral cortical cells 16-18 um high, the medullary cells 15-20 um in diam.

Leaves laxly imbricated, when moist erecto-patent and not squarrose. Lobe broadly ovate, 0.9-1.5 mm long, 0.7-1.0 mm wide, inserted along 1/2 of the length of the merophyte, the apex blunt to minutely apiculate, the apical region plane to slightly incurved, when spread out the ventral margin forming an angle of $160-180^{\circ}$ with the keel; keel straight to weakly concave, at an angle of \pm 45° with the axis, shortly decurrent; median leaf cells 23-38 x 16-24 um, margin cells 12-20 um high; intermediate thickenings scarce, elliptic-rounded, when present one per each larger cell wall.

Lobule ovate-rectangular to ovate-triangular, 0.40-0.55 mm long, 0.25-0.30 mm wide, 0.5 x the length of the lobe, rather abruptly flattened towards the free margin, the flattened part plane; free margin \pm straight and abruptly curved near the apex, with four inflexed teeth; teeth consisting of (1-)2-5 cells in total with 1-2 cells at the base, separated from each other by 3-7 marginal cells; hyaline papilla 1-2 cells below the proximal base of the first tooth.

Underleaves distant to barely imbricated, suborbicular, 0.30-0.35 mm long, 0.30-0.40 mm wide, the apex plane and widely rounded, the margins plane, the bases rounded and shortly decurrent, the line of insertion cuneate, 0.10-0.12 mm deep; median cells $23-36 \times 14-23$ um, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc tristratose in longitudinal section, shortly elongated like a stalk, 39-63 um long; rhizoid disc suborbicular, consisting of many thinwalled cells.

Androecia located 1-2 series of vegetative leaves below the gynoecium; bracts and bracteoles in 1-3 series, the bract lobe ovate, 0.70-0.80 mm long, 0.50-0.65 mm wide, the lobule with three (rarely four!) reduced teeth of 3-4 cells; antheridium c. 100 um in diam.

Gynoecium terminating stems and long or short *Frullania*-type and *Lejeunea*-type branches, with two innovations; bracts and bracteoles in one series, the bract lobe plane to weakly concave, obovate, 0.85-1.05 mm long,

0.50-0.65 mm wide, the apex blunt, the keel rounded, bracts frequently without wing or with a reduced, narrow linear to elliptic wing at the keel, 170-200 um long, 30-75 um wide, the lobule rectangular, 0.3-0.4 x the length of the lobe, the apex truncate, apical tooth of 3-4 cells in total with 1-2 cells at the base; bracteole obovate-spathulate, 0.60-0.65 mm long, 0.40-0.50 mm wide, the apex widely rounded-truncate to emarginate, slightly recurved, the basal part not inserted on the innovations. Perianth exserting the bracts for 1/2-2/3 when mature, frequently stalked, the stalk up to 440 μ m long, obovoid to obovoid-oblong, 1.2-1.6 x 0.8-0.9 mm, the three plicae extending over the upper 1/5-1/2 of the perianth; beak 5-6 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four spreading valves; spores not observed; elaters 34 per capsule, marginal elaters 270-420 μm long, c. 20 μm wide, with one colourless, incompletely developed, c. 4 um wide spiral.

Sporeling of the Lejeunea-type.

Distribution (PI. XXVII): CHILE, endemic to the Juan Fernandez Islands, at 600-915 m altitude.

<u>Ecology</u>: growing epiphytic on fronds of *Blechnum schottii* and on culms of Chusquea fernandeziana, in the subtropical evergreen forests of the wet eastern parts of Masatierra (REICHE 1907).

Differentiation: *B. fernandeziana* is characterized by 1) the broadly ovate leaves that are not falcate, 2) the straight to weakly concave keel of the leaves, 3) the ovate-rectangular to ovate-triangular leaf lobule bearing four teeth on the free margin (PI. VII, fig. 7), 4) the wide angle between the keel and the ventral leaf margin (160-180°), and 5) the distant to only barely imbricated underleaves (PI. VII, fig. 1a-b).

The first four characters are unique in the genus *Brachiolejeunea* and warrant, in my opinion, a distinction of this taxon at the species level. *B. fernandeziana* is related to *B. spruceana* (see under the latter species).

Specimens examined (B. fernandeziana):

CHILE, JUAN FERNANDEZ ISLANDS. <u>Masatierra</u>: El Yunque near summit, Kunkel H298, 6.111.1955 (S), type collection of *Brachiolejeunea fernandeziana* S. Arnell; Valle Ingles, high central ridge, on culms of *Chusquea fernandeziana*, Sparre H254, 28.11.1955 (S). 2. BRACHIOLEJEUNEA LAXIFOLIA (Tayl.) Schiffn. (Plates VIII-X)

in Engl. & Prantl, Nat. Pfl.-fam. 1, 3(1): 128 (1893); Evans (1908a: 155); Stephani (1912: 120); Verdoorn (1934c: 54); Vanden Berghen (1948: 43); Mizutani (1961: 165); Bonner (1963: 453); Bischler (1965: 407); Schuster (1961: 157), (1963: 104), (1980b: 759); Gradstein (1974a: 328); Grolle (1983: 7).

- Phragmicoma laxifolia Tayl., London J. Bot. 6: 431 (1847); Mitten (1851: 359); Stephani (1889: 167).
- Lejeunea (subg. Brachiolejeunea) laxifolia (Tayl.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 130 (1884); Stephani (1890: 134). Type: Ecuador, Pichincha, Jameson s.n., XI.1846 (FH-Taylor holo, BM).

Heterotypic synonyms:

Lejeunea (subg. Brachiolejeunea) laxifolia var. obliquata Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 131 (1884) <u>syn. nov.</u> Syntypes: Ecuador, "Ad pedem montis Tunguragua juxta pagos Banos et Puela", Spruce s.n. (B, BM, MANCH 14074, 14077 & 14079, NY).

- Brachiolejeunea laxifolia fo. condensata Herz., Hedwigia 74: 95 (1934) nom. nud. Based on: Colombia, páramo El Boquerón, Troll 2176a & 2180, 1929 (JE, NY) & 2203, 1929 (B, JE).
- Brachiolejeunea laxifolia fo. obtusata Herz., Beih. Bot. Centralbl. (B) 61: 577 (1942) nom. nud. Based on: Ecuador, Pichincha, an der Rinde von Bäumen im Matorral, Espinosa s.n., VIII.1933 (B, JE).
- Brachiolejeunea laxifolia fo. minor Herz., Feddes Repert. 57: 176 (1955) <u>syn</u>. <u>nov</u>. Type: Colombia, Norte de Santander, road from Pamplona to Toledo, crossing the divide between Rio La Teja and Rio Mesme, Killip & Smith 19918, 27-28.II.1927 (JE holo).
- Brachiolejeunea mandoni Steph., Spec. Hep. 5: 121 (1912); Herzog (1955: 176) syn. nov. Type: Bolivia, Mandon 795 (G 20198 holo).
- Brachiolejeunea thomeensis Steph., Spec. Hep. 5: 113 (1912); Vanden Berghen (1951: 88) <u>syn. nov.</u> Type: Africa (!), San Thomé, Moller s.n., 1885 (G 20360 holo).
- Brachiolejeunea uleana Steph., Spec. Hep. 5: 123 (1912); Arnell (1964: 93) syn. nov. Type: Brazil, Sierra Itatiaia, Ule 451, 1884 (G 20369 holo).

Phragmicoma leiboldiana var. β Lindenb. & Gott., Syn. Hep.: 744 (1847)

= Phragmicoma leiboldiana var. gracilior Gott., Mex. Leverm.: 270 (1863) syn. nov.

Type: Mexico, Chinantla, Liebmann 430b ("530" Gottsche I.c. pro err.), V.1841 (W (hb. Lindenberg 5985) holo, C, FH-Schiffner, G 20166, S).

Plants paroecious, medium-sized to large, up to 5.5 cm long, 1.75-2.40 mm wide, olive-green, becoming light to dark brown when dry, sparsely branched, parts of the plants with a dichotomous appearance due to floriferous innovations; branches mainly long but also short, *Frullania*-type, only occasionally *Lejeunea*-type; shoots with a well developed, lamellate paraphyllium, (120-)170-270(-360) µm long, located at the dorsal interlocking of the lateral merophytes and only separated from each other by the dorsal leaf insertion cells, unistratose, the antical part (2-)3-4(-5) cells high $(50-70(-105) \mu m)$, gradually decreasing in height towards the postical part of 1-2 cells high $(30-40 \mu m)$, the paraphyllia present on all merophytes except from the offspring to the second leafy appendage of a *Frullania*-type branch.

Stem rigid (in weakly developed specimens rather flaccid!). 0.15-0.20(-0.25) mm in diam.; ventral merophyte 4-6(-8) cell rows wide, the ventral cortical cells rectangular to longly so, 70-125 x 24-35 µm, the walls unevenly thickened, the dorsal cortical cells rectangular, $45-90 \times 24-40 \ \mu m$; stem in transverse section with 13-23(-30) thickwalled cortical cells surrounding 28-55(-82) thinwalled medullary cells, the dorsal cortical cells 20-40 um high, the ventral cortical cells 18-25 µm high, the medullary cells 16-30 um in diam., the walls of the cortex, especially ventrally, distinctly thicker and darker in colour than the walls of the medullary cells.

Leaves laxly imbricated, when moist widely spreading. Lobe ovate-falcate, 1.0-1.4 mm long, 0.6-0.9 mm wide, inserted along 2/3-1/1 of the length of the merophyte, the apex rounded to minutely apiculate, the apical region incurved, when spread out the ventral margin forming an angle of 90-125° with the keel; keel smooth, at an angle of 45-60° with the axis, curved near the base, not decurrent; median leaf cells $(22-)34-47 \times 17-28 \mu m$, margin cells 11-17 μm high; intermediate thickenings frequently present, one per each larger cell wall, elliptic-rounded; oil bodies *Massula*-type, 16-27 per cell, ellipsoid-fusiform, sphaerical when seen from the side, 5-6 μm long, glistening, in the stem cortex cells much smaller and more numerous, c. 45-50 per cell.

Lobule broadly ovate-triangular, 0.30-0.45 mm long, 0.35-0.45 mm wide, $0.3-0.4 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part weakly concave; free margin plane, with (2-)3(-4) inflexed teeth; teeth consisting of 3-5 cells in total with two cells at the base, separated by 3-7 free marginal cells; hyaline papilla two cells below the proximal base of the first tooth.

Underleaves barely imbricated, suborbicular, 0.50-0.70 mm long, 0.50-0.75 mm wide, the apex rounded, recurved, the lateral margins incurved, giving the underleaves in situ a rectangular to obtriangular appearance, the bases rounded and shortly decurrent, the line of insertion cuneate, 0.15-0.20 mm

deep; median cells 19-28 x 16-20 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc tristratose in longitudinal section, elongated like a stalk, 80-180 μ m long; rhizoid disc suborbicular, consisting of many small, thin-walled cells or fewer, larger cells.

Androecia located 1-3 series of vegetative leaves below the gynoecium; bracts and bracteoles in 2-4 series, the bract lobe ovate-oblong, 0.5-0.7 mm long, 0.3-0.4 mm wide, the lobule bearing 1-3 reduced teeth of 2-4 cells; antheridium c. 135 µm in diam.

Gynoecium terminating stems and long or short *Frullania*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe plane, ovate-falcate, the apical region slightly concave, 1.0-1.3 mm long, 0.6-0.7 mm wide, the apex blunt to minutely apiculate, the keel rounded, bracts with a narrow linear wing at the keel, 290-580 μ m long, 60-110 μ m wide, the lobule rhomboid-rectangular, 0.5-0.6 x the length of the lobe, the apex blunt, without distinct apical tooth; bracteole obovate, 0.9-1.1 mm long, 0.6-0.7 mm wide, the apex widely rounded and recurved, the basal part not inserted on the innovations. Perianth exserting the bracts for 1/2-2/3 when mature, frequently stalked, the stalk up to 360 um long, obovoid to obovoid-oblong, 1.4-2.2 x 0.7-1.0 mm, the three plicae extending over the upper 1/3-2/3 of the perianth; beak 5-6 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four spreading valves; spores green, more or less rectangular when dry, 70-105 μ m long, covered with numerous compound verrucae; elaters 34 per capsule, marginal elaters 320-470 μ m long, c. 20 μ m wide, with one colourless, incompletely developed, c. 4 μ m wide spiral.

Sporeling of the Lejeunea-type.

Distribution (PI. XXVII): tropical SOUTH and CENTRAL AMERICA, north to Mexico, and the WEST INDIES (Jamaica, Dominican Republic). Mainly distributed along the Andes chains from Bolivia to Northeastern Colombia and the adjacent region of Venezuela, but also recorded from the higher parts of Central and Southern Brazil (Sierra Itatiaia). Occurring between (1500-)2000-3500 m altitude.

Ecology: mainly on bark of living trees and shrubs in Andean forests, subpáramos and páramos. In the Andean forest rather heliophilous, usually growing on rather exposed locations where temporarily drought may occur. The plants are usually ramicolous in loose patches or tufts, more or less ascendent (obs. S.R. Gradstein), and rarely pendulous (coll. Gradstein 3589). Occasionally *B. laxifolia* grows on rotten tree trunks, rocks or peaty soils. In the Colombian páramos and subpáramos the species is present in shrubby communities of e.g. *Aragoa* spp. or *Diplostephium revolutum* (CLEEF 1981). The species is sometimes found growing intermingled with species of the related genera *Blepharolejeunea* (e.g. *B. securifolia*: colls. Grubb & Guymer B102e; Aguirre et al. 4617) and *Frullanoides* (e.g. with *F. densifolia*, HERZOG 1952). Differentiation: B. laxifolia is easily to be distinguished from the other species of Brachiolejeunea by: 1) its well developed lamellate paraphyllium along the dorsal interlocking border of the lateral merophytes (PI. VIII, figs. 3-4, 7; VAN SLAGEREN & GRADSTEIN 1981). These paraphyllia are easily observed after (partial) removal of the leaves under a dissecting microscope, 2) the rectangular to longly rectangular ventral cortical cells, 70-125 x 24-35 μ m in size and with unevenly thickened walls (PI. IX, fig. 8), and 3) the sparse branching of the plants, with long *Frullania*-type branches (mainly) and an occasional short *Lejeunea*-type branch.

Variation: the specimens examined show a conspicuous variation in general size (2.5-5.5 cm). This variation is correlated with variation in: 1) the density of the foliation, 2) the length and height of the paraphyllia, and 3) in the outline of the ventral cortical cells.

Poorly developed plants may resemble *B*. *leiboldiana*, but *B*. *laxifolia* is always distinguishable by: 1) the paroecious male bracts (dioecious in *B*. *leiboldiana*), 2) the antical part of the paraphyllia, which is at least two cells high (one cell in *B*. *leiboldiana*), and 3) the ovate-falcate leaves (broadly obovate to suborbicular in *B*. *leiboldiana*).

Notes:

- Schiffner collections from Brazil, enumerated by ARNELL (1964) under the name B. uleana, belong to Frullanoides densifolia (mainly), Blepharolejeunea securifolia (one coll.), Brachiolejeunea leiboldiana (one coll.) and to B. laxifolia (Schiffner 2269).
- 2. Stems of well developed plants (cross section) may possess several thickened cell layers (Mandon 796 and Cleef 2795b; Pl. IX, figs. 1-2). In longitudinal section, these stems show much shorter cortical cells than medullary cells. This indicates that a thickening of the outer cell layers of the medulla has taken place.
- The type of B. thomeensis Steph. (= B. laxifolia) is the only collection of Brachiolejeunea, recorded from Africa and thus provokes a remarkable disjunction. Because of the brief data on the label, the scanty material and Stephani's well known carelessness I consider this African record as doubtful.

Specimens examined (B. laxifolia):

- MEXICO. Chinantla, Liebmann 430b, V.1841 (C, FH-Schiffner, G 20166, S, W (hb. Lindenberg 5985), type collection of *Brachiolejeunea leiboldiana* var. gracilior Gott.; Popocatepetl, Amecameca, den Held & van Rhijn, HH5, 21.IV.1973 (U); Movelos, road Cuernavacca-Tres Cumbres, Schwab 58, 1.IV.1973 (U); Federal District, Pringle 15338, 9.VI.1908 (G 20179, U).
- COSTA RICA. Cartago: Aledano, Chaverri & López 1519, 22.VI.1983 (CR, U); s. loc., Werckle 6243, V.1900 (G 20165).

JAMAICA. s.loc., Wilson s.n. (NY).

DOMINICAN REPUBLIC. La Vega, Constanza, Steere 22623, 28.IV.1982 (NY).

- BRAZIL. Santa Catharina: Serra Geral, Ule 237 (B, G 20370); Minas Gerais: Serra Itatiaia, Ule 451, 1884 (G 20369), type collection of *Brachiolejeunea uleana* Steph., & 452 p.p. (G 20273); ibid., Vital s.n., 26.1X.1974 (SP, U); ibid., Schiffner 2269, 17.1X.1901 (S); <u>Sao Paulo</u>: Lugar, Serra do Rocinha, Baptista s.n., 4.XII.1971 (U); <u>s.loc.</u>: Spruce s.n. (MANCH 14078); Sellow s.n. (BM); Ule 348 (G 20372) & 457 (BM).
- VENEZUELA. Mérida: Sierra Nevada de Mérida, Onraedt 78.V.5903, 19.VII.1978 (hb Onraedt, U); La Mucuy, oberhalb Tabay, Hertel & Oberwinkler 10245b, 9.IV.1969 (JE); páramo de la Culata, Sierra del Norte, Griffin & Dugarte PV-856, 14.II.1985 (FLAS); s.loc., Goebel s.n. (BM); Tachira: El Zumbador, Griffin PV-208, 29.VI.1984 (FLAS, U); Trujillo: páramo El Jabón, Griffin & Lopez PV-1463, 6-9.III.1985 (FLAS); s.loc. Funck & Schlim s.n. (G 20169).
- COLOMBIA. Magdalena: punta de Borrero, Funck & Schlim 287, 1845/1846 (NY); Norte de Santander: páramo de las Vegas, Killip & Smith 15743, 20-21.VII.1926 (JE, S); road Pamplona-Toledo, Killip & Smith 19918, 27-28.11.1927 (JE), type collection of Brachiolejeunea laxifolia fo. minor Herz.; Antioquía: Llanos de Quivá, Onraedt 83.A.10461, 19.11.1983 (hb. Onraedt, U); Boyacá: road Sogamoso-Pajarito, Bischler 1723, 2.11.1959 (COL, PC, U); Sácama, Aguirre et al. 3095, 17.VIII.1982 (COL, U); Rio San Pablin valley, Grubb & Guymer B102e, 28.VII.1957 (S) & B51, 29.VII.1957 (BM, S); Ritacuba, Grubb & Guymer s.n., 4.VIII.1957 (S); Sierra Nevada de Cocuy, Grubb & Guymer B3, 27.VII.1957 (BM), B375 & B379, 22.VIII.1957 (BM); Cundinamarca: Rio Colorado, sur la Laguna de Chisacá, Bischler 2312 & 2332, 1.V.1959 (COL, PC, U); Páramo de Chisacá, Gradstein & Aguirre 3642a, 6.VIII.1980 (COL, U); ibid., Aguirre & Gradstein 4617 & s.n., 4.IX.1984 (COL, U); Grange der Ceja gegen den páramo östlich von Bogotá, Troll 2032, 1929 (NY); Páramo El Boguerón, Troll 2176a, 2180 (JE, NY) & 2203, 1929 (B, JE), material of Brachiolejeunea laxifolia fo. condensata Herz.; ibid., 2181a (JE, NY), 2188b (NY), 2204 (B, S) & s.n., 1929 (S); Páramo de Cruz Verde, Daniel Guevara 6294, 7.VIII.1978 (NY); ibid., Grabant & Idrobo 125, 3 6.VIII.1974 (COL); ibid., Cleef 2795b, 11.IV.1972 & 3186, 26.IV.1972 (COL, U); ibid., Onraedt 78.A.5993, 78.A.6000, 78.A.6002 & 78.A.6041, 7.VIII.1978 (JE, hb. Onraedt, U); Airededores de la Merced, Breure B87, 25.IV.1975 (COL, U); road Bogotá-Choachi, van der Hammen & Jaramillo 2455, 20.IX.1967 (COL, U); Páramo de Choachi, Mägdefrau 1429, 14.-III.1967 (JE, M); Páramo de Guasca, Cleef 398b, 29.XII.1971 (COL, U); Páramo de Palacio, Cleef 3690a, 3698a, 3750b & 3973b, 12-22, V.1972, (COL, U); ibid., Mägdefrau 1566a, 9.IV.1967 (U); Valle Rio Neusa, Cleef & Jaramillo 4193, 26.V.1972 (COL, U); páramo between Cógua and San

Cayetano, Cleef 6394 & 6438b, 15.X1.1972 (COL, U); road San Gayetano-Cógua near Las Mercedes, Cleef 6626a, 19.XI.1972 (COL, U); near Alba, Schaeck 72.A.70, 2.IV.1972 (hb. Onraedt); Alto de los Patios, Onraedt 78.A.6182 & 78.A.6186, 6.VIII.1978 (hb. Onraedt); La Pena, Lindig s.n. (G. 20172); Pacho, s.coll., s.n. (S); Cordilleren von Bogotá, Apollinaire 203, 1905 (G 20237); Andes of Bogotá, Weir c185 & s.n. (NY-several collections); Bogotá, Florschütz 4465 (COL, U); Risaralda: Sta. Rosa de Cabal, between Termales and volcano Otún, Gradstein & Aguirre 3570a & 3589, 16-19.VII.1980 (COL, U); Tolima: Santa Isabel, Aquirre & Gradstein 1487, 1630 & 1649, 28-30.VII.1980 (COL, U); Nevado del Tolima, van der Hammen & Jaramillo 3375, 12.VIII.1975 (COL, U); Meta: Páramo de Sumapaz, Cleef 942, 24.1.1972 (COL, U), 1170, 27.1.1972 (COL, U), 7801a, 14.1.1973 (COL) & 8254a, 23.1.1973 (COL); Huila: Monte de Morro, Lindig s.n. (G 20173); Cauca: Valle de Las Papas, Bischler 801, 7.IX.1958 (COL, PC, U) & 1102, X.1958 (COL, PC); volcán Puracé, Cleef & Fernandez 506, 5.1.1972 & 612a, 6.1.1972 (COL, U); s.loc.: Wallace s.n. (NY); Weir s.n. (NY); Funck & Schlim s.n., 1847 (NY); Liebmann s.n. (FH-Schiffner, G 20167, S, W (hb. Lindenberg 5984); Lindig s.n. (BM); s.coll., s.n. (BM).

ECUADOR. Carchi: Páramo de El Angel, Gradstein et al. 3389 & 3413, 3-4.1V.1976 (U); San Gabriel, Spruce s.n. (NY); Napo: Rio Napo, Villanicentia s.n. (YU); Pichincha: above Pangor, Spruce s.n. (MANCH 14067); Pallatanga, Spruce s.n. (MANCH 14068); Mt. Guayrapata, Spruce s.n. (BM, G 20171, 20174 & 20175, MANCH 14065, 14066, 14070, 14071 & 14082, NY-several collections, S, W, YU); Andes Quitensis, Spruce s.n. (BR, G 11010); ibid., Jameson s.n. (MANCH 14075); Quito, Jameson s.n. (BM, FH-Taylor), type collection of Brachiolejeunea laxifolia (Tavl.) Schiffn.; ibid., Jameson 53 & 148 (NY), 232 (BM), 1354 (G 20168) & s.n. (BM, G 20095, NY-several collections); s.loc., Spruce L74 (MANCH 14073); Quito, s.coll., s.n. (G 20089); An der Rinde von Baumen im Matorral, Espinosa s.n., 7.VIII.1933 (B, JE), material of Brachiolejeunea laxifolia fo. obtusata Herz.; Tungurahua: Abitagua, Spruce s.n. (NY); above Puela, Spruce L164 (MANCH 14074); Banos, at the foot of Mt. Tungurahua, Spruce s.n. (B, BM, MANCH 14074, 14077 & 14079, NY), syntypes of Brachiolejeunea laxifolia var. obliquata Spruce; Azuay: Cuenca, Harling 2205 p.p., 11.111.1947 (JE, S) & 2306, 11.V.1947 (JE); s.loc.: Jameson, s.n. (MANCH 14076 & 14080); Spruce s.n. (B).

PERU. <u>Amazonas</u>: Chachapoyas, road Chachapoyas-Cajamarca, Frahm et al.
974 (B, G, U); Bongará, Pomacochas, E. & P. Hegewald 7060, 1.1X.1973 (hb. Hegewald, U); <u>Cajamarca</u>: Contumazá, cerro Cumanten, E. & P. Hegewald 7323, 16.1X.1973 (hb. Hegewald, U); <u>San Martin</u>: Rioja, road Chachapoyas-Moyobamba, Frahm et al. 657, 31.VIII.1982 (B, G, U), 796, 1.1X.1982 (B, G, U) & 1248, 10.1X.1982 (B, G, U); <u>Junín</u>: Huancayo, E. & P. Hegewald 9261, 8.VII.1977 (hb. Hegewald, U); <u>s.loc.</u>: Spruce s.n. (MANCH 14072); Poeppig s.n. (BM).

- BOLIVIA. Santa Cruz, along road Cochabamba-Santa Cruz, Hermann 24701, 25.11.1972 (PC, S); Unduavi, Brooke 6824A & 6863A, 12-13.X.1950 (BM), 6871A, 14.X.1950 (BM, hb. Fulford) & 6915C, 16.X.1950 (BM); Unduavi, Sorata, Rusby 3087 & 3089 p.p., II.1886 (MANCH 14069, NY); ibid., Mt. Illampu, Irahola 10122A, 8.IV.1972 (FLAS); Yacacoma, Williams 2242, 10.VI.1902 (NY, U, YU); Arrique, Lechler s.n. (NY); Cunuca, Herzog s.n. (NY); Cochabamba, Incacorral, Herzog s.n., I.1908 (YU) & 4953, VI.1911 (L); ibid., Herzog s.n. (hb. Levier 5884) (G 20170); Estradillas, Herzog 3331, VI.1911 (B, L) & 3344 (B); Coranital, Herzog 3380, V.1911 (JE, L) & 3398, V.1911 (B, JE); Rio Saniri, Herzog 3271, X.1911 (B, L); s.loc., Mandon 795 (G 20198), type collection of *Brachiolejeunea mandoni* Steph., Mandon 796 (G 20199) & 1662 (S).
- AFRICA, SAN THOME. S.loc., Moller s.n., 1885 (G 20360), type collection of Brachiolejeunea thomeensis Steph. Doubtful record.

3. BRACHIOLEJEUNEA LEIBOLDIANA (Gott. & Lindenb.) Schiffn (Plates X-XII)

Hedwigia 33: 182 (1894); Stephani (1912: 126); Bonner (1963: 454). *Phragmicoma leiboldiana* Gott. & Lindenb., Syn. Hep.: 296 (1845), 744 (1847); Gottsche (1863: 269).

- Lejeunea (subg. Brachiolejeunea) leiboldiana (Gott. & Lindenb.) Steph., Hedwigia 29: 134 (1890).
- Marchesinia leiboldiana (Gott. & Lindenb.) Kuntze, Rev. Gen. Pl. II: 837 (1891).

<u>Type</u>: Mexico, Leibold s.n. (118?) (W (hb. Lindenberg 5983) holo, B, G 20176, S).

Heterotypic synonyms:

Phragmicoma leiboldiana var. & Lindenb. & Gott., Syn. Hep.: 744 (1847)
= Phragmicoma leiboldiana var. fastigiata Gott., Mex. Leverm.: 270 (1863);
Schiffner (1894: 182) syn. nov.
Type: Mexico, Mirador, Liebmann 191, III.1842 (W (hb. Lindenberg 5986)
holo, C, FH-Schiffner, G 21078, L, S). Cited erroneously as Lindenberg 5956 by Schiffner (I.c.).

Brachiolejeunea mamillata Steph., Spec. Hep. 5: 121 (1912) syn. nov. Type: Mexico, s.coll., s.n., ex hb. Nees, "dedit Jack" (G 20194 holo) Brachiolejeunea sulcata Evans ex Steph., Spec. Hep. 6: 382 (1923) syn. nov. Type: Jamaica, Cinchona, on trunk of *Podocarpus*, Evans 406, VIII.1906 (G 20354 holo).

Plants dioecious(?), medium-sized, up to 2.5 cm long (but rarely up to 5 cm), 1.40-1.75 mm wide, green to olive-green, becoming light to dark brown when dry, irregularly branched, parts of the female plants with a dichotomous appearance due to floriferous innovations; branches mainly *Frullania*-type, only occasionally *Lejeunea*-type; shoots with a lamellate paraphyllium, (130-)160-230(-270) µm long, located at the dorsal interlocking border of the lateral merophytes and separated only from each other by the dorsal leaf insertion cells, unistratose, one cell high (27-56 um), the paraphyllia present on all merophytes except from the offspring to the second leafy appendage of a *Frullania*-type branch.

Stem flaccid to rather rigid, 0.15-0.20(-0.25) mm in diam.; ventral merophyte four cell rows wide, the ventral cortical cells subquadrate to rectangular, $41-75 \times 18-45 \mu$ m, the dorsal cortical cells subquadrate to rectangular, $45-60 \times 30-54 \mu$ m; stem in transverse section with 11-21 thick-walled cortical cells surrounding 31-67(-75) thin-walled medullary cells, the dorsal cortical cells $23-35 \mu$ m high, the ventral cortical cells $16-30 \mu$ m high, the medullary cells $16-25 \mu$ m in diam.

Leaves imbricated, when moist distinctly squarrose. Lobe broadly obovate to suborbicular, 1.0-1.4 mm long, 0.8-1.4 mm wide, inserted along the whole length of the merophyte, the apex blunt to rounded, rarely minutely apiculate, the apical region plane to only slightly incurved, when spread out the ventral margin forming an angle of 150(-170°) with the keel; keel smooth, at an angle of 45-90° with the axis, only weakly curved, not decurrent; median leaf cells 33-54 x 20-36 µm, margin cells 13-22 µm high; intermediate thickenings frequently present, one per each larger cell wall. elliptic-rounded; oil bodies Massula-type, 16-30 per cell, ellipsoid-fusiform, 6.5-7.5 µm long, 1.5-2.5 µm wide.

Lobule rectangular to broadly ovate, 0.45-0.60 mm long, 0.25-0.40 mm wide, $0.3-0.6 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part plane to weakly concave; free margin plane, with 2(-3) inflexed teeth; teeth consisting of 3-5 cells in total with two cells at the base, separated by 7-10(-14) free marginal cells, the free margin with a distinct angle of \pm 150° at the second tooth; hyaline papilla 1-2 cells below the proximal base of the first tooth.

Underleaves imbricated, suborbicular, 0.5-0.6 mm long, 0.6-0.8 mm wide, the apex rounded, plane to recurved, the lateral margins plane to incurved, the base rounded and shortly decurrent, the line of insertion cuneate, 0.15-0.20 mm deep; median cells 27-41 x 18-27 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc tristratose in longitudinal section, elongated like a stalk, frequently with an extra cell layer developed between the superior central cell and the underleaf lamina cell, 55-200 μ m long; rhizoid disc suborbicular, consisting of many small, thin-walled cells.

Androecia not observed.

Gynoecium terminating stems and long or short Frullania-type branches, with 1-2 innovations; bracts and bracteole in one series, the bract lobe plane, obovate, the apical region concave, 1.0-1.5 mm long, 0.5-1.0 mm wide, the apex blunt to rounded, the keel with an angle of \pm 90°, bracts with a narrow-linear to more elliptic wing at the keel, 350-630 µm long, 90-250 µm wide, the lobule rectangular to rhomboid-rectangular, 0.45-0.55 x the length of the lobe, the apex without tooth or with a small tooth of 1-2 cells; bracteole obovate, 0.8-1.1 mm long, 0.6-0.8 mm wide, the apex widely rounded and slightly recurved, the basal part not inserted on the innovations. Perianth exserting the bracts for 1/5-1/3 when mature. frequently stalked, the stalk up to 350 um long, obovoid to obovoid-oblong, 1.2-1.5 x 0.6-0.8 mm, the three plicae extending over the upper 1/3-2/3 of the perianth; beak 2-4 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four spreading valves; spores green, more or less rectangular when dry, 57-87 μ m long, covered with numerous compound verrucae; elaters 34 per capsule, marginal elaters 220-430 μ m long, c. 20 μ m wide, with one colourless, incompletely developed, c. 4 μ m wide spiral.

Sporeling of the Lejeunea-type.

Distribution (PI. XXVII): tropical CENTRAL and SOUTH AMERICA, WEST INDIES (Jamaica). Main distribution in Mexico and Colombia, but also recorded from Ecuador and Brazil and from Jamaica (West Indies). Occurring at 800-1650 m altitude.

Ecology: growing epiphytic in rather loose mats on stems and trunks of living trees in xerophytic secondary forests (Brazilian cerradaos) or at forest edges, along rivers, in arable fields, etc. where temporarily drought may occur. Occasionally epilitic at higher altitude (coll. Gradstein & Aguirre 2956: 1650 m). *B. leiboldiana* frequently grows intermingled with other Lejeuneaceae (a.o. *B. laxifolia*, coll. Aguirre et al. 2995) or with *Frullania*.

<u>Differentiation</u>: *B. leiboldiana* is distinguished by a number of characters: 1) the obovate to suborbicular leaves which are distinctly squarrose when moist, 2) the rectangular to broadly ovate leaf lobule with only two, rarely three, teeth on the free margin (PI. XI, figs. 5-6), 3) the free margin of the leaf lobule, which has a distinct angle of \pm 150° at the location of the second tooth, 4) the stalked underleaf base at the rhizoid disc, frequently with cells between the superior central cell and the underleaf lamina cell (PI. XI, figs. 6-7), 5) the presence of a paraphyllium, which is one cell high (PI. XI, figs. 2-3) (up to 3-4 cells in height at their antical part in *B. laxifolia*, and 6) the rather irregular habitus of the plants, due to the frequent occurrence of single innovations (PI. XI, fig. 1). Single innovations are observed in all species of *Brachiolejeunea* but never as frequent as in *B. leiboldiana*. This character may serve to distinguish *B. leiboldiana* habitually when growing mixed with the related *B. laxifolia* (as in the collection Aguirre et al. 2995).

When only one innovation is developed the bracts are, in addition, anisomorphic: the bract subtending the innovation has a lobule and a wing as usual, whereas the other bract presumably represents a modified vegetative leaf with a somewhat more inflated lobule (PI. X, fig. 7).

Poorly developed *B. laxifolia* with reduced paraphyllia and weakly thickened ventral cortical cells may resemble *B. leiboldiana* but the former species is then distinguished by: 1) the ovate-falcate leaves with ovate lobules, 2) the paroecious male bracts, and 3) the more regular dichotomous growth. *B. leiboldiana* is seemingly dioecious but male plants have unfortunately not been found.

<u>Variation</u>: morphologically *B*. *leiboldiana* is a stable species, only varying in: 1) general size (2.5-5 cm long), together with a conspicuous variation in the density of foliation, and 2) the number of innovations (see above).

Specimens examined (B. leiboldiana):

- MEXICO. Mirador, Liebmann 191, III.1842 (C, FH-Schiffner, G 20178, L, S, W (hb. Lindenberg 5986), type collection of *Phragmicoma leiboldiana* var. *fastigiata* Gott.; s.loc., Leibold s.n. (118?) (B, G 20176, S, W (hb. Lindenberg 5983), type collection of *Brachiolejeunea leiboldiana* (Gott. & Lindenb.) Schiffn.; s.loc., Liebmann s.n. (BM); s.loc., Leibold s.n. (BM, G 20177, S); s.loc., s.coll., s.n. "dedit Jack" (G 20194), type collection of *Brachiolejeunea mamillata* Steph.
- JAMAICA. Cinchona, Evans 406, 28.VIII.1906 (G 20354), type collection of Brachiolejeunea sulcata Evans ex Steph.; s.loc., Evans 406 (?), 1913 (G 20355).
- BRAZIL. Bahia, Serra de Agua de Rega, Irwin et al. 31124, 26.II.1971 (U); Minas Gerais, Nova Lima, Vital 8871, 11.IV.1980 (JE, SP); Sao Paulo, Rio Grande, Schiffner 1591, 7.VI.1901 (S); Sao Paulo, Apiaky, Puiggari 664 (B, G 20371).
- COLOMBIA. Boyacá, Sácama, Aguirre et al. 2956, 2995 & 3097, 16-17.VIII.1982 (COL, U); Caldas, Manizales, Chichina, Aguirre & Gradstein s.n., 20.IX.1984 (COL, U); Risaralda, Santa Rosa de Cabal, El Lembo, Gradstein & van Zanten Z 569, 20.IX.1984 (COL, GRO, U).

ECUADOR. Tungurahua, Banos, Spruce s.n. (MANCH 14096).

4. BRACHIOLEJEUNEA SPRUCEANA (Mass.) Schiffn. (Plates XII-XIII)

in Engl. & Prantl, Nat. Pfl.-fam. I, 3(1): 128 (1893); Stephani (1912: 139); Bonner (1963: 460); Solari (1983: 536).

Lejeunea spruceana Mass., Nuovo Giorn. Bot. Ital. 17(3): 246 (1885).

Phragmicoma spruceana (Mass.) Steph., Hedwigia 28: 168 (1889).

<u>Type</u>: Argentina, Staten Island, "Ad ramulos Berberidis ilicifoliae ex Insula Statuum prope Port Cook", Speggazini 132, II-III.1882 (VER holo, G 16169, MANCH 14081).

Plants paroecious, small to medium-sized, up to 2.0 (rarely 2.5) cm long, 1.0- 1.8 mm wide, green, becoming light brown when dry, irregularly branched, parts of the plants with a dichotomous appearance due to floriferous innovations; branches mainly *Frullania*-type, only occasionally *Lejeunea*-type; shoots without a lamellate paraphyllium at the dorsal interlocking border of the lateral merophytes, but a tendency to form a one cell high paraphyllium sometimes present (PI. X111, figs. 2-3).

Stem rather flaccid, 0.10-0.18 mm in diam.; ventral merophyte four cell rows wide, the ventral cortical cells rectangular, $33-75 \times 16-33 \mu$ m; the dorsal cortical cells subquadrate-rectangular, $20-63 \times 18-36 \mu$ m, stem in transverse section with 12-17 thick-walled cortical cells surrounding 16-33 thin-walled medullary cells, the dorsal cortical cells 18-32 μ m high, the ventral cortical cells 15-27 μ m high, the medullary cells 12-27 μ m in diam.

Leaves rather densely imbricated, when moist distinctly squarrose. Lobe ovate-falcate, 0.60-0.95 mm long, 0.50-0.80 mm wide, inserted along 1/2-2/3 of the length of the merophyte, the apex rounded, the apical region not to slightly incurved, when spread out the ventral margin forming an angle of 120-145° with the keel; keel smooth, at an angle of 45-80° with the axis, curved near the base, not decurrent; median leaf cells 22-40 x 13-33 μ m, margin cells 9-16 um high; intermediate thickenings frequently present, one per each larger cell-wall, elliptic-rounded.

Lobule broadly ovate-rectangular, $0.25-0.40 \text{ mm} \log 0.20-0.30 \text{ mm}$ wide, 0.4-0.6 x the length of the lobe, gradually flattened towards the free margin, the flattened part weakly concave; the free margin plane, with three inflexed teeth; teeth consisting of 3-5 cells in total with 1-2 at the base, separated from each other by 4-8 free margin cells; hyaline papilla one cell below the proximal base of the first tooth.

Underleaves imbricated to barely so, suborbicular, 0.35-0.45 mm long, 0.35-0.40 mm wide, the apex plane and rounded, the margins plane, the bases rounded and shortly decurrent, the line of insertion cuneate, 0.07-0.10 mm deep; median cells $18-30 \times 12-18 \mu$ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc tristratose in longitudinal section, shortly elongated like a stalk, 30-60 μ m long; rhizoid disc suborbicular, consisting of many small, thin-walled cells.

Androecia located 1-3 series of vegetative leaves below the gynoecium; bracts and bracteoles in 2-4 series, the bract lobe ovate, 0.65-0.75 mm long, 0.55-0.60 mm wide, the lobule bearing 2-3 reduced teeth of 2-3 cells;

antheridium c. 125 µm in diam.

Gynoecium terminating stems and long or short *Frullania*-type and *Lejeunea*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe plane, obovate, the apical region concave, 0.85-0.95 mm long, 0.50-0.55 mm wide, the apex blunt to rounded, the keel with an angle of \pm 90°, bracts frequently without wing at the keel, occasionally a reduced, narrow linear wing developed, 100-250 µm long, 35-135 µm wide, the lobule rhomboid-rectangular, 0.5-0.6 x the length of the lobe, the apex blunt, without distinct apical tooth; bracteole obovate, 0.7-0.8 mm long, 0.5-0.6 mm wide, the apex widely rounded-truncate, the basal part not inserted on the innovations. Perianth exserting the bracts for 1/3-1/2 when mature, frequently stalked, the stalk up to 260 um long, obovoid to obovoid-oblong, 0.95-1.20 x 0.60-0.75 mm, the three plicae extending over the upper 1/4-3/4 of the perianth; beak 5-8 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.45 mm in diam., splitting to near base into four spreading valves; spores green, more or less rectangular when dry, 45-80 μ m long, covered with numerous compound vertucae, which sometimes show a tendency towards rosette formation; elaters 34 per capsule, marginal elaters 290-380 μ m long, c. 16 μ m wide, with one colourless, incompletely developed, c. 4 μ m wide spiral.

Sporeling of the Lejeunea-type.

<u>Distribution</u> (PI. XXVII): temperate SOUTH AMERICA (Chile, Argentina). Occurring in the southern parts of Chili and Argentina between 40-56° S, including the Tierra del Fuego area. Altitudinal data are lacking on labels, but DUSEN (in STEPHANI 1901) mentions occurrence up to 400 m.

Ecology: growing in dense patches on trees and shrubs (e.g. Berberis ilicifolia) in the very wet, species-rich, evergreen forests of Nothofagus betuloides and (locally) Drymis winteri. In the southernmost parts around Tierra del Fuego also in forests of Nothofagus antarctica. The forests are restricted to the western slopes of the Andes and are characterized by their great abundance of terrestric liverworts (DUSEN in STEPHANI 1901; ENGEL 1978).

Differentiation: this small species is distinguished from *B. laxifolia* and *B. leiboldiana* by: 1) the lack of a dorsal lamellate paraphyllium. In stem cross section a tendency towards paraphyllium development is sometimes seen (PI. XIII, figs. 2-3), 2) the plane underleaves (PI. XIII, fig. 6), 3) the lack of a wing on the female bracts, except for the occasional presence of a strongly reduced wing (PI. XII, fig. 3), and 4) the strongly inflated lobule of the paroecious male bracts (PI. XII, fig. 1).

Besides these morphological and anatomical features, *B. spruceana* is distinguished geographically by its restricted occurrence in temperate South America (mainland only), thus separated from the tropical *B. laxifolia* and *B. leiboldiana*.

The first three characters mentioned above are also present in B. *fernandeziana* from the Juan Fernandez Islands, but the latter species is

easily distinguished by several characters unique to *Brachiolejeunea* (see under *B. fernandeziana*).

Both sterile and fertile material of *B. spruceana* may be confused with *Blepharolejeunea securifolia* when observed at a glance. The latter species occurs in the tropical parts of the Andean chains as well as in Southeastern Brazil (VAN SLAGEREN & KRUIJT 1985) and is, besides its different distribution, to be distinguished by: 1) its rotundate-rectangular leaf lobule with a truncate apex and two, dissimilar teeth: the apical tooth blunt and inflexed, the second tooth straight and sharp, 2) its triangular to weakly cordate trigones, and 3) its dorsal cortical cells that are equal in size to the ventral cortical cells when observed in stem cross section. The two species are similar in 1) the outline of leaves, underleaves, perianth, paroecious male bracts and female bracts, including the frequent absence of a wing on the keel, and 2) the reduced and sometimes only scale-like leafy appendages of the *Frullania*-type branches.

Variation: morphologically B. spruceana is a very stable species.

Note: ARNELL's (1959: 18) record of *B. spruceana* from the Juan Fernandez Islands (coll. Sparre H254) represents misidentified material of *B. fernandeziana*. *B. spruceana* is thus far not reported from these islands.

Specimens examined (B. spruceana):

- CHILE. Valdivia: Corral, Quitaluto, Hosseus 613 p.p., II.1935 (JE); Termas de Puyehue, Schwabe 74b p.p., 27.VII.1940 (JE); s.loc., Hahn s.n. (G 20350); Llanquihue: Calbuco, Schwabe s.n., 18.IX.1937 (S); Puerto Varas, Quebrada del Diavolo, Dusén s.n. (380 ?), 7.V.1897 (NY); Lago Llanquihue, Quebrada del Diavolo, Dusén 466, VI.1897 (G 16171, S); Chiloë: Petrohue, Hosseus 524 p.p., 1935 (JE); s.loc., Skottsberg s.n., 1908 (G 16170, UPS), with coll. nr. 94 according to SOLARI (1983); Magellanes: Groppler Bay, Douglas s.n., 1893 (YU); Lago San Raphael, Bachman s.n., I.1921 (JE); Borja Bay, s.coll., 333 (G 20349); Isla Desolacion, Puerto Angusto, Dusén 209, 20.III.1896 (G 16173, UPS) & s.n. (380 ?), 13.IV.1896 (G 16172, UPS); Gray Harbour, Cunningham s.n. (NY); Cape Horn, s.coll., s.n. (NY); s.loc., s.coll., s.n. (NY-several collections); s.loc., Lechler s.n. (NY).
- ARGENTINA. Staten Island, Port Cook, Spegazzini 132, II-III.1882 (G 16169, MANCH 14081, VER), type collection of *Brachiolejeunea spruceana* (Mass.) Schiffn.; s.loc. (Albatros Voyage), s.coll., s.n., II.1888 (U, YU).

FRULLANOIDES Raddi

Crittogame Brasiliane: 13 (1822, prep. repr.), Mem. Math. Fis. Soc. Ital. Modena 19: 37 (1823); Bonner (1965: 470); Gradstein (1974a: 327); Farr et al. (1979: 691); Gradstein et al. (1982: 749); Grolle (1983: 17).

Ptychocoleus Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3(4): 404 (1877); Gradstein (1974a: 327); Gradstein et al. (1982:749) <u>nom. illeg.</u> <u>p.p</u>.

Lectotype (Trevisan 1877): Frullanoides densifolia Raddi (= Brachiolejeunea densifolia (Raddi) Evans).

Heterotypic synonym:

Brachiolejeunea subg. Plicolejeunea Schust., Beih. Nova Hedwigia 9: 104 (1963); Schuster (1980b: 763). Type: Brachiolejeunea bahamensis Evans (= Frullanoides bahamensis (Evans) van Slageren).

Plants dioecious, autoecious or paroecious, growing in densely or rather loosely appressed mats on corticolous, occasionally saxicolous or terrestric substrates, rarely pendulous, small to medium-sized, 11-5 cm long, occasionally large and then up to 10-12 cm long, blackish to deep olive-green, when dry becoming yellowish to darkish brown to black, irregularly branched; branches of the Frullania-type and of the Lejeunea-type, the Frullania-type branches usually long, vegetative or sexual (short in F. bahamensis and F. corticalis), with the dorsal stem half-leaf partially inserted on the branch, the first branch underleaf (un)equally bilobed and the first branch acroscopic leaf (un)equally bilobed, the Lejeunea-type branches short, vegetative or sexual, the gynoecia with two innovations of the Radula-type that may be repeatedly floriferous, giving parts of the shoots a dichotomous appearance.

Stem c. 0.1-0.2 x the width of the leafy plant, rigid or flaccid, 0.10-0.35 mm in diam., ventral merophyte (4-)6-8(-14) cell rows wide; dorsal cortical cells arranged in oblique zig-zag rows, the lateral merophytes interlocking dorsally; stem in transverse section with (11-)15-25(-37) thin-walled cortical cells (ventral cortical cells thick-walled in *F. densifolia* and *F. laciniatiflora*) surrounding (17-)36-74(-115) medullary cells with wall thickenings of variable size, the dorsal cortical cells larger than both the medullary cells and the ventral cortical cells, the medullary cells and the ventral cortical cells is with secondary blackish pigmentation; medullary cells in longitudinal section tapering towards relatively wide, truncate ends.

Leaves incubous, with a large dorsal lobe and a smaller ventral lobule, imbricated, suberect-convoluted when dry, when moist widely spreading and erectopatent to squarrose. Lobe (broadly) ovate to ovate-falcate to ovate-oblong, inserted along 2/3-1/1 of the length of the lateral merophyte, the dorsal base straight or auriculate, not to slightly arching beyond the

stem, the ventral and dorsal margins entire to serrulate (F. laciniatiflora), the apex rounded to obtuse to minutely or longly apiculate, never acute, the apical region plane to incurved, the ventral margin plane or incurved, when spread out forming an angle of 150-180° with the keel, the keel smooth, weakly curved to ± straight to weakly concave, not decurrent; cells arranged in \pm diverging rows, elongate-hexagonal, the median cells 21-54 x 14-33 µm, slightly larger at the leaf base, towards the margins becoming gradually smaller, at the margins rectangular to subquadrate, 11-28 µm high; vitta and ocelli absent; trigones and intermediate thickenings present, the trigones to medium-sized, small cordate, the intermediate thickenings scarce. elliptic-rounded to elongated, when present one per each larger cell wall; cuticula smooth; oil bodies present in all cells of leaves, underleaves, involucrum, perianth and stem cortex, Massula-type, in the lobe 15-30 per cell, homogeneous, ellipsoid to fusiform, or cylindrical-oblong, up to 8 µm long, upon degeneration becoming septate and subsequently desintegrating into minute granulae.

Lobule 0.3-0.7 x the length of the lobe, <u>never reduced</u>, ovate to broadly so or ovate-triangular, inflated along the keel and gradually flattened towards the free margin, the flattened part plane to concave, the free margin plane, straight to gradually curved towards the apex or irregularly arched with triangular segments (*F. liebmanniana*), with (3-)5-9(-11) inflexed teeth, beyond the apex <u>continuing over a short distance into the ventral margin of the lobe</u>; hyaline papilla inserted on the inner side of the lobule, 1-2(-6)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, $2.5-6.0 \times$ the width of the stem, varying from suborbicular to elliptic or obtrapezoid (*F. mexicana*), the apex undivided, rounded to truncate, plane or recurved, the margins entire, plane or slightly recurved, the bases without ears or with minute to large ears, the line of insertion subtransverse, arched or cuneate; underleaf base with <u>4-8 superior</u> <u>central cells</u>, the underleaf base at the rhizoid disc in longitudinal section <u>bistratose</u>, the stalk of attachment short, only (22-)35-60(-90) µm in length; the primary rhizoid disc consisting of up to 78 bulging cells giving rise to bundles of pale rhizoids.

Androecia terminal or intercalary on stems, Frullania-type and Lejeunea-type branches, bracts and bracteoles in 3-23 series, the bracts very much resembling leaves but usually smaller in size, the lobules with a more strongly inflated basal part and a concave distal part, <u>epistatic</u> (but hypostatic for the major part in *F. corticalis*!), the free margin without or with 1-7 reduced teeth, enveloping <u>one or two</u> antheridia subtended by a curved, uniseriate stalk; the bracteoles similar to underleaves, present throughout the male spike.

Gynoecium terminating stems and long or short *Frullania*-type or *Lejeunea*-type branches, bracts and bracteole in one series; bract lobe squarrose or plane to concave, ovate to obovate-elliptic or obovate-oblong, the apex rounded, blunt or (minutely) apiculate, the margins entire, in the apical region entire or ciliate, the keel sharp, or $\pm 90^{\circ}$, or blunt to rounded,
with a small linear to large elliptic-rounded wing, <u>running along the keel and</u> <u>transversally inserted on the innovation</u>, hence curved in situ (the wing often reduced to absent in *F. liebmanniana* and *F. mexicana*); bract lobule 1/4-3/4x the length of the lobe, narrow rectangular or rectangular-rhomboid, the apex truncate or rounded, without or with a 1-4-celled apical tooth; bracteole rectangular or rectangular-spathulate, the apex widely rounded-truncate to emarginate (in *F. laciniatiflora* truncate to bifid and ciliate), smaller in size than the bract lobe, basal part inserted on innovations or only on the main stem.

Perianth immersed or emergent for 1/5-1/3(-1/2) of its length when mature, (ob)ovoid-cylindrical or obovoid-oblong, frequently stalked, terete and isoplicate with 5-11 plicae in the upper 1/3-3/4 or broadly 3-keeled (*F. liebmanniana* and *F. mexicana*), the plicae occasionally extending down to base, the plicae smooth on their backs; beak 4-18 cells long; basal perianth cells large and thin-walled with small trigones, apical cells smaller with larger trigones and intermediate thickenings.

Calyptra entirely enveloping the sporophyte until maturity, the upper part (surrounding the capsule) 1(-2) stratose, the lower part (surrounding seta and foot) 2-6 stratose, the 1-2 outer cell layers of the lower part identical to the cells of the upper part, the 1-4 inner layers consisting of much smaller and \pm isodiametrical cells, the calyptral stalk very short.

Mature sporophyte exserted up to 0.8 mm above the perianth, the foot consisting of a few bulging cells, the seta articulate, with 16(-17, SCHUSTER 1980b) evenly tiered longitudinal rows of outer cells and 4(-6, SCHUSTER 1980b) longitudinal rows of inner cells, the capsule globose, dark brown, splitting to near base into four valves; valves widely spreading, especially the apical region, alternatively with 9 or 16 elaters in the apical region in a (1+3+5) or (1+3+5+7) arrangement or with 6 or 18 elaters in the apical region in a (2+4) or a (2+4+6+6) arrangement, the capsule valves bistratose in the apical part, the outer cells with asymmetrically-nodulose trigones and intermediate thickenings, the thickenings weaker at the extreme base, the cells of the inner valve layer covered by a yellow-brown, plurifenestrate sheet of thickening, the capsule base 3-5 stratose, consisting of thin-walled cells; elaters 30-68 per capsule, 260-550 um long, 15-20 um wide, with one (rarely two in F. liebmanniana), yellow-brown, c. 4 um wide spiral(s); spores with precocious germination, ± isodiametrical (with eight facets inside the capsule), angular when dry, 38-65 um in diam., the outer surface covered with numerous spinulae and eight rosettes of radially oriented spinae.

Sporelings of the Lopholejeunea-type (sensu NEHIRA 1983).

Chromosome number unknown.

Distribution: NEOTROPICAL (F. tristis PANTROPICAL), ranging in altitude from sea level up to 3650 m; the highest records from Mexico, Colombia, Peru and Nepal (3000-3650 m). Main centre of diversity in Central and South America (Mexico, Brazil and Peru: four species; Colombia: three species). All African and Asian localities concern F. tristis, which is also present in Central and South America. Ecology: mostly epiphytic, tolerating temporarily drought and maritime conditions. Preferably growing on stems, trunks and branches of living trees or shrubs in rather dense to more open rain forests or mountain forests, in mesophytic to xerophytic woodlands, on open hillsides, in savannas, along roadsides and in cultivated areas (plantations, gardens etc.), more rarely in moist riparian woods, in hammocks, swamps and mangrove; occasionally on decaying wood, rocks or on soil; \pm not epiphyllous (one collection known). Frequently species of the genus are growing intermingled, with other Lejeuneaceae or with *Frullania*; less frequent with other Hepaticae or Musci.

Differentiation: important diagnostic characters are underlined in the description.

KEY TO THE SPECIES OF FRULLANOIDES

1.	Ventral cortical cells of the stem thick-walled; underleaf auricles large,
	0.15-0.35 x 0.13-0.25 mm, appressed to the ventral-lateral side of the
	stem
1.	Ventral cortical cells of the stem thin-walled; underleaf auricles absent to
	minute or medium-sized, up to 0.07-0.15 \times 0.03-0.10 mm, not appressed to
	the ventral-lateral side of the stem
	2. Leaf apex blunt to minutely apiculate; apical margin of leaf, subgynoe-
	cial underleaf, female bracts and female bracteole entire
	2. Leaf apex long apiculate; leaf apical margin serrulate to ciliate; apical
	margin of subgynoecial underleaf and female bracteole as well as margin
	of female bracts dentate to ciliate 4. F. laciniatiflora (Peru)
3.	Branches predominantly Frullania -type, less frequent Lejeunea-type;
	underleaf auricles medium-sized, up to $0.07-0.15 \times 0.03-0.10$ mm;
	vegetative leafy shoots 1.4-2.7 mm wide
3.	Branches predominantly Lejeunea -type, only few Frullania-type; underleaf
	auricles absent to minute (a few cells only); vegetative leafy shoots
	1.0-1.7 mm wide
	4. Plants paroecious 7. F. tristis (America, Africa, India, Nepal)
	4. Plants dioecious
5.	Leaf lobule narrow triangular, with 8-11 teeth; teeth consisting only of a
	protruding cell of the lobule free margin; underleaf obtrapezoid
5.	Leaf lobule large, ovate-rectangular, with 3-5 teeth; teeth consisting of
	1-2 cells that are superimposed on the apex of triangular segments of the
	leaf lobule free margin; underleaf suborbicular to reniform
	5. F. liebmanniana (C. and S. America)

- 2. F. corticalis (S. and C. America, West Indies, Florida)
 6. Plants autoecious (rarely paroecious); male bracts in spikes of 4-9(-12) series, epistatic; leaf lobule with 5-6 teeth of (1-)3-5 cells with 1-2 cells at base; first tooth not situated at the extreme end of the lobule free margin; hyaline papilla at the proximal base of the first tooth .
 1. F. bahamensis (West Indies, Florida)

- FRULLANOIDES BAHAMENSIS (Evans) van Slageren comb. nov. (Plates XIV-XV)
- Brachiolejeunea bahamensis Evans, Bull. Torrey Bot. Club 35: 383 (1908a);
 Stephani (1912: 127); Schuster (1963: 104), (1980b: 768).
 <u>Type</u>: Bahamas, Crooked Island, Coppice, Stopper Hill, L.J.K. Brace 4816, 9-23.1.1906 (YU holo).

Heterotypic synonym:

Brachiolejeunea longispica Steph., Spec. Hep. 5: 125 (1912) syn. nov. Type: Cuba, Wright 1086 (G 20191 holo).

Plants autoecious (rarely paroecious), small to medium-sized, up to $1\frac{1}{2}$ cm long, 1.0-1.6 mm wide, at male spikes 0.60-1.15 mm, blackish to deep olivegreen (SCHUSTER 1980b), becoming darkish brown to black when dry, irregularly branched, parts of the plants with a dichotomous appearance due to floriferous innovations, parts with male spikes slender and more elongated; branches short or long, mainly *Lejeuneg*-type, only few *Frullania*-type.

Stem flaccid, 0.10-0.15 mm in diam.; ventral merophyte four cell rows wide, the ventral cortical cells subquadrate to short rectangular, 18-50 x 18-27 μ m, the dorsal cortical cells subquadrate to short rectangular, 27-36 x 22-31 μ m; stem in transverse section with 11-15 thin-walled cortical cells surrounding 17-26 thick-walled medullary cells, the dorsal cortical cells 22-40 um high, the ventral cortical cells 18-30 μ m high, the medullary cells 14-28 um in diam.

Leaves imbricated. Lobe ovate, sometimes ovate-oblong, 0.50-0.80 mm long, 0.40-0.55 mm wide, inserted along 3/4 of the length of the merophyte, the dorsal base straight, the apex rounded, the apical region plane to slightly incurved, the ventral margin plane, when spread out forming an angle of 150--170° with the keel; keel smooth, slightly curved, at an angle of 60-90° with the axis; median leaf cells 28-36 x 18-28 μ m, margin cells 11-22 μ m high; intermediate thickenings scarce, when present one per each larger cell-wall, elliptic-rounded to elongated, oil bodies (SCHUSTER & HATTORI 1954, SCHUSTER 1980b) *Massula*-type, (15-)20-30 per cell, ellipsoid to fusiform, 1.5-2 x 3-6(-8) μ m.

Lobule ovate to broadly so, 0.30-0.35 mm long, 0.20-0.30 mm wide, $0.40-0.55 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part concave; free margin gradually curved towards the apex, with 5-6 well developed teeth; teeth consisting of (1-)3-5 cells in total with 1-2 cells at the base, straight with only the top cells inflexed, separated from each other by (1-)3-4 free marginal cells; hyaline papilla one cell below the proximal base of the first tooth.

Underleaves imbricated, suborbicular, 0.3-0.4 mm long, 0.3-0.4 mm wide, the apex widely rounded, the margins plane, the bases without or with minute ears of a few cells only (Pl. XV, fig. 4), the line of insertion subtransverse, 0.02-0.10 mm deep; median cells $20-36 \times 15-22$ µm, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, very short, only 22-36 um in length; rhizoid disc suborbicular, consisting of a few thin-walled cells.

Androecia terminal or intercalary on stems and long or short Lejeunea-type branches; bracts and bracteoles in 4-9(-12) series, rarely below the gynoecium and then in 1-5 series, the bract lobe ovate to broadly so, 0.50-0.60 mm long, 0.40-0.45 mm wide, the lobule with a more strongly inflated basal part and a concave distal part bearing 1-2 distinct teeth of 1-3 cells and 1-2 indistinct teeth; bracts mono- and diandrous, antheridium c. 140 um in diam.

Gynoecium terminating stems and long or short Lejeunea-type branches, occasionally on Frullania-type branches, with two innovations; bracts and bracteole in one series, the bract lobe plane, obovate, the apical region plane to slightly concave, 0.85-1.00 mm long, 0.40-0.55 mm wide, the apex blunt to rounded, the keel sharp, bracts with a small elliptic-rounded wing at the reduced to a linear fold, (110-)160-320 um keel, occasionally lona. (50-)100-180 um wide, the wing occasionally absent, the lobule large, (narrow) rectangular to rectangular-rhomboid, 0.5-0.7 x the length of the lobe, the apex acute with a distinct apical tooth of 1-4 cells; bracteole rectangular-spathulate, 0.6-0.7 mm long, 0.3-0.4 mm wide, the apical part widely rounded, plane to slightly recurved, the basal part shortly inserted on the innovations. Perianth exserting the bracts for 1/5-1/4 when mature, occasionally stalked, the stalk up to 150 um long, (ob)ovoid-cylindrical, 0.8-1.1 x 0.4-0.5 mm, with 9-10 smooth, rounded plicae extending over the upper 1/2-3/4 of the perianth; beak 5-7 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 59-64 um long, covered with numerous spinulae and eight rosettes; elaters 30 per capsule, 260-360 um long, c. 18 um wide, with one brownish, c. 4 um wide spiral.

Sporeling of the Lopholejeunea-type.

Distribution (PI. XXIX): WEST INDIES, FLORIDA. Reported from the Bahamas, Puerto Rico, Cuba and the southern tip of Florida, U.S.A. Occurring in lowland areas (0-350 m) but data on altitudinal distribution are scarce.

Ecology: on bark of trees and on logs in lowland forest as well as in degraded and mesophytic woodlands; rarely epilitic. In Florida present at margins of open harmock forest where regular drought periods occur, in *Taxodium* swamps and in harmock adjoining salt marshes and mangrove, thus tolerating maritime conditions (SCHUSTER 1980b). Usually occurring associated with various Lejeuneaceae and with *Frullania* spp. Though *F. bahamensis* and *F. corticalis* are both found in the southern tip of Florida, U.S.A. in more or less the same habitats, they are surprisingly not reported growing together (SCHUSTER 1980b).

<u>Differentiation</u>: this is the smallest species of the genus *Frullanoides*, with the stems not exceeding $1\frac{1}{2}$ cm in total length. It is also the only autoecious species (the paroecious condition is only rarely present). Size, colour and general habit are very similar to *F. corticalis*, with which it has several characters in common (see under *F. corticalis*).

F. bahamensis is distinguished from F. corticalis by: 1) the male bracts, which are always epistatic and resembling the leaves (Pl. XIV, fig. 9), 2) the perianth with 9-10 smooth, rounded plicae (Pl. XIV, fig. 5), 3) the lobule of the female bract, which has a distinct apical tooth of 1-4 cells (Pl. XIV, fig. 5; Pl. XV, figs. 2-3), 4) the teeth of the leaf lobule, which are well developed, consisting of (1-)3-5 cells in total with 1-2 at the base, and which are not inflexed except for the top cells (Pl. XIV, fig. 8), and 5) the subgynoecial leaves, which are similar to the other vegetative leaves (widely different in F. corticalis).

A difference between F. bahamensis and F. corticalis that can almost serve as diagnostic is the distribution of the reproductive organs: F. bahamensis is autoecious and F. corticalis dioecious. A few specimens of F. bahamensis are, however, paroecious (colls. Pócs and colls. Wright from Cuba) and one specimen of F. corticalis was found autoecious (Ule 94 from Brazil).

Variation: morphologically F. bahamensis is a very stable species.

Specimens examined (F. bahamensis):

- U.S.A. Florida: Dade Co., Madeira Bay, Small 7557, 16.IV.1916 (FH, NY, YU); Monroe Co., Big Pine Key, R.M. & O.M. Schuster 31748b, 25.XII.1953 (G 11009, hb. Schuster); ibid., R.M. Schuster 42082 (B, hb. Schuster) & 42083, 29.XII.1958 (S, hb. Schuster).
- BAHAMAS. Abaco: Old Kerr's Point, Brace 2027, 2.1.1905 (YU); New Providence: s.loc., Brace 3, VII.1921 (YU) & Brace 9966 (YU); s.loc., Coker 1 p.p., 18.VI.1903 (YU) & Coker 2, 24.VI.1903 (YU); Fox Hill, Britton & Millspaugh 2090, 26.1.1905 (YU); Grantstown, Britton 562, 584 6.IX.1904 (YU);s.loc., Britton p.p., 6.IX.1904 (YU): Watling's Island: Cockburn Town, Britton & Millspaugh 6120, 12-13.111.1907 (YU); Crooked Island: Vauxhall, Brace 4746, 9-23.1.1906 (YU); Coppice, Brace 4816, 9-23.1.1906 (YU), type collection of Frullanoides bahamensis (Evans) van Slageren; ibid., Britton 3191, 31.1.1905 (U, YU).
- CUBA. Oriente: Holguin, Pócs 9019/D, 16.X.1978 (EGR, G 210389, HAC, U), Pócs 9040/B & 9041/G, 23.X.1978 (EGR, HAC, U), Pócs & Catasus 9025/N, 18.X.1978 (EGR, U); Santiago de Cuba, Sierra Maestra, Pócs 9056/F & 9056/J, 16.XI.1978 (EGR, HAC, U); <u>Matanzas</u>: Playa, Britton & Wilson 81, 28.VIII.1903 (YU); <u>Pinar del Rio</u>: Carabelita, Schubert M32, 2.XII.1967 (JE); <u>s.loc</u>., Wright 489 (G 20110), 1072 (G 20193) & 1086 (G 20191, type collection of *Brachiolejeunea longispica* Steph.).

PUERTO RICO. Mona Island, Britton et al. 1798, 20-26.1.1914 (YU).

- FRULLANOIDES CORTICALIS (Lehm. & Lindenb.) van Slageren <u>comb</u>. <u>nov</u>. (Plates XVII-XVIII)
- Jungermannia corticalis Lehm. & Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pug. 4: 50 (1832).
- Phragmicoma corticalis (Lehm. & Lindenb.) Lehm. & Lindenb., Syn. Hep.: 297
 (1845); Stephani (1890: 8).
- Ptychocoleus corticalis (Lehm. & Lindenb.) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3(4): 405 (1877).
- Lejeunea (subg. Brachiolejeunea) corticalis (Lehm. & Lindenb.) Steph., Hedwigia 28: 167 (1889), (1890: 134).
- Marchesinia corticalis (Lehm. & Lindenb.) Kuntze, Rev. Gen. Pl. II: 836 (1891). Brachiolejeunea corticalis (Lehm. & Lindenb.) Schiffn., Hedwigia 33: 180 (1894); Evans (1902: 131), (1908a: 160); Stephani (1912: 127); Bonner (1963: 449); Schuster (1980b: 764).
 <u>Type</u>: Jamaica, Lehmann s.n. (S holo, G 20105 & 20115, W (hb. Lindenberg 5990).

Heterotypic synonyms:

- Frullania leprieurii Nees & Mont., Ann. Sci. Nat. Bot. 2(14): 333 (1840); Syn. Hep.: 297 (1845).
- Phragmicoma leprieurii (Nees & Mont.) Mont., Syll. Gen. Spec. Crypt.: 86
 (1856).
- Phragmicoma melanophloea Mont. & Nees, Syn. Hep.: 297 (1845); Evans (1902: 132): nom. inval. pro syn.

Syntypes: Guiana (MONTAGNE 1840: "in corticibus crescentiae cujetae ad radices montis Baduel prope Cayennam"), Leprieur 273 & 277, V.1837 (PC-Montagne holo, BM).

- Acrolejeunea linguaefolia (Tayl.) Bonner, Index Hep. II: 19 (1962); Gradstein (1975: 127).
- Lejeunea linguaefolia Tayl., London J. Bot. 5: 390 (1846); Syn. Hep.: 754 (1847); Evans (1902: 132); Stephani (1890: 134), (1912: 127). Type: St. Thomas, Richard s.n., 1814 (BM, G 20112, MANCH 14042, PC, S, W (hb. Lindenberg 6262). The holotype, which should be in FH-Taylor, has not been available).

Brachiolejeunea surinamensis Steph., Spec. Hep. 5: 124 (1912); Herzog (1951: 136) syn. nov.

Type: Guiana, Leprieur 115, s.d. (G 20356 holo).

Ptychocoleus torulosus (Lehm. & Lindenb.) Trev. fo. parvistipula Herz., Rev. Bryol. Lichénol. 20: 135 (1951); Gradstein (1975: 129) <u>syn. nov.</u> Type: Honduras, Lancetilla Valley, near Tela, 20-600 m, Standley 54496, 14.XII.1927-15.III.1928 (JE holo).

Plants dioecious, (rarely autoecious), small to medium-sized, up to 2.5 cm long, 1.25-1.70 mm wide, at male spikes 0.55-0.95(-1.25) mm, brown to blackish-green (SCHUSTER 1980b), becoming darkish-brown to black when dry, irregularly branched, female plants with a dichotomous appearance due to floriferous innovations, male plants more sparsely branched and with a more slender appearance; branches short or long, mainly *Lejeunea*-type, *Frullania*-type less frequent.

Stem flaccid, 0.15-0.20 mm in diam.; ventral merophyte four cell rows wide, the ventral cortical cells subquadrate to short rectangular, 29-54 x 21-26 μ m, the dorsal cortical cells subquadrate to short rectangular, 36-68 x 29-50 μ m; stem in transverse section with 11-14 thin-walled cortical cells surrounding 17-36(-45) thick-walled medullary cells, the dorsal cortical cells 25-40 μ m high, the ventral cortical cells 18-25 μ m high, the medullary cells 14-25 μ m in diam.

Leaves imbricated. Lobe ovate, 0.6-0.9 mm long, 0.5-0.6 mm wide, inserted along the whole length of the merophyte, the dorsal base straight, the apex rounded, the apical region plane to incurved, the ventral margin plane, when spread out forming an angle of 150-170° with the keel; keel smooth, curved to only slightly so, at an angle of 60-90° with the axis; median leaf cells 29-43 x 18-32 μ m, margin cells 14-21 μ m high; intermediate thickenings scarce, elliptic rounded, when present one per each larger cell wall.

Lobule ovate to broadly so, 0.35-0.45 mm long, 0.2-0.3 mm wide, 0.40-0.55 x the length of the lobe, rather abruptly flattened towards the free margin, the flattened part concave; free margin straight with the basal part curved, with 3-6 teeth; teeth consisting of 1-3 cells in total with one cell at the base, inflexed, separated from each other by 2-4 free marginal cells, the second and the third tooth separated by 3-8 cells, the first tooth located at the extreme end of the lobule; hyaline papilla 1-2 cells below the proximal base of the second tooth.

Underleaves imbricated, suborbicular, 0.35-0.45 mm long, 0.40-0.55 mm wide, the apex widely rounded to truncate, the margins plane, the bases without ears or with minute ears of a few cells only, the line of insertion arched to subtransverse, 0.05-0.10 mm deep; median cells 25-46 x 18-25 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, very short, only 27-54(-63) μ m in length; rhizoid disc suborbicular, consisting of a few thin-walled cells.

Androecia terminal or intercalary on stems and long or short Frullania-type

and Lejeunea-type branches; bracts and bracteoles in 4-15(-22) series, the bracts epistatic in the basal and apical series, in the largest, central part hypostatic (PI. XVII, fig. 1b); the bract lobe variable in outline: from resembling the leaves with a more strongly inflated lobule to much shorter and broadly ovate with a very large, ovate-rectangular lobule, which has a large, rounded to rather acute apex (PI. XVII, fig. 8), the lobule 0.45-1.00 x the length of the lobe, the free margin without teeth or with one blunt tooth; bracts 0.45-0.80 mm long, 0.35-0.50 mm wide; bracts diandrous, antheridium c. 130 μ m in diam.

Gynoecium terminating stems and long or short Frullania-type and Leieunea-type branches, with two innovations; bracts and bracteole in one series, the bract lobe plane, ovate-oblong, the apical region concave, rarely squarrose, 0.85-1.25 mm long, 0.45-0.65 mm wide, the apex rounded, the keel blunt to rounded, bracts with an elliptic-rounded and rather small wing at the keel, (0.25-)0.30-0.60 long, (0.15-)0.20-0.30 mm wide, the lobule large, narrow rectangular-rhomboid, $0.60-0.75 \times$ the length of the lobe, the apex acute-rounded, without apical tooth; bracteole rectangular, 0.75-1.05 mm long, 0.45-0.70 mm wide, the apex widely rounded to truncate-emarginate, slightly recurved, the basal part inserted on the main stem only, the basal 2/3 of the bracteole in situ canaliculate; the stem leaves directly below the bracts with narrow rectangular, oft hypostatic lobules, 0.65-0.75 x the length of the lobe, with only one (apical) tooth of 2-6 cells. Perianth exserting the bracts for 1/5-1/3 when mature, occasionally stalked, the stalk 215-535 um long, obovoid to obovoid-oblong, $0.70-1.25 \times 0.50-0.70$ mm, with 5-8(-10)smooth and narrowly-rounded plicae extending over the upper 2/5-1/2 of the perianth; beak 4-7 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 50-60 μ m long, covered with numerous spinulae and eight rosettes; elaters 30 per capsule, 290-400 μ m long, c. 15 μ m wide, with one brownish, c. 4 μ m wide spiral.

Sporeling of the Lopholejeunea-type.

Distribution (PI. XXVIII): tropical SOUTH and CENTRAL AMERICA, WEST INDIES, FLORIDA. A common species in the West Indies, the southern tip of Florida, U.S.A. and the Bahamas. Also reported from tropical Brazil, the Guianas and in Central America north to Mexico. A lowland species (0-200 m) but data on altitudinal distribution are scarce. In Cuba collected at 600-650 m.

Ecology: in dense to more loose patches, closely adnate to the cortex of stems and trunks of living trees, rarely on rocks or on sheltered terrestric substrates. Occurring in both natural and degraded habitats and with a wide drought tolerance. Present in rain forests as well as more open mesophytic to xerophytic woodlands (VAN SLAGEREN 1979). In Florida found at edges of hammock forest, brackish areas and on mangrove (SCHUSTER 1980b). Often occurring together with various Lejeuneaceae and with *Frullania* spp. <u>Differentiation</u>: *F. corticalis* is easily distinguished from the other species of *Frullanoides* by: 1) the male spike of 4-15(-22) series of hypostatic bracts except for the most basal and apical series (PI. XVII, figs. 1b, 8), 2) the stem leaves, directly below the female bracts, which have a narrow, often hypostatic, rectangular lobule (PI. XVII, fig. 2), 3) the presence of a small tooth on the extreme end of the leaf lobule and the location of the hyaline papilla below the proximal base of the second tooth (PI. XVIII, fig. 3), a configuration similar to *Acrolejeunea pycnoclada* (GRADSTEIN 1975: 110), and 4) the perianth, which has only 5-8 rather sharp plicae (PI. XVII, fig. 7a-b) (ten \pm rounded plicae, however, may be occasionally present).

It must be noted that the first three characters are unique in *Frullanoides* and allow easy distinction from the other species in the genus. *F. corticalis* and *F. bahamensis* have several characters in common, which distinguish them from the other species in *Frullanoides*: 1) the reduced number of elaters: 30, divided alternatively over valves with (1+3+5) and with (2+4) elaters (the other species with 56-68 elaters), 2) the branches, which are predominantly of the *Lejeunea*-type (in the other species of the *Frullania*-type), 3) the small size of the plants: not exceeding 2.5 cm in length and 1.65 mm in width (other species at least 2 cm long and 1.40 mm wide), 4) the number of cortical cells: 11-14 (other species at least 14 and up to 37), 5) the minute to even absent auricles of the underleaves (in other species medium-sized to large: 0.05-0.35 mm long, (0.03-)0.10-0.25 mm wide), and 6) the plane female bracts with incurved apical region (in the other species at least partially squarrose).

When sterile, F. corticalis might be confused with Acrolejeunea torulosa (GRADSTEIN 1975). Sterile A. torulosa differs by: 1) dull yellowish-brown to darkish- or grayish-brown colour when dry, 2) the more strongly squarrose leaves, 3) the presence of vegetative reproduction via caducous leaves, and 4) the male bracts, which are epistatic instead of hypostatic.

<u>Variation</u>: *F. corticalis* is morphologically constant throughout its range with the most important variation observed in the number of plicae of the perianth and in the outline of the male bracts and their lobules. Usually there are 5-8 rather sharp plicae, but 10 rounded plicae may be occasionally present. When 10 plicae are developed, the perianth is similar to *F. bahamensis* and this character then fails to separate *F. corticalis* from the latter species. Size and outline of the male bracts may vary considerably: shorter and more broadly ovate lobes have (relatively) larger and ovate-rectangular lobules, up to an extent where the length of the lobule and the lobe are equal (Pl. XVII, fig. 8).

<u>Note</u>: similarly to *F*. bahamensis this species is, in fact, polyoecious: one autoecious specimen has been found (Ule 94 from Brazil). As the specimen is identical to the dioecious specimens in all other respects, no separate taxonomic status is given based on this feature (cf. CRADSTEIN 1975).

Specimens examined (F. corticalis):

- U.S.A. Florida: Everglades National Park, Verdoorn s.n. (hb. Fulford); Sanford, Quer (Büer ?) 8.R., 8-19.1912 (FH); Dade Country, Small s.n., 1915 (FH); Everglade Keys, Brogdon Hammock, Small & Mosier 6227 & 6230, 19.VI.1915 (FH, NY, YU); Breckell's Hammock, Britton 35, 18.III.1904 (YU); Dade, Monroe County, N.C. & E.G. Britton 554, 4.XII.1919 (NY, YU); Fairchild's Tropical Garden, Jephson 1996, 18.II.1960 (NY); s.loc., Underwood 303, 1891 (YU); Lake Worth, Underwood 2178 (NY, YU); s.loc., Underwood 2590 (G 20107); s. loc., J.D.S. s.n., 1877 (MANCH 14044 & 14047).
- MEXICO. Mirador, Liebmann s.n., III.1842 (S, W (hb. Lindenberg 5973); s.loc., Liebmann s.n. (BM).
- BELIZE. Nicolas Cay, Spellman & Stoddart B127b, 5.VII.1972 (EGR, HAC, U); Lime Cay, Spellman & Stoddart B128b, 5.VII.1972 (EGR, HAC, MO, U); Frank Cay, Spellman & Stoddart B129b, 6.VII.1972 (EGR, HAC, MO, U).
- HONDURAS. Atlantida, Lancetilla Valley, near Tela, Standley 54496, 14.XII.-1927-15.III.1928 (JE), type collection of *Ptychocoleus torulosus* fo. *parvistipula* Herz.
- COSTA RICA. Golfo Duice, Taylor 39-754, 26.111.1939 (hb. Fulford).
- PANAMA. Panama, playa langosta, Salazar 870 (hb. Fulford); Canal Zone, Gatún, Howe s.n., 1.1.1910 (NY, YU); Canal Zone, Colon, Howe s.n., 29.XII.1909 (NY, YU).
- CUBA. Isle of Pines: Ensanada de Siguanea, Britton & Wilson 15428, 13.111.1916 (YU); Siguanea, Britton et al. 15389, 12.111.1916 (YU); Matanzas: s.loc., Underwood & Cook 144, II.1891 (BM, G 20109, MANCH 14043, YU); Las Villas: Santa Clara, Bahia de Cochinos, León & Loustalot 9574, 14.VIII.1920 (HAC, NY, U); Santa Clara, Amaro, León & Loustalot 9589, 11.VIII.1920 (YU); Oriente: Guantánamo, Baracoa, Reyes 699, 719 & 732, 7-8.IX.1974 (HAC, U); Gran Piedra, Reyes 733, 25.IX.1970 (HAC, U); Guantánamo, Cuchillas de Baracoa, Pócs & Reyes 9065/AC, 9065/AE, 9065/AF & 9065/C, 27.XI.1978 (EGR, U); Guantánamo, Puriales de Canjeri, Pócs et al. 9185/D, 22.X.1980 (EGR, HAC, U); Baracoa, Rio Toa, Schubert M325, 6.II.1968 (JE); Baracoa, Lippold 10106, 10114, 10118 & 10118C, 3.XI.1968 (JE); Baracoa, base of El Junque Mt., Underwood & Earle 313, III.1903 (YU); <u>s.loc.</u>: Underwood 2073 (BM, G 20108) & 2106a (G 20111); Wright s.n. (YU).
- JAMAICA. Mansfield, near Bath, Evans 337, 1.VIII.1903 (B, BM, YU), 343b & 350, 1.VIII.1903 (YU); ibid., Maxon 1850, 3.V.1903 (YU); ibid., Underwood 2814, 2-4.V.1903 (YU); Portland, Hermitage Farm, Orcutt 4549,

18.II.1928 & 4759A, 22.II.1918/19 (?) (hb. Fulford); St. Ann's Bay, Farr 1484, 19.III.1955 (hb. Fulford); John Crow Peak, Underwood 784 p.p. (YU); St. Mary Parish, Castleton Botanic Garden, von der Porten 286 & 287, 29.I.1949 (WTU); s.loc., Davies 4 & s.n., V.1882 (BM); s.loc., Curnow 1 (BM, G 20192); s.loc., Lehmann s.n. (G 20105 & 20115, S, W (hb. Lindenberg 5990), type collection of *Frullanoides corticalis* (Lehm. & Lindenb.) van Slageren.

- BAHAMAS. <u>Great Bahama</u>: Pinder's Point, Britton & Millspaugh 2533, 5-13.11.1905 (YU); Golden Grove, Britton & Millspaugh 2719 & 2723, 5-13.11.1905 (YU); Barnett's Point, Britton & Millspaugh 2646, 5-13.11.1905 (YU); <u>Cat Island</u>, The Bight, Britton & Millspaugh 5899, 1-6.111.1905 (YU).
- HAITI. Tortue Island: Vicinity of La Vallée, E.C. & G.M. Leonard 11613, 28.XII.1928-9.1.1929 (JE); Vicinity of Basse Terre, E.C. & G.M. Leonard 12542, 21-29.III.1929 (JE).
- DOMINICAN REPUBLIC. St. Domingo, Eggers s.n. (BM).
- PUERTO RICO. Vieques Island, Cerro Ventana, Schafer 2989b, 20-21.11.1914 (YU); s.loc., Sintenis s.n. (BM).
- ST. THOMAS. s.loc., Richard s.n. (BM, G 20112, MANCH 14042, PC, S, W (hb. Lindenberg 6262), type collection of *Acrolejeunea linguaeifolia* (Tayl.) Bonner.
- GUADELOUPE. s.loc., Marie s.n. (BM).
- ST. LUCIA. Road Castries to Morne Fortuné, Evans 84b & s.n., 30.VIII.1926 (YU); Castries, Evans s.n., 5.IX.1926 (YU).
- CURAÇAO. Christoffelberg, near Piedro Molina, van Slageren & Stoffers 8129 & 8133a, 23.XII.1976, 8151b, 29.XII.1976 & 8401, 25.I.1977 (U); Pos Kayuda, van Slageren & Stoffers 8086, 20.XII.1976 (U); Christoffelberg, Florschütz 3456a, III.1965 (U); ibid., Suringar s.n., I-V.1885 (L).
- TRINIDAD. Manzanilla, N.L. & E.G. Britton 2203, 9.111.1921 (YU); North Post Road, Britton et al. 788 & 789, 19.111.1920 (YU).
- FRENCH GUIANA. Cayenne, "ad truncas Byrsonima in plaitibus circa Cayenne", Leprieur s.n., V.1838 (PC-Montagne); ibid., Jardin Botanique, Cremers 3811, 12.VIII.1976 (U); ibid., Gradstein 5772, III.1985 (U); ibid., Place des Palmistes, Aptroot 15077, III.1985 (U); ibid., around Montabo mountain, Gradstein 5753, 5757 & 5764, III.1985 (U); vicinity of Cayenne, Reservoir Hill, Broadway 790 (NY) & 799, 12.VII.1921 (YU); s. loc., Leprieur 115 (G 20356), type collection of Brachiolejeunea

surinamensis Steph.; s.loc., Leprieur 273 & 277, V.1837 (BM, PC-Montagne), syntypes of Frullania leprieurii Nees & Mont.; s.loc., Leprieur s.n. (BM, MANCH 14048); s.loc., Montagne s.n. (S, W (hb. Lindenberg 5991).

- GUYANA. Near Berbice, Aiken s.n., 1910 (BM, BP, U); s.loc., Goebel s.n. (BM); s.loc., s.coll., s.n. (MANCH 14045).
- BRAZIL. <u>Mato Grosso</u>: Mirando, Vital 2374, 12.VI.1973 (SP, U); <u>Minas Gerais</u>: Rio de Janeiro, Ule 94, 1889 (BM, G 20106, 20114); Sierra d'Estrella, Beyrich 21 (BM, G 20113, S, W); s.loc., Martius s.n. (B).
- COLOMBIA. Narino: El Charco, La Vigia, Linares 033, 1983 (COL); Isla de Providencia, M.C. Ramirez 014, 1983 (COL, U).

3. FRULLANOIDES DENSIFOLIA Raddi (Plates XVIII-XXI)

Crittogame Brasiliane: 14 (1822 prep. repr.), Mem. Mat. Fis. Soc. Ital. Sci. Modena 19: 38 (1823); Bonner (1965: 470); Gradstein (1974a: 327); Farr et al. (1979: 691); Grolle (1983: 17).

Ptychocoleus densifolius (Raddi) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3(4): 405 (1877); Grolle (1983: 33) nom. illeg.

Brachiolejeunea densifolia (Raddi) Evans, Bull. Torrey Bot. Club. 35: 158 (1908a); Evans (1912b: 62); Stephani (1912: 118); Bonner (1963: 449); Gradstein (1974a: 328).

<u>Type</u>: Brazil, "Trovasi com' essa sugl' alberi negl' ombrosi boschi del Corcovado, Montagne prossima a Rio-janeiro", Raddi s.n. (Pl holo, BM, FH-Taylor, PC, NY).

Heterotypic synonyms:

- Brachiolejeunea appendiculistipa Steph., Spec. Hep. 6: 381 (1923); Herzog (1955: 199): syn. nov. Type: Bolivia, Herzog 3365 p.p. (G 20062 holo).
- Brachiolejeunea appendiculistipa var. bifida Herz., Svensk Bot. Tidskr. 51: 190 (1957) <u>syn. nov.</u>
 Type: Ecuador, Pichincha, zwischen San Juan und Saloya, E. Asplund s.n., 11.IX.1939 (JE holo, G 20063, S).

Brachiolejeunea bicolor (Nees) Schiffn. in Engl. & Prantl, Nat. Pfl.-fam. I,

3(1): 128 (1893); Evans (1912b: 62), (1914: 325); Bonner (1963: 446). Jungermannia bicolor Nees in Martius, Flor. Bras. 1(1): 349 (1833); Gradstein (1974a: 328); Bonner (1976: 48).

Lejeunea bicolor (Nees) Mont., Flor. Boliv.: 66 in d'Orbigny, Voy. dans l'Amér. Mérid., Bot. 7(2) (1839); Spruce (1884: 131); Stephani (1890: 7, 134).

Phragmicoma bicolor (Nees) Nees, Syn. Hep.: 294 (1845); Gottsche (1857: 344), (1863: 268), (1864: 145); Stephani (1889: 167), (1912: 136).

Marchesinia bicolor (Nees) Kuntze, Rev. Gen. Pl. II: 836 (1891). Type: Brazil, Minas Geraes, Martius s.n., 1832 (STR holo not seen, FH-Taylor, M, S, W (hb. Lindenberg 5956).

Phragmicoma bicolor var. armata Gott., Lindenb. & Nees, Syn. Hep.: 743 (1847); Gottsche (1863: 268) <u>syn. nov.</u> Type: Mexico, Pico de Orizaba, Liebmann 389b (C holo).

Phragmicoma bicolor var. conferta Gott., Lindenb. & Nees, Syn. Hep.: 743 (1847); Spruce (1884: 132); Schiffner (1894: 180) <u>syn. nov.</u> Lectotype: Colombia, Merida, Moritz s.n. (W holo, BM G 20079, STR). The holotype, which has been in B, has been destroyed.

Brachiolejeunea canaliculata Steph., Spec. Hep. 5: 117 (1912) syn. nov. Type: Mexico, s.d., s.coll., s.n. (G 20099 holo).

Brachiolejeunea columbica Steph., Spec. Hep. 6: 382 (1923) syn. nov. Type: Colombia, s.d., s.coll., s.n., hb. Cardot 29 (G 20101 holo).

Brachiolejeunea rupestris (Gott.) Steph., Spec. Hep. 5: 122 (1912) <u>syn. nov.</u> Phragmicoma rupestris Gott., Ann. Sci. Nat. Bot. 5(1): 146 (1864); Stephani (1889: 168). Type: Colombia, Padua, Lindig 224 (G 20242 holo, B).

Brachiolejeunea succisa Steph., Hedwigia 34: 65 (1895a), Spec. Hep. 5: 122 (1912) syn. nov.

Lejeunea (subg. Brachiolejeunea) succisa Steph., Hedwigia 28: 168 (1889) nom. nud.

Type: Ecuador, s.d., s.coll., s.n., hb Renauld 524 (G 20351 holo).

- Dicranolejeunea boliviensis Steph., <u>in</u> Herzog, Biblioth. Bot. 87: 253 (1916); Spec. Hep. 6: 385 (1923); Herzog (1955: 199) <u>syn</u>. <u>nov</u>. Type: Bolivia, Incacorral, Herzog 4971, VI.1911 (G 22658 holo, L).
- Dicranolejeunea nudiflora Steph., in Herzog, Biblioth. Bot. 87: 254 (1916); Spec. Hep. 6: 383 (1923) syn. nov. Type: Bolivia, in valle Corani, Herzog 4753, V.1911 (G holo, L).

Marchesinia coniloba Steph., Spec. Hep. 5: 147 (1912) syn. nov.

Type: Costa Rica, Cartago, Werckle s.n. (G 21836 holo).

- Mastigolejeunea decurrens Steph., in Herzog, Biblioth. Bot. 87: 249 (1916); Spec. Hep. 6: 561 (1924) syn. nov.
 Syntypes: Bolivia, Florida de San Mateo, Herzog 3695 & 3697 (G 21810); Bolivia, Rio Tocorani, Herzog 4089 & 4094 (G 21810).
- Ptychanthus boliviensis Steph., in Herzog, Biblioth. Bot. 87: 249 (1916);
 Spec. Hep. 6: 559 (1924) syn. nov.
 Type: Bolivia, Rio Tocorani, Herzog 4113 (G holo).

Ptychocoleus boliviensis Steph., in Herzog, Biblioth. Bot. 87: 250 (1916);
Gradstein (1975: 127) nom. nud.
Material: Bolivia, Florida de San Mateo, Herzog 3639, IV.1911 (B, G 14604, L, M, MANCH, S, W).

Plants dioecious, medium-sized to large, average length 4-5 cm, occasionally up to 10-12 cm, 1.9-3.0 mm wide, at male spikes 1.65-2.35 mm, green, becoming yellowish or darkish-brown to black when dry, irregularly branched, female plants with a dichotomous appearance due to floriferous innovations, male plants more sparsely branched and with a more slender appearance; branches long, sometimes short, mainly *Frullania*-type, *Lejeunea*-type occasionally present.

Stem rigid, 0.15-0.25(-0.35) mm in diam.; ventral merophyte 8-10(-14) cell rows wide, the ventral cortical cells rectangular, $54-80 \times 21-32$ um, in well developed plants becoming elongated rectangular, $54-104 \times 18-29$ um, with irregularly thickened walls, the dorsal cortical cells subquadrate to short rectangular, $36-78 \times 18-40$ um; stem in transverse section with 20-31(-37) cortical cells that are thin-walled to only slightly thickened on the dorsal and lateral side and strongly thickened on the ventral side, the dorsal cortical cells 25-40(-47) um high, the ventral cortical cells 18-27 um high, the medulla consisting of 46-90(-115) thick-walled cells, 22-29(-40) um in diam., the walls of the medullary cells less thickened than of the ventral cortical cells.

Leaves loosely imbricated. Lobe ovate-falcate, 1.00-1.80 mm long, 0.75-1.40 mm wide, inserted along 3/4-1/1 of the length of the merophyte, the dorsal base auriculate, the apex blunt to minutely apiculate, the apical region incurved, the ventral margin upcurved, when spread out forming an angle of $160-180^\circ$ with the keel; keel smooth, in outline varying from slightly convex to slightly concave, at an angle of $60-80^\circ$ with the axis; median leaf cells $25-40 \times 18-33$ um, margin cells 15-22 um high; intermediate thickening scarce, elliptic-rounded, when present one per each larger cell wall; oil bodies homogeneous, *Massula*-type, 15-27 per cell, ellipsoid to fusiform, sphaerical when seen from the side, $2.5-6.0 \times 1.5-2.5$ um, glistening.

Lobule ovate-triangular with an oblique apex, 0.45-0.80 mm long, 0.35-0.70 mm wide, $0.4 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part plane; free margin gradually curved to almost straight towards the apex of the lobule, with (5-)7-9 teeth; teeth consisting

of 1-4 cells in total with 1-2 cells at the base, inflexed, better developed near the apex and there at a greater distance of each other: 5-11 viz. 4-6 free marginal cells; hyaline papilla two cells below the proximal base of the first tooth.

Underleaves imbricated, outline, including auricles, in situ varying from suborbicular to transversally elliptic to subquadrate-rectangular, 0.50-1.10 mm long, 0.85-1.30 mm wide, the rounded to truncate apical region strongly recurved, the margins plane to slightly recurved, the bases with large, rounded to broadly ovate ears, 0.15-0.35 x 0.15-0.20 mm in size, appressed to the ventral-lateral side of the stem, the line of insertion arched, 0.17-0.22 mm deep; median cells 21-46 x 18-25 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, short, 36-63(-80) μ m in length; rhizoid disc elliptic to small reniform, consisting of many, thin-walled cells.

Androecia terminal or intercalary on stems and long or short *Frullania*-type and *Lejeunea*-type branches; bracts and bracteoles in 3-20 series, the bract lobe ovate-oblong, 0.80-1.25 mm long, 0.50-0.85 mm wide, the lobule with a very strong inflated basal part that is cylindrical in situ and a small, concave, distal part bearing 2-7 teeth of 1-3 cells or which outline occasionally only indicates teeth; bracts diandrous, antheridium c. 200 μ m in diam.

Gynoecium terminating stems and long or short *Frullania*-type and *Lejeunea*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe squarrose, ovate to obovate, 1.80-2.20 mm long, 1.10-1.35 mm wide, the apex apiculate, occasionally blunt, the apical region concave, the keel forming an angle of \pm 90°, bracts with a large elliptic wing at the keel, 0.7-1.2(-1.4) mm long, 0.3-0.6 mm wide, the lobule narrow rectangular, 0.3-0.4 x the length of the lobe, the apex with a tooth of (1-)3-4 cells; bracteole rectangular, 1.00-1.40 mm long, 0.80-0.85 mm wide, the apical region truncate-emarginate to occasionally bifid, plane to slightly recurved, the basal part inserted on the innovations. Perianth usually not emergent when mature, sometimes exserting the bracts for 1/4 when mature, obovoid-cylindrical, $1.25-1.65 \times 0.60-0.90$ mm, with 10(-11) smooth, rounded plicae extending over the upper 1/3-2/3 of the perianth, occasionally extending down to base; beak 8-10 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 45-55 μ m long, covered with numerous spinulae and eight rosettes; elaters 68 per capsule 435-550 μ m long, c. 18 μ m wide, with one brownish, c. 4 μ m wide spiral.

Sporeling of the Lopholejeunea-type.

Distribution (PI. XXIX): temperate and tropical SOUTH AMERICA, CENTRAL AMERICA. Widespread in South and Central America and reported by several authors from temperate Northern Argentina through Brazil, the Andean countries and the Galapagos Islands. In central America present north to Mexico. Most altitudinal data indicate a lowland distribution (0-1000 m), but in the

Andes reported from 600-2500 m (SPRUCE 1884) and recently found up to 3650 m (Colombia: coll. van Reenen 1192; coll. Aguirre & Gradstein 1669). In Central America reported from 1000-1800 m altitude; in Mexico up to 3000 m (coll. Liebmann 389b).

Ecology: mainly in loose and ascending, occasionally in rather dense and appressed mats. Almost exclusively corticolous on stems, branches and trunks of trees and shrubs. The species has a wide drought tolerance and is reported from mountain and lowland rain forests, cloud forests, as well as from xerophytic, shrubby, secondary forests (cerradaos of Southeastern Brazil). In Peru and Colombia extensive mats may be found at forest edges and along roads (Gradstein, pers. comm.). Often growing intermingled with other *Frullanoides* species, other Lejeuneaceae or *Frullania*. Occasionally recorded terrestric (coll. Spruce L158) or from granite boulders and exposed rocks at higher altitudes (1500-2200 m).

Differentiation: F. densifolia and its ally F. laciniatiflora are easily distinguished from the medium-sized species of Frullanoides (e.g. F. tristis, F. liebmanniana, F. mexicana) by: 1) the rigid stems (PI. XVIII, figs. 5-7), 2) the ventral merophyte of 8(-14) cells (PI. XVIII, fig. 5), 3) the ventral cortical cells, which are usually narrow rectangular with irregular thickenings (PI. XVIII, figs. 6-7), 4) the underleaves with large auricles, 0.15-0.35 x 0.13-0.20 mm, appressed to the ventral-lateral side of the stem (PI. XIX, fig. 7; PI. XX, figs. 3-4), 5) the male bracts, deviating from the leaves by their strongly inflated lobules, which are \pm cylindrical in situ (PI. XIX, fig. 1), and 6) the large size of the shoots, at least 4-5 cm long, but F. densifolia up to 10-12 cm.

The differences between F. densifolia and F. laciniatiflora are discussed under the latter. Sterile plants might be confused, but F. densifolia is recognisable by: 1) the entire apical margin of the subgynoecial underleaf (ciliate in F. laciniatiflora; Pl. XXI, fig. 8a-b), 2) the blunt to only small apiculate leaves (long apiculate in F. laciniatiflora; Pl. XXII, fig. 7a-b), 3) the generally shorter and more rectangular ventral cortical cells (long and narrow in F. laciniatiflora; Pl. XXII, fig. 6), and 4) the entire apical region of the leaves (usually serrulate to ciliate in F. laciniatiflora; Pl. XXII, fig. 8).

Variation: several characters of this widespread species are subject to substantial variation: 1) the size of the specimens: 4-5 cm average, but in favourable conditions (e.g. mist forest) the length reaches 10-12 cm (coll. Griffin & Eakin 244; coll. Nishida D-11-1-a), 2) the ventral cortical cells vary from rectangular, 54-80 x 21-32 um, and hardly thickened to long and narrow rectangular, 54-104 x 18-30 um, with conspicuous, irregular wall thickenings; the latter condition present in better developed specimens (PI. XVIII, figs. 6-7), 3) the number of ventral merophyte cells: 8-10(-14), 4) the blunt, almost rounded or small apiculate leaf apices, 5) the transversally elliptic to suborbicular to subquadrate-rectangular outline of the underleaves *in situ*

(PI. XIX, fig. 7; PI. XX, figs. 3-4), 6) the truncate to emarginate to bifid apex of the female bracteole (PI. XIX, fig. 4), and 7) the series of male bracts: 3-20. HERZOG (1957) based his *Brachiolejeunea appendiculistipa* var. *bifida* on the bifid female bracteole, but examination of female specimens revealed that this feature is an extreme within the variation width.

Key to the subspecies of F. densifolia:

- a. plants dioecious; leaf lobule teeth 5-9, each consisting of 1-4 cells in total; underleaves with large and distinct ears, $0.15-0.35 \times 0.15-0.20$ mm in size; male bracts with strongly inflated lobules that are ± cylindrical in situ.....ssp. densifolia
- b. plants paroecious; leaf lobule teeth 5-6, each consisting of (2-)4-9 cells in total; underleaves with small, indistinct ears, 0.03-0.10 x 0.05-0.08 mm in size; male bract lobules only slightly more inflated than the lobules of vegetative leaves.....ssp. grandidentata
- 3a F. densifolia ssp. densifolia: see under the species
- 3b F. densifolia ssp. grandidentata (Clark) van Slageren comb. nov. (Plate XX)

Brachiolejeunea grandidentata Clark, Proc. California Acad. Sci. 27: 595 (1953).

<u>Type</u>: Ecuador, Galapagos Islands, Abermarle Island (= Isabela), above Santo Tomás, Villamil Mountain, on trees, Howell 211A, 29.IV.1932 (WTU holo, not in CAS!).

Plants paroecious, size similar to ssp. densifolia, becoming darkish-brown to black when dry, irregulary branched; parts of the plants with a dichotomous appearance due to floriferous innovations; branches short or long, *Frullania*-type only.

Stem rigid, 0.15-0.25 mm in diam., ventral merophyte eight cell rows wide, the ventral cortical cells rectangular, $(29-)38-72 \times 15-32 \mu$ m, with irregular thickened walls; stem in transverse section with 18-25 cortical cells, not to only slightly thickened on the dorsal and lateral side and strongly thickened on the ventral side, the medulla consisting of 46-69 thick-walled cells.

Leaves loosely imbricated. Lobe ovate, 1.0-1.2 mm long, 0.6-0.8 mm wide, the dorsal base auriculate, the apex apiculate, the apical region incurved; keel smooth, in outline varying from slightly convex to slightly concave, leaf cells as in ssp. *densifolia*.

Lobule ovate-triangular, $0.35-0.45 \times$ the length of the lobe, 0.40-0.50 mm long, 0.30-0.45 mm wide, the free margin with 5-6 teeth; teeth consisting of (2-)4-9 cells in total with 1-3 cells at the base.

Underleaves imbricated, outline, including auricles, suborbicular, 0.65-0.80 mm long, 0.70-0.85 mm wide, the rounded apical margin slightly recurved,

the lateral margins plane to slightly incurved, the bases rounded with small ears that are only distinct near the arched insertion and indistinct on the lateral margin of the underleaves, ears not appressed to the ventral-lateral side of the stem, $0.30-0.10 \times 0.05-0.08$ mm in size; cells and rhizoid disc as in ssp. densifolia.

Androecia located 1-4 series of vegetative leaves below the gynoecium; bracts and bracteoles in 3-6 series, the bracts resembling the leaves but the lobes smaller, ovate to ovate-oblong, the lobule with a slightly more inflated basal part than the vegetative leaves, the distal part concave, the free margin bearing 4-6 teeth of (2-)4-8 cells in total with 1-2 cells at the base; antheridium not observed.

Gynoecium as in ssp. *densifolia*. Sporophyte and sporelings not observed.

Distribution (PI. XXIX): ECUADOR, GALAPAGOS ISLANDS, at 450-750 m altitude. Apart from the type a few recent collections only.

Ecology: on twigs and stems in wind exposed, evergreen forests, bushes or scrubs as well as in pampas, occasionally pendulous. Plants tolerating temporarily drought.

Differentiation: this subspecies, endemic to the Galapagos Islands, is to be distinguished from the subspecies densifolia by: 1) the 3-6 paroecious male bracts with only slightly more inflated lobules than in vegetative leaves (PI. XX, figs. 5, 9), 2) the suborbicular underleaves with small and rather indistinct auricles (PI. XX, figs. 7, 10), and 3) the well developed teeth of the leaf lobule, consisting of (2-)4-9 cells in total with 1-3 cells at the base (PI. XX, figs. 6, 8).

As is already indicated by CLARK (1953) the two (sub)species are habitually very similar and only close examination will reveal the diagnostic differences of the ssp. grandidentata described above. Together with "a geographical distribution, distinct from the distribution of the other subspecies" (LAWRENCE 1951), I think that the category of subspecies reflects best the status of the Galapagos populations.

Specimens examined (F. densifolia):

a. ssp. densifolia:

MEXICO. Pico de Orizaba, Liebmann 389b (C), type collection of *Phragmicoma bicolor* var. armata Gott., Lindenb. & Nees; Orizaba, Sierra de San Cristobal, Müller s.n. (BM, C); Vera Cruz, Fortin de las Flores, Düll 2/102, 13.VIII.1975 (DUIS, JE, U); s.loc., Leibold s.n. (BM); s.loc., s.coll., s.n. (BM); s.loc., s.coll., s.n. (G 20099), type collection of *Brachiolejeunea canaliculata* Steph.

COSTA RICA. San José: Santa Maria de Dota, Standley & Valerio 43152 (JE)

& 43158, 26.XII.1926-3.I.1927 (JE, S); Cartago: Tapantí Forest Reserve, Griffin III & Eakin 222 (FLAS) & 244, 10.IX.1973 (B, FLAS, HAC, U); s.loc., Werckle s.n. (G 21836), type collection of Marchesinia coniloba Steph.; Puntarenas: San Vito, Sipman 11941, 31.XII.1978 (U).

GUIANA. s.loc., s.coll., s.n. (G 20280).

BRAZIL. Pará: s.loc., J.L.R. s.n., III.1841 (BM); Bahia: Lugar, Tapera Garazinho, Sehnem 5700, 26.111.1951 (U); Minas Gerais: Caldas, Mosén Du, 20.VIII.1873 (G 20093, S), ibid., Mosén Jo, 25.VIII.1873 (G 20075, S), Mosén Hi, 30.VIII.1873 (G 20074, S), Mosén Jk, 1.IX.1873 (G 20077, G 20096, S), Mosén Ex, 30.VIII.1875 (BM, G 20078, S) & Mosén Hj, 15.1X.1897 (G 20353, S); ibid., Lindberg 31, VII-XII.1854 (S), Lindberg 33, 25.VI.1854 (BM, S), Lindberg s.n., 25.VII.1854 (BM) & Lindberg s.n., 1854 (BM, U); ibid., Henschen s.n. (S-several collections); Sierra d'Estrella, Beyrich 16a & 54 (S); Sta. Cruz, celle Leguar do Herval do Paredoc, Jürgens s.n., XII.1916 (S); Sierra Itatiaia, Dusén 54, 8.VI.1902 (NY); Rio de Janeiro, Glaziou 5620 & s.n. (NY) & 7410 p.p. (BM); ibid., Schiffner 595, 17.IX.1901 (S, W); s.loc., Martius s.n., 1832 (FH-Taylor, M, S, W (hb. Lindenberg 5956), type collection of Brachiolejeunea bicolor (Nees) Schiffn.; s.loc., Robert s.n., X1.1900 (BM); s.loc., Wainio s.n. (BM); Serro, s.coll., s.n. (PC, NY); s.loc., s.coll., s.n., (G 20084); Sao Paulo: prope S. Bernardo, Schiffner 16, 1.VII.1901 (S. W): Itapetininga, Schiffner 265, 14.VIII.1901 (S, W); prope Lapa, Schiffner 305, 14.VIII.1901 (S, W); prope Rio Grande, Schiffner 892, 7.VI.1901 (S, W) & Schiffner 2228, VII.1901 (S, W); prope Taipas, Schiffner 1769, 8.VI.1901 (S, W) & Schiffner 1045 & s.n., 1.VI.1901 (S, W); Cerqueia Cesar-Facendo, Schiffner 1233 & 1497, 22.VII.1901 (S, W); Itapecirica, Schiffner 1475, 13.VI.1901 (S, W), 1337 & 1522, 17.VI.1901 (S, W) & 2069, 22.VI.1901 (S, W); Mangaguá, Schiffner 1348, 4.VII.1901 (S, W); prope Faxino, Schiffner 1369, 20.VIII.1901 (S, W); prope Rio Chepeo, Schiffner 1485, VIII.1901 (S, W); prope Butatan, Schiffner 1601 & 1787, 27.V.1901 (S, W); prope Facenda Paranapanema, Schiffner 1669, 15.VIII.1901 (S, W); prope Xiririca, Schiffner 2211, XI.1901 (S, W); Campos de Jordao, Vital 9593, 22.XI.1980 (JE, SP, U); Apiaky, Souza 1410 (G 20197); ibid., Puiggari 270 (S, W), 883 (G 20081), 884 (G 20082) & s.n. (BM, G 20080); s.loc., Lindberg 27 (BM, S), 29 (MANCH 14056, S) & s.n., IV.1854 (BM, PC, S); s.loc., Robert s.n., 14.1.1901 (BM); s.loc., s.coll., s.n., (MANCH 14062); Paraná: Dusén 12077, 13.VII.1901 (S, W); Rio Grande do Sul: Sarandi, Vital 5712 & 5715, 12.111.1976 (SP, U); s.loc., Kunert s.n. (G 20068); s.loc.: Raddi s.n. (BM, FH-Taylor, PC, PI, NY), type collection of Frullanoides densifolia Raddi; s.loc., Raddi 58 (BM); s.loc., Swainson s.n. (BM, NY); s.loc., Steward s.n. (NY); s.loc., Burchell 2037, 11.11.1926 (BM, NY); s.loc., Sowerby s.n. (NY); s.loc., Bischoff s.n. 1.1849 (S); s.loc., Lindenberg s.n. (S); s.loc., Beyrich s.n., 1833 (BM, G 20083); s.loc., Lehmann s.n., I.1833 (BM); s.loc., Ule 153 (BM) & 510 (G 20069); s.loc., Sellow s.n. (BM); s.loc., s.coll., s.n. (several

collections: G 20085, 20086, 20090 & 20091, JE, NY, S).

- VENEZUELA. <u>Mérida</u>: Mucuy, Onraedt 78.V.5599, 5.VII.1978 (JE, hb. Onraedt, U); s.loc., Moritz s.n. (BM, G 20079, W), type collection of *Phragmicoma bicolor* var. *conferta* Gott., Lindenb. & Nees; <u>Táchira</u>: Junin, páramo de Tamá, Griffin III et al. 772, VIII.1975 (FLAS, U); <u>s.loc.</u>: s.col., s.n.(L).
- COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, Winkler C166, C183, C186 & C313, 16.1.1967-24.11.1967 (hb. Winkler); Santander: vicinity of Charta, Killip & Smith 19337, 1-11.11.1927 (JE, NY); between El Roble and Tona, Killip & Smith 19438, 17.11.1927 (JE, NY); Sacorro, San Gil, s.coll., s.n. (BM); Antioquía: Llanos de Quivá, Onraedt 83.A.10196, 19.11.1983 (hb. Onraedt, U); Montanita à San Pedro, Onraedt 83.A.10317, 2.111.1983 (hb. Onraedt, U); Padua, Lindig 224 (B, G 20242), type collection of Brachiolejeunea rupestris (Gott.) Steph.; Boyacá: road Chiquinquig-Paun, van der Hammen et al. 2474, 2.IX.1967 (COL, U); Cundinamarca: Sácama, Aguirre & Gradstein 2952, 16.VIII.1982 (COL, U); Laguna de Pedro-Palo, Bischler 2216, 21.IV.1959 (PC, U); vallée du Rio Checua, Schaeck s.n., 2.IV.1972 (hb. Onraedt 72.Am.59); Pacho, Lindig 198 (G 20240); Bogotá, páramo Choache, Lindig s.n., IX.1860 (BM); Bogotá, Tequendoma, Lindig s.n. (S); Fuzagaruza, Lindig s.n. (G 20196); Andes Bogotensis, Weir s.n. (NY-several collections); Risaralda: Santa Rosa de Cabal, van Reenen et al. 1559, 18.VII.1980 (COL, U); ibid., Aguirre et al. 6223 & 6363, 19.IX.1984 (COL, U); Tolima: Santa Isabel, van Reenen et al. 1192, 1.11.1980 (COL, U); ibid., Aguirre & Gradstein 1669, 30.VII.1980 (COL, U); s.loc.: Webeter 1 (NY); s.loc., Lindig 201 (G 20067) & 205 (G 20241); Wallis s.n. (BM); s.loc., s.coll., s.n., (G 20101), type collection of Brachiolejeunea columbica Steph.; s.loc., Blagbome s.n. (BM); s.loc., s.coll., s.n. (BM).
- ECUADOR. Azuay, Cuenca, Harling 2200a, 2205 p.p. & 2206, 11.V.1947 (JE, S); Oriënte, Allioni 6486, V.1909 (G 20092); Quito, Jameson s.n. (MANCH 14052, NY); Pichincha, between San Juan and Saloya, Asplund s.n., 11.1X.1939 (G 20063, JE, S), type collection of *Brachiolejeunea appendiculistipa* var. *bifida* Herz.; Tunguragua, Spruce s.n. (G 20087, MANCH 14058); Tunguragua, Agoyan, Spruce s.n. (NY); Banos, Spruce L158 & s.n. (MANCH 14050 & 14060); Chimborago, Spruce L117 (MANCH 14051); Pastusa superior, Spruce s.n. (B, BM, BR, G 20071, 20094 & 20250, MANCH 14057, NY, S, YU); Azuay, s.coll., s.n. (MANCH 14064); s.loc., s.coll., s.n. (G 20351), type collection of *Brachiolejeunea succisa* Steph.
- PERU. <u>Amazonas</u>: Chachapoyas, road Cajamarca-Chachapoyas, Frahm et al. 507, 1001, 7.IX.1982 (B, G, U) & 1148, 7.IX.1982 (B, BA, BM, C, COL, COLO, F, FLAS, G, hb. Grolle, H, MEXU, NY, NICH, PRC, S, SP, TNS, U, USJ, VBI); Chachapoyas, Las Palmas, E. & P. Hegewald 7011,

31.VIII.1973 (hb. Hegewald, U); Bongará, Pomacochas, E. & P. Hegewald 7058, 7073, 7077 & 7102, 1.IX.1973 (hb. Hegewald, U); Cajamarca: Cerro Huayllaconga, E. & P. Hegewald 6556, 29.VIII.1973 (hb. Hegewald, U); Celeudin, E. & P. Hegewald 6656, 30.VIII.1973 (hb. Hegewald, U); Cafetal, Panayaco grande, Büer 1584a, X.1919 (YU); San Martin: Rioja, road Chachapoyas-Moyabamba, Frahm et al. 1312, 11.IX.1982 (B, G, U); Mt. Lamas, Spruce L174 (MANCH 14049); Huanuco: Churubamba, Mexia 8246a, 1.X.1936 (hb. Fulford, NY); Cuzco: Coromilla, sobre Chanpimayo, Büer 1528a, XI.1920 (YU); San Miquel, Foote 8, 24.VII.1911 (YU); Sandia, Weberbauer 736, 1902 (G 20072); Paucertambo, Jay 15 (NY), 31 (YU) & 104, X.1893 (NY, YU); Urubamba, Macchu Picchu, E. & P. Hegewald 5578, 6.V.1973 (hb. Hegewald, U); <u>Arequimpa</u>: Uchumayo, Büer 1540, VI.1920 (YU); <u>s.loc</u>.: d'Orbigny 192 (PC-Montagne); s.coll., s.n. (PC-Montagne); s. coll., s.n. (BM); Location unknown: Jatanara, Lechler s.n. (NY); Sachapata, Lechler c3118 (NY).

- BOLIVIA. Corani, Herzog 3375, V.1911 (B, L, MANCH, S, W); ibid., Herzog 3398b (B, JE, S); ibid., Herzog 4753, V.1911 (G, L), type collection of Dicranolejeunea nudiflora Steph.; Tablas, Herzog s.n., V.1911 (S); Cunuca, Herzog s.n., X.1907 (YU); Velasco, Rio Blanco, Herzog 5852,, VIII.1907 (G 20239, YU); Rio Tocorani, Herzog 4113 (G), type collection of Ptychanthus boliviensis Steph.; Incacorral, Herzog 4971, VI.1911 (B, G 22658, L), type collection of Dicranolejeunea boliviensis Steph.; ibid., Herzog 5857, I.1908 (G 20238); Comarapa, Herzog s.n., IV.1911 (B, JE, NY, S); Florida de San Mateo, Herzog 3693, IV.1911 (B, G 14604, L, M, MANCH, S, W), material of Ptychocoleus boliviensis Steph.; Tres Cruces, Herzog 3910, II.1911 (B, JE, S); Cerro Amboro, Herzog s.n. (Bryotheca Levier 5859 p.p.) (G 20195); s.loc., Herzog 3500a, 1911 (G, L 20352); s.loc., Herzog 3695, 3697, 4089 & 4094, 1913 (G 21810), syntypes of Mastigolejeunea decurrens Steph.; s.loc., Herzog 3805, 1913 (G 12484), 3896 (G 12486), 3990 (G), 4142 (G 12487), 4334 (G), 4747 (G 12485), 3365 p.p. (G 20062 - type collection of Brachiolejeunea appendiculistipa Steph.) & s.n. (JE); Lagunillas, Brooke 6163B, 6.111.1950 (BM); Unduavi, Pearce s.n. (BM, G 20070, NY, U); Chedes, Pearce s.n. (G 20073); s.loc., Pearce s.n. (BM); Tipuani, Buchtieu 148, 1920 (NY); s.loc., Buchtieu 258 p.p. (JE) & s.n. (G 20206); Siberia, Comarapa, Nishida et al. D-11-1-a, 11.XII.1974 (U); Cochabamba, Chaparé, Hermann 24677, 22.II.1972 (G 20164, NY); near Paucartambo, Jay 20, 1893 (NY, U, YU).
- ARGENTINA. Rio Serro bei San Andrès, Oran, Lorentz s.n., 17.1X.1873 (B, BM, BP, G 20088, S, U).

CHILE. Valdivia, Sainthill s.n. (NY).

b. ssp. grandidentata:

ECUADOR, GALAPAGOS ISLANDS. Santa Cruz: top of Cerro Maternidad, van der Werff 1777, 5.XII.1974 (U); between Puntudo and Mt. Crocker, Gradstein & Weber H11, 14.IV.1976 (BM, COLO, FLAS, hb. Fulford, G 156081, U); s.loc., Gradstein & Weber H105, 17.IV.1976 (COLO, U); San Cristobal: El Junco, Gradstein & Lanier H254, 21.V.1976 (U); Pinzon, Gradstein & Sipman H485, 2.VII.1976 (U); Isabela: Santo Tomás, Villamil Mountain, Howell 211A, 29.IV.1932 (WTU), type collection of Frullanoides densifolia ssp. grandidentata (Clark) van Slageren.

- 4. FRULLANOIDES LACINIATIFLORA (Loitl.) van Slageren comb. nov. (Plates XXI-XXII)
- Lejeunea (subg. Brachiolejeunea) laciniatiflora Loitl., in Szyszylowicz, I. (ed.): Diagn. Plant. Nov., Diss. Cl. Math. Phys. Acad. Litt. Cracow 29: 233 (1894).

Brachiolejeunea laciniatiflora (Loitl.) Steph., Spec. Hep. 5: 120 (1912); Bonner (1963: 453).

<u>Type</u>: Peru, Cuitervo, ad corticem inter Frullanias, Jelski 536 (W holo, G 20163, H, JE, KRA, S, U).

Plants dioecious, medium-sized, up to 4-5 cm long, (1.5-)1.7-3.0 mm wide, at male spikes 1.0-1.5 mm, green, becoming light to darkish-brown to black when dry, irregularly branched, female plants with a dichotomous appearance due to floriferous innovations, male plants more sparsely branched, and with a more slender appearance; branches short or long, *Frullania*-type, rarely *Lejeunea*-type.

Stem rigid, (0.15-)0.20-0.30 mm in diam.; ventral merophyte (6-)8(-10) cell rows wide, the ventral cortical cells narrow rectangular, 54-108 x 15-36 µm, with irregular thickened walls, the dorsal cortical cells narrow rectangular, 54-108 x 21-36 µm; stem in transverse section with (16-)24-36 cortical cells, which are thin-walled to only slightly thickened on the dorsal and lateral side and strongly thickened on the ventral side, the dorsal cortical cells 21-29 µm high, the ventral cortical cells 11-25 um high and dark in colour, the medulla consisting of (35-)45-92 thick-walled cells which are 18-36 um in diam., the walls of the medullary cells less thickened than of the ventral cortical cells.

Leaves loosely imbricated. Lobe ovate-falcate, $1.0-1.7 \text{ mm} \log 0.6-1.0 \text{ mm}$ wide, inserted along 2/3-1/1 of the length of the merophyte, the dorsal base auriculate, the apex long apiculate, the apical region plane to incurved, the margin of the apical region smooth to irregular serrulate-ciliate, the ventral margin upcurved, when spread out forming an angle of $150-180^\circ$ with the keel; keel smooth, in outline varying from straight to slightly concave, at an

angle of $45-90^{\circ}$ with the axis; median leaf cells $21-40 \times 21-25 \mu$ m, margin cells 14-21 um high; intermediate thickenings scarce, elliptic-rounded, when present one per each larger cell wall.

Lobule ovate-triangular with a rounded to oblique apex, 0.35-0.80 mm long, 0.30-0.50 mm wide, 0.3-0.5 x the length of the lobe, gradually flattened towards the free margin, the flattened part plane, the free margin gradually curved towards the apex of the lobule, with 7-9 teeth; teeth consisting of 1-3 cells in total, inflexed, the first tooth separated from the second by 7-9 free marginal cells, the other teeth separated from each other by (2-)4-6 free marginal cells; hyaline papilla 2-3 cells below the proximal base of the first tooth.

Underleaves imbricated, outline, including auricles, varying from suborbicular to obtrapezoid to \pm rectangular, 0.6-1.0 mm long, 0.6-1.1 mm wide, the rounded to truncate apical region slightly recurved, the margins plane, the bases with large, rounded to obovate ears, 0.15-0.30 x 0.15-0.25 mm in size, appressed to the ventral-lateral side of the stem, the line of insertion arched, 0.13-0.20 mm deep, the underleaf directly below the female bracteole rectangular, 1.10-1.20 x 0.95-1.10 mm, the widely rounded apical margin ciliate; median cells 21-40 x 14-21 um, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, very short, only 27-45 µm in length; rhizoid disc small reniform, consisting of many, rather thick-walled cells.

Androecia terminal or intercalary on stems and long or short *Frullania*-type branches; bracts and bracteoles in 3-12 series, the bract lobe ovate, 0.90-1.00 mm long, 0.60-0.65 mm wide, the lobule with a very strong inflated basal part that is cilindrical in situ and a small, concave distal part bearing 3-6 teeth of 1-3 cells; bracts diandrous, antheridium c. 120 µm in diam.

Gynoecium terminating stems and long or short *Frullania*-type and *Lejeunea*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe squarrose, obovate-elliptic, 1.9-2.3 mm long, 0.9-1.4 mm wide, the apex irregularly ciliate, the apical region concave, the keel sharp, bracts with a large, elliptic wing present at the keel, 0.70-1.40 mm long, 0.20-0.35 mm wide, the lobule narrow rectangular, 0.25-0.35 x the length of the lobe, the apex with a tooth of 2-3 cells or without a distinct tooth; bracteole \pm rectangular, 1.00-1.50 mm long, 0.65-0.90 mm wide, the apical region varying from truncate with 4-6 large ciliae to bifid in the upper 1/3-1/2 of the bracteole with sharply acute lobes, the basal part inserted on the innovations. Perianth not emergent when mature, obovoid-cylindrical, 1.25-1.30 x 1.65-0.80 mm, with (9-)10 smooth, isomorphous plicae extending over the upper 1/3-2/3 of the perianth; beak 15-18 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, $38-54 \mu m$ long, covered with numerous spinulae and eight rosettes; elaters per capsule $270-325 \mu m$ long, c. 18 μm wide, with one brownish, c. 4 μm wide spiral.

Sporeling not observed.

Distribution (PI. XXVIII): PERU. Only known from a few scattered localities in the Andes of North and Central Peru at 2000-3200 m altitude.

<u>Ecology</u>: growing or rather loose mats on branches of trees in mountain forests and on open hillsides, sometimes intermingled with other *Frullanoides* species (e.g. *F. densifolia*), with species of *Brachiolejeunea* (e.g. *B. laxifolia*) and with *Frullania* spp.

Differentiation: *F. laciniatiflora* is easily distinguished from the other species of *Frullanoides* by: 1) its dentate to ciliate margin of the female bracts and bracteole (PI. XXI, figs. 5-7, 9), apical region of the leaves (PI. XXII, figs. 7a, 8) and of the subgynoecial underleaf (PI. XXI, fig. 8a-b), and 2) the apical region of the female bracteole, which varies from truncate to deeply bifid with narrow acute lobes (PI. XXI, figs. 5-6). The species is most closely related to *F. densifolia* (see under that species).

Variation: though only a limited number of collections is known from this species, conspicuous variation is observed in: 1) the outline of the apical region of the female bracteole: truncate-ciliate to deeply bifid with narrow acute lobes, and 2) to a lesser extent in the ciliae of the female bract margins and the apical region of the leaves.

Specimens examined (F. laciniatiflora):

PERU. Cuitervo, Jelski 536 (G 20163, H, JE, KRA, S, U), type collection of *Frullanoides laciniatiflora* (Loitl.) van Slageren; ibid., Jelski 535, 538 & s.n. (KRA, U); Ayacucho, Pampalca, between Huanta and Rio Apurimac, Killip & Smith 22229, 4-18.V.1929 (JE, NY); Amazonas, Chachapoyas, road Chachapoyas-Cajamarca, Frahm et al. 744 & 975, 4-7.IX.1982 (B, G, U).

- 5. FRULLANOIDES LIEBMANNIANA (Lindenb. & Gott.) van Slageren <u>comb</u>. <u>nov</u>. (Plates XXIII-XXIV)
- Phragmicoma liebmanniana Lindenb. & Gott., Syn. Hep.: 744 (1847); Gottsche (1863: 270).
- Lejeunea (subg. Brachiolejeunea) liebmanniana (Lindenb. & Gott.) Steph., Hedwigia 29: 8, 134 (1890).
- Marchesinia liebmanniana (Lindenb. & Gott.) Kuntze, Rev. Gen. Pl. 11: 837 (1891).
- Brachiolejeunea liebmanniana (Lindenb. & Gott.) Schiffn., Hedwigia 33: 183 (1894); Bonner (1963: 454).

Type: Mexico, Comaltepec, Liebmann 197, VII.1842 (W holo (hb. Lindenberg 5992), B, BM, C, FH-Schiffner, G 20180, S).

Heterotypic synonyms:

Brachiolejeunea anguliloba Steph., Spec. Hep. 5: 128 (1912) syn. nov. Type: Bolivia, Herzog 5851 p.p., 1907 (G 20060 holo).

Dicranolejeunea gigantea Steph., Spec. Hep. 5: 160 (1912) syn. nov. Type: Bolivia, Cochabamba, im Bergwald bei Incacorral, Herzog s.n. (hb. Levier 5856), 1.1908 (G 22669 holo).

Plants dioecious, medium-sized, up to 4 cm long, 1.75-2.30 mm wide, at male spikes 1.35-1.80 mm, green, becoming light to darkish-brown to black when dry, irregularly branched, female plants with a dichotomous appearance due to floriferous innovations, male plants more sparsely branched and with a more slender appearance; branches short or long, mainly *Frullania*-type, less frequently *Lejeunea*-type branches.

Stem flaccid, 0.2-0.3 mm in diam.; ventral merophyte 4-6(-8) cell rows wide, the ventral cortical cells subquadrate to short rectangular, 36-61 x 28-46 μ m, the dorsal cortical cells subquadrate to short rectangular, 32-57 x 28-54 μ m; stem in transverse section with 18-25 thin-walled cortical cells surrounding 51-84 thick-walled medullary cells, the dorsal cortical cells 28-43 μ m high, the ventral cortical cells 21-28 μ m high, the medullary cells 18-32 μ m in diam.

Leaves closely imbricated. Lobe ovate, $0.95-1.50 \text{ mm} \log 0.80-1.10 \text{ mm}$ wide, inserted along the whole length of the merophyte, the dorsal base straight, the apex blunt to rounded, the apical region plane to weakly incurved, the ventral margin plane, when spread out forming an angle of 170-180° with the keel; keel smooth, almost straight, at an angle of $60-90^{\circ}$ with the axis; median leaf cells $29-47 \times 18-33 \mu m$, margin cells $14-22 \mu m$ high; intermediate thickenings scarce, elliptic-rounded, when present one per each larger cell wall; oil bodies (Gradstein, pers. comm.) Massula-type, 15-25 per cell, small cylindrical-oblong, $2-3 \times 6-8 \mu m$.

Lobule ovate-rectangular with the apex blunt to rectangular, 0.55-0.80 mm long, 0.35-0.55 mm wide, $0.50-0.65 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part concave; free margin irregularly arched with triangular segments, with 3-5 teeth; teeth located at the apex of a triangular segment and consisting of 1-2 cells in total, inflexed, or teeth only indicated by the triangular segment which then has a rounded apex, teeth separated from each other by 5-9 free marginal cells, near the apex at a distance of 7-15 cells; hyaline papilla 3-6 cells below the proximal base of the first tooth.

Underleaves imbricated, suborbicular to reniform, 0.50-0.70 mm long 0.60-0.95 mm wide, the apex widely rounded to truncate, slightly recurved, the margins plane, the bases with small ears, $0.07-0.15 \times 0.03-0.07$ mm in size, the line of insertion arched, 0.07-0.12 mm deep; median cells 29-43 x 18-29

 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, short, 40-65 μ m in length, rhizoid disc reniform, consisting of many thin-walled cells.

Androecia terminal or intercalary on stems and long or short *Frullania*-type and *Lejeunea*-type branches; bracts and bracteoles in 4-9 series, the bract lobe ovate to broadly so, 0.80-0.95 mm long, 0.55-0.75 mm wide, the lobule with a more strongly inflated basal part and a concave distal part bearing three one celled teeth at the apex of, sometimes indistinct, triangular segments; bracts mono- and diandrous, antheridium c. 150 µm in diam.

Gynoecium terminating stems and long or short Frullania-type branches, with two innovations; bracts and bracteole in one series, the bract lobe squarrose in the apical region, obovate-oblong, 1.10-1.25 mm long, 0.55-0.60 mm wide, the apex blunt, the keel sharp, bracts usually without a wing at the keel, occasionally a small to somewhat larger, elliptic wing developed 0.15-0.25 x 0.07-0.10 mm (small forms) up to 0.40-0.65(-1.00) x 0.10-0.25 mm (large forms) in size, the lobule narrow rectangular-rhomboid, 0.55-0.65 x the length of the lobe, the apex rounded with a one celled tooth; bracteole rectangular to rectangular-spathulate, rather small, 0.70-1.10 mm long, 0.45-0.75 mm wide, the apex truncate to (deeply) emarginate, plane to slightly recurved, the basal part shortly inserted on the innovations. Perianth exserting the bracts for \pm 1/5 when mature, occasionally stalked, the stalk up to 150 um, obovoid, 1.20-1.30 x 0.65-0.75 mm, with 9-10 smooth and rounded plicae in the upper 1/3-1/2, the plicae divided over two large lateral keels and one large ventral keel, occasionally terete and isoplicate; beak 5-7 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.45 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 47-63 μ m long, covered with numerous spinulae and eight rosettes; elaters 68 per capsule, 260-540 μ m long, c. 20-25 μ m wide, with 1(-2!) brownish, c. 4 μ m wide spiral(s).

Sporeling not observed.

Distribution (PI. XXVIII): CENTRAL and SOUTH AMERICA, WEST INDIES. Known from rather isolated localities in Mexico, Jamaica, Colombia, Peru, Southeastern Brazil and Bolivia. Occurring at low to medium altitudes: 200-1000 m.

<u>Ecology</u>: growing in loose patches on bark of trees; in Southeastern Brazil also in riparian forest.

Differentiation: F. liebmanniana is easily distinguished from the other species of *Frullanoides* its large leaf lobules with a free margin that bears only 3-5 teeth at the apex of triangular segments (PI. XXIII, fig. 4). To a lesser extent the species is distinguished by: 1) the close imbricated leaves, 2) the reduced size and only occasional presence of a wing on the female bract keel, and 3) the relatively small size of the underleaf ears. F. liebmanniana most closely resembles F. mexicana with which it has several characters in common:

1) the closely imbricated leaves, 2) the morphology of the female bract wing, 3) the outline of the perianth, and 4) the small size of the underleaf ears. *F. mexicana* is, however, easily distinguished from *F. liebmanniana* by: 1) the narrow triangular leaf lobules, bearing 8-11 teeth, and 2) the obtrapezoid underleaves.

F. liebmanniana differs from the large F. densifolia and F. laciniatiflora (when specimens are of \pm the same length as F. liebmanniana) in: 1) the leaf lobule, 2) the thin-walled ventral cortical cells (compare PI. XXIII, fig. 8 with PI. XVIII, fig. 5 and PI. XXII, figs. 3-4), and 3) the male bract lobules, which are less strongly inflated.

The underleaf auricles of F. liebmanniana are similar to F. mexicana (see above) and F. tristis. F. tristis differs from F. liebmanniana in: 1) the paroecious male bracts, and 2) the leaf lobule, which is ovate with (4-)6-9 teeth.

The number of teeth on the leaf lobule of *F*. *liebmanniana* corresponds more or less with *F*. *corticalis*. The latter species, however, differs widely because of: 1) the reduced number of plicae on the perianth: 5-8(-10), 2) the plane underleaves without ears or with ears of a few cells only, 3) the ovate leaf lobule, 4) the number of teeth of the male bracts: 0-1, 5) the smaller number of cortical (11-14) and medullary (17-36, rarely up to 45) cells, and 6) the smaller size of the plants, not exceeding 2.5 cm in length.

<u>Variation</u>: morphologically *F. liebmanniana* is a rather stable species. The most important variation is observed in: 1) the ventral merophyte: 4-6(-8) cell rows, 2) the series of male bracts: 4-9, and 3) the development of the wing on the keel of the female bract (when present!): length from 0.15-0.25 mm up to 0.40-0.65 (-1.00) mm, width varying from 0.07-0.10(-0.25) mm.

Notes:

- Though quite uncommon, this species is remarkably well discussed in the literature, e.g. GOTTSCHE et al. 1845, GOTTSCHE 1863, STEPHANI 1890, SCHIFFNER 1894. All the discussions and descriptions, however, deal only with the type collection!
- 2. The name *liebmanniana* is spelled both *liebmanniana* and *liebmaniana* in the literature as well as on herbarium labels. *Liebmaniana* must be considered as an orthographic variant since the correct spelling of the collectors name is Liebmann. *Liebmanniana* is therefore the correct name of the species (see STAFLEU & COWAN 1981: 12).

Specimens examined (F. liebmanniana):

- MEXICO. Comaltepec, Liebmann 197, VII.1842 (BM, C, FH-Schiffner, G 20180, S, W (hb. Lindenberg 5992), type collection of *Frullanoides liebmanniana* (Lindenb. & Gott.) van Slageren; ibid., Liebmann s.n. (BM).
- JAMAICA. Cataclupe bei Montego Bay, Hegewald s.n., X.1973 (hb. Hegewald, U).

- TRINIDAD. S.loc., Fendler s.n. (NY-several collections); s.loc., s.coll., s.n. (NY).
- BRAZIL. <u>Goiás</u>: Morrinhue, Vital 6148, 10.IV.1976 (SP, U); Caldas novas, Vital 8635, 27.VIII.1979 (SP, U); <u>Mato Grosso</u>: Bonito, Vital 8596, 28.XI.1979 (SP, U); <u>Minas Gerais</u>: Joao Pinheiro, along road Presedente Olegário-Joao Pinheiro, Vital 6222, 16.IV.1976 (SP, U); Paracatu, Vital 6250, 17.V.1976 (SP, U); near Cimento Tocantius, Irwin et al. 31670, 10.III.1971 (NY, U); <u>Paraná</u>: river Paranapanema, Schiffner 134 & 2231, 24.VII.1901 (S, UPP, W).
- COLOMBIA. Santander: San Gil, Micholitz s.n., V.1901 (G, U); <u>Cundinamarca</u>: road Fusagasugá-Melgar, van der Hammen et al. 2147, 20.XII.1967 (COL, U); Andes Bogotensis, Weir s.n. (NY); <u>Tolima</u>: Venadillo, Vereda de la Sierrita, Finca El Cidro, van Reenen et al. 2508, 12.VIII.1980 (COL, U); ibid., alrededores del Rio Venadillo, van Reenen et al. 2530, 13.VIII.1980 (COL, U); <u>s.loc</u>.: Weir s.n. (NY); Moritz s.n. (G 20181, L); Pehlke s.n. (G 20061).
- VENEZUELA. Lara, road Gamelotal-Yaritagua, Griffin et al. 130, 24.V.1978 (FLAS, U).
- PERU. San Martin, Lamas, road Yurimaguas-Tarapoto, Frahm et al. 1833, 15.IX.1982 (B, G, U).
- BOLIVIA. Cochabamba, im Bergwald bei Incacorral, Herzog s.n. (hb. Levier 5856), I.1908 (G 22669), type collection of *Dicranolejeunea gigantea* Steph.; Chiquitos, im Bergwald bei Santiago, Herzog s.n., V.1907 (YU); s.loc., Herzog 5851 p.p., 1907 (G 20060), type collection of *Brachiolejeunea anguliloba* Steph.

6. FRULLANOIDES MEXICANA van Slageren spec. nov. (Plates XXIV-XXVI)

Planta dioica, a F. liebmanniana cui affinis est, differt lobulis foliorum anguste triangularibus, 8-11 denticulatis; dentibus unicellularibus; amphigastris obtrapezoideis.

<u>Type</u>: Mexico, Chiapas, Umgebung der Ruinas von Palenque, an alten Laubbaum in Palenque-dorf, Eggers & Frahm MX 22.7, 8.111.1979 (hb. Eggers holo, hb. Frahm 792229, U).

Plants dioecious, medium-sized, up to 4 cm long, 2.15-2.70 mm wide, at male

spikes 1.75-2.15 mm, green, becoming darkish-green to black when dry, irregularly branched, female plants with a dichotomous appearance due to floriferous innovations, male plants more sparsely branched and with a more slender appearance; branches short or long, mainly *Frullania*-type, *Lejeunea*-type only rarely present.

Stem rigid, 0.20-0.35 mm in diam.; ventral merophyte 6-8 cell rows wide, the ventral cortical cells subquadrate to short rectangular, 32-61 x 25-43 μ m, the dorsal cortical cells subquadrate to short rectangular, 50-72 x 32-57 μ m; stem in transverse section with 20-28 thin-walled cortical cells surrounding 70-115 thick-walled medullary cells, the dorsal cortical cells large, 47-54 μ m high, the ventral cortical cells 22-25 μ m high, the medullary cells 18-40 μ m in diam.

Leaves closely imbricated. Lobe ovate to broadly so, 1.10-1.70 mm long, 0.85-1.30 mm wide, inserted along the whole length of the merophyte, the dorsal base weakly auriculate, the apex rounded to obtuse, the apical region plane to weakly incurved, the ventral margin plane, when spread out forming an angle of 150-160° with the keel; keel smooth, straight to only slightly curved, at an angle of 60-90° with the axis; median leaf cells 29-54 x 18-25 cells 15-28 high; intermediate thickenings μm, margin μm scarce, elliptic-rounded, when present one per each larger cell wall.

Lobule narrow triangular with a narrowly rounded apex, 0.65-0.85 mm long, 0.30-0.40 mm wide, 0.45-0.55 x the length of the lobe, rather abruptly flattened towards the free margin, the flattened part concave; free margin straight, rounded at the apex of the lobule, with 8-11 teeth; each tooth consisting of one protruding cell of the lobule margin, separated from each other by (2-)4-5 free marginal cells, near the apex separated by 4-7 free marginal cells; hyaline papilla 1-2 cells below the proximal base of the first tooth.

Underleaves imbricated, obtrapezoid, 0.55-0.80 mm long, 0.75-1.15 mm wide, the apex widely rounded to truncate, sometimes emarginate, plane or slightly recurved, the margins plane to slightly recurved, the bases with small ears, only 0.07-0.13 x 0.05-0.10 mm in size, the line of insertion arched, 0.14-0.17 mm deep; median cells 25-40 x 18-25 μ m, at the margins smaller and subquadrate; the underleaf base at the rhizoid disc bistratose in longitudinal section, very short, only 28-36 μ m in length; rhizoid disc reniform, consisting of many thin-walled or fewer and then more thick-walled cells.

Androecia terminal or intercalary on stems and long or short *Frullania*-type branches; bracts and bracteoles in 8-23 series, the bract lobe ovate to broadly so, 1.10-1.20 mm long, 0.90-0.95 mm wide, the lobule with a more strongly inflated basal part and a concave distal part bearing 3-5 teeth of one cell; bracts diandrous, antheridium c. 130 µm in diam.

Gynoecium terminating stems and long or short *Frullania*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe squarrose in the apical part, obovate-oblong, 1.75-2.00 mm long, 0.90-1.00 mm wide, the apex blunt to rounded, the apical region concave, the keel rounded, bracts usually without wing at the keel, occasionally a small linear

wing developed, 0.4 mm long, 0.1 mm wide, obliquely inserted on the innovation, the lobule narrow rectangular, $0.35-0.45 \times the length of the lobe, the apex with a one-celled tooth; bracteole rectangular-spathulate, 1.00-1.15 mm long, 0.75-0.80 mm wide, the apical region widely rounded to emarginate, plane to slightly recurved, the basal part inserted on the main stem only. Perianth not emergent when mature, obovoid-cylindrical, 1.4-2.0 <math display="inline">\times$ 0.9-1.0 mm, \pm dorso-ventrally compressed with the ventral side inflated, with 5-6 unequal, smooth and rounded plicae, divided over two narrowly rounded lateral keels and one broad ventral keel with 1-2 small plicae and 1(-2) small and rounded, dorsal plicae, the plicae extending over the upper 1/4-1/2 of the perianth but the ventral plicae sometimes extending almost down to base; beak 8-10 cells long.

Sporophyte: seta with a 16+4 cell pattern, articulate (?, only one observation of a mature seta in bad condition); capsule c. 0.6 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 57-72 μ m long, covered with numerous spinulae and eight rosettes; elaters 56 per capsule (one observation only, see Note), 400-435 μ m long, c. 20 μ m wide, with one brownish, c. 4 μ m wide spiral.

Sporeling not observed.

Distribution (PL. XXVIII): CENTRAL AMERICA (Mexico, Honduras). Only known from Southern Mexico, at 180-250 m, and from Honduras, at 20-600 m altitude.

<u>Ecology</u>: growing in rather loose mats on trees and logs in, sometimes disturbed, localities in lowland rain forest. Growing intermingled with other Lejeuneaceae (e.g. *Frullanoides tristis* or *Acrolejeunea torulosa*) and with Musci (e.g. *Calymperes* spp.).

<u>Differentiation</u>: this species stands out by a number of characters: 1) the narrow triangular leaf lobule with a straight keel and a free margin that bears 8-11 teeth, which consist only of one large cell, protruding from the free margin (PI. XXVI, fig. 5), 2) the obtrapezoid underleaf with its small auricles of only $0.07-0.13 \times 0.04-0.09$ mm in size (PI. XXV, figs. 5-6; compare with the underleaf auricles of the often equally large species *F*. *densifolia* and *F*. *laciniatiflora*: $0.15-0.35 \times 0.15-0.25$ mm), 3) the perianth with only 5-6 plicae, divided over three keels (PI. XXVI, figs. 2, 9), and 4) the absence of a wing on the keel of the female bracts, except for an occasionally developed, small linear wing (PI. XXVI, figs. 6-7).

The first two characters are unique in the genus *Frullanoides*. The shape of the perianth and the occurence and shape of the female bract wing are \pm similar to *F*. *liebmanniana* but this species furthermore differs widely (see under *F*. *liebmanniana*). The shape of the perianth resembles, besides *F*. *liebmanniana*, also the perianth of some species of *Mastigolejeunea*, most notably of the sect. *Brachiolejeuneoides* (e.g. *M. recondita*, see MIZUTANI 1969b, GRADSTEIN 1975). The obtrapezoid outline of the underleaves also resembles the underleaves of *Mastigolejeunea* but differs from the latter genus in the development of auricles. *F. mexicana* is, in my opinion, a good species of *Frullanoides*, which complies with all diagnostic characters of the genus (see genus description).

Variation: morphologically F. mexicana is a very stable species.

Notes:

- The number of elaters, 56 divided over two valves of (1+3+5+7) and two valves of (2+4+6), is seemingly aberrant within the genus. Due to the size of the plants and the development of its sporophyte, the number should most logically be 68 (or 72, see Chapter III). The number of 56 is based on only one observation of a mature seta and theca, available thus far. Since the elaters may easily break off from the valves, the actual number may be the expected 68 when more material becomes available.
- 2. The seta most probably is articulate. My conclusion with respect to this character is, however, somewhat preliminary since I have observed only one mature, elongated seta, which was unfortunately in very bad condition. More material is needed to draw a definite conclusion. In a young stage, the arrangement of the outer cells of the seta is rather irregularly (PI. XXVI, fig. 3), contrary to young setae of other *Frullanoides* species.
- HERZOG (1951) published three formae of Brachiolejeunea mamillata Steph. (fo. typica, fo. brevifolia, fo. obtusifolia), all of them based on misidentified material of F. mexicana (see specimens examined).

Specimens examined (F. mexicana):

- MEXICO. Chiapas, Palenque, Eggers & Frahm MX 22.7/792229, 8.111.1979 (hb. Eggers, hb. Frahm, U), type collection of *Frullanoides mexicana* van Slageren; Chiapas, Agua Azul, between Palenque and Ocosingo, Eggers & Frahm 792625, 9.111.1979 (hb. Frahm, U).
- HONDURAS. Atlantida, Lancetilla Valley, near Tela, Standley 54372 & 55428
 (in HERZOG (1951) sub nom. Brachiolejeunea mamillata fo. brevifolia Herz. nom. nud.), 54358, 54423, 54496, 54526 (in HERZOG (1951) sub nom. Brachiolejeunea mamillata fo. obtusifolia Herz. nom. nud.), 55249 (in HERZOG (1951) sub nom. Brachiolejeunea mamillata fo. typica Herz. nom. nud.), 55295, 55428 & 56075a, 6.X11.1927-20.111.1928 (JE).

- 7. FRULLANOIDES TRISTIS (Steph.) van Slageren comb. nov. (Plates XV-XVI)
- Lejeunea (subg. Brachiolejeunea) tristis Steph., Hedwigia 29(1): 8, 29(3): 134 (1890).
- Brachiolejeunea tristis (Steph.) Steph., Spec. Hep. 5: 112 (1912); Arnell (1961: 400), (1963: 225); Vanden Berghen (1951: 88), (1960: 114).
 <u>Type</u>: Ethiopia, "Inter Lichenes, Hampe sub Phragm. tristis" (W (hb Lindenberg 5996) holo, G 739, S).

Heterotypic synonyms:

Brachiolejeunea camerunensis E. Jones & Vand. Bergh., Bull. Jard. Bot. Etat 21: 88 (1951), Vanden Berghen (1960: 115); Arnell (1961: 400), (1962a: 55), (1963a: 225); Jones (1968: 565) syn. nov.
Syntypes: Cameroun, Victoria, Ukile, on tree trunk in forest, Jones 404B, 30.111.1948 (BM, hb. Vanden Berghen) and Cameroun, on stem of *Hypericum* in the upper region of the forest, Jones 432, 2.1V.1948 (BR, hb. Vanden Berghen).

- Brachiolejeunea camerunensis var. angolensis S. Arnell, Svensk Bot. Tidskr.
 56: 55 (1962) syn. nov.
 Type: Angola, Cuanza Sul, Faz. Chipepe, D.G. Degelius s.n., 20.11.1960 (UPP holo, S).
- Brachiolejeunea chinantlana (Gott.) Schiffn., Hedwigia 33: 180 (1894); Evans (1908a: 160); Stephani (1912: 117); Bonner (1963: 448); Grolle (1966: 293, 296) syn. nov.
- Phragmicoma bicolor var. chinantlana Gott., Mex. Leverm.: 268 (1863).
- Lejeunea (subg. Brachiolejeunea) bicolor var. chinantlana (Gott.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 132 (1884).
 Lectoype: Mexico, Chinantla, Liebmann 456b, V.1841 (C holo, FH-Schiffner, G 20100, S, W (hb. Lindenberg 5957). The holotype, located in B, has been destroyed.
- Brachiolejeunea confertifolia Steph., Spec. Hep. 5: 113 (1912); Arnell (1953: 281), (1963a: 225) <u>syn. nov</u>. Type: Madagascar, Mathieu s.n., hb. Cardot 75 p.p. (G 738 holo).
- Brachiolejeunea crenata Sim, Trans. Roy. Soc. South Africa 15: 56 (1926);
 Vanden Berghen (1951: 88); Arnell (1963a: 225) <u>syn. nov.</u>
 Syntypes: South Africa, Natal, Sim 8298, 9770, 9771, 9773 (PRE);
 Transvaal, Sim 9765 (PRE). SIM (1926: 56) cites nr. 7965 instead of 9765.
- Brachiolejeunea hildebrandtii Steph. var. pluriplicata Gola, Mem. Reale Acca. Sci. Torino, Ser. II, vol. 65(1): 9 (1916) <u>syn. nov.</u> Type: the type collection has not been available (see Note 3).

- Brachiolejeunea insularis Evans, Bull. Torrey Bot. Club 35: 159 (1908a); Stephani (1912: 126) <u>syn. nov.</u> Type: Puerto Rico, vicinity of Cayey, on tree, Evans 97, 23-26.VII.1900 (YU holo).
- Brachiolejeunea jackii Steph., Spec. Hep. 5: 119 (1912) syn. nov. Type: Mexico, Tlapacoyo, Liebmann s.n., V.1841 (G 20158 holo, W).
- Brachiolejeunea mohriana Steph., Spec. Hep. 5: 125 (1912) syn. nov. Type: Mexico, Huatusco, Mohr 35, 1847 (G 20204 holo).
- Brachiolejeunea parva Herz., Rev. Bryol. Lichénol. 20: 135 (1951) syn. nov. Type: Honduras, Lancetilla Valley, near Tela, Standley 56075a (JE holo).
- Brachiolejeunea parviflora Steph., Spec. Hep. 5: 116 (1912) <u>syn</u>. nov. Type: Madagascar, Betsileo, Villaume s.n., hb. Lacouture 126 (G 20222 holo).
- Brachiolejeunea poeltii Mizut. & Grolle, Ergebn. Forsch.-Untern. Nepal Himalaya 1 (4): 293 (1966) syn. nov.
 Type: Nepal, Vorhimalaya, Abies-Rhododendron-Wald um Thodung, 3000 m, Poelt H 208/B, 1962 (M holo, JE, NICH).
- Brachiolejeunea wrightii Steph., Spec. Hep. 5: 123 (1912) syn. nov. Type: Cuba, Wright 1186 (G 20375 holo).

Plants paroecious, medium-sized, 2-4 cm long, 1.40-2.25 mm wide, dull-yellowish to brownish green (EVANS 1908a), becoming light to darkish brown to black when dry, irregularly branched, parts of the plants with a dichotomous appearance due to floriferous innovations; branches short or long, mainly *Frullania*- type, *Lejeunea*-type less frequent.

Stem flaccid, 0.15-0.25 mm in diam.; ventral merophyte 4-6 cell rows wide (but see Note 2), the ventral cortical cells subquadrate to short rectangular, 25-50 x 21-36 μ m, the dorsal cortical cells subquadrate to short rectangular, 36-60 x 29-40 μ m; stem in transverse section with 14-20 thin-walled cortical cells surrounding (22-)26-48(-91!) thick-walled medullary cells; the dorsal cortical cells 25-40 um high, the ventral cortical cells 21-36 μ m high, the medullary cells 14-36 um in diam.

Leaves imbricated. Lobe ovate to ovate-falcate, 0.70-1.30 mm long, 0.50-0.95 mm wide, inserted along 3/4-1/1 of the length of the merophyte, the dorsal base straight, the apex varying from rounded to blunt to (occasional) minutely apiculate, the apical region incurved, the ventral margin upcurved, when spread out forming an angle of 150-170° with the keel; keel smooth, slightly curved to \pm straight, at an angle of 45-90° with the axis; median leaf cells 25-47 x 14-32 µm, margin cells 14-21 µm high; intermediate thickenings scarce, elliptic-rounded, when present one per each larger cell wall.

Lobule broadly ovate to ovate-oblong, (0.35-)0.50-1.00 mm long, 0.25-0.60 mm wide, $0.4-0.6 \times$ the length of the lobe, gradually flattened towards the free margin, the flattened part plane; free margin gradually curved towards the apex of the lobule, sometimes with a distinct, blunt angle at the apical tooth (PI. XV, fig. 9), with (4-)6-9 teeth; teeth consisting of 1-4(-5) cells in total with 1-2 at the base, inflexed, separated from each other by 2-5(-10) free marginal cells, apical and second tooth separated by (4-)7-12 free marginal cells; hyaline papilla one cell below the proximal base of the first tooth.

Underleaves imbricated, suborbicular to (occasionally) reniform, 0.45-0.75 mm long, 0.45-0.80 mm wide, the apex widely rounded-truncate, the margins slightly recurved, the basis with small to medium sized ears, 0.05-0.15 x 0.05-0.10 mm (Pl. XVI, fig. 6), the line of insertion arched, 0.05-0.10 mm deep; median cells 29-43 x 18-25 μ m, at the margins smaller and subquadrate, the underleaf base at the rhizoid disc bistratose in longitudinal section, short, (36-)40-63(-90) μ m in length; rhizoid disc suborbicular to elliptical, consisting of many thin-walled cells.

Androecia located 1-3(-5) series of vegetative leaves below the gynoecium; bracts and bracteoles in 1-3(-5) series, the bract lobe ovate, 0.7-1.2 mm long, (0.4-)0.7-0.9 mm wide, the lobule with a more strongly inflated basal part and a concave distal part bearing 2-6 teeth of 2-5 cells in total with two cells at the base or represented by small triangular segments only; bracts monandrous, antheridium c. 130 µm in diam.

Gynoecium terminating stems and long or short *Frullania*-type and *Lejeunea*-type branches, with two innovations; bracts and bracteole in one series, the bract lobe squarrose, (ob)ovate to broadly so, the apical region concave, 1.20-1.60 mm long, 0.60-0.95 mm wide, the apex blunt to minutely apiculate, the keel widely rounded, bracts with an elliptic to long and narrow wing at the keel, 0.45-0.70(-0.80) mm long (0.10-)0.20-0.50 mm wide, the lobule narrow rectangular, 0.35-0.50 x the length of the lobe, the rounded to acute apex with a tooth of 1-2 cells; bracteole rectangular, 0.80-1.15 mm long, 0.55-0.85 mm wide, the apex widely rounded to truncate-emarginate, the basal part inserted on the innovations. Perianth exserting the bracts for 1/4-1/3(-1/2) when mature, occasionally stalked, the stalk up to 350 µm, obovoid-cylindrical, $1.15-1.55 \times 0.55-0.80$ mm, with 10 smooth, rounded plicae extending over the upper 1/2-2/3 of the perianth; beak 5-10 cells long.

Sporophyte: seta articulate with a 16+4 cell pattern; capsule c. 0.5 mm in diam., splitting to near base into four widely spreading valves; spores green, angular when dry, 43-65 μ m long, covered with numerous spinulae and eight rosettes; elaters 68 per capsule, 290-350 μ m long, c. 20 μ m wide, with one brownish, c. 4 μ m wide spiral.

Sporeling of the Lopholejeunea-type.

Distribution (PI. XXIX): CENTRAL and SOUTH AMERICA, WEST INDIES, AFRICA, ASIA (India, Nepal). A widely distributed species, known from tropical areas, but also from the temperate regions of South Africa and Nepal. In Central and South America present from Mexico (SCHIFFNER 1894, EVANS

1908a sub Brachiolejeunea chinantlana) through Panama, Colombia, Venezuela and Peru to the Guianas and Eastern Brazil. Also recorded from the West Indian islands of Cuba, Jamaica and Puerto Rico (EVANS 1908a sub B. insularis) and from the Galapagos Islands (CLARK 1953 sub R grandidentata); GRADSTEIN & WEBER 1982 sub B. bahamensis). In Africa described by several authors under various names from Ethiopia to South Africa, Angola and Madagascar (see Note 1). Also known from Western Africa: Sierra Leone, Nigeria and Cameroun (VANDEN BERGHEN 1951 sub B. camerunensis; JONES 1968, JONES & HARRINGTON 1983 sub B. tristis). In Asia known only from two disjunct localities: the mountains of Southern India and in Nepal (GROLLE 1966 sub B. poeltii). The American localities are generally at lower altitude (0-1000 m, occasionally up to 2200 m) than the African localities (± 1000-2600 m). In Nepal collected at 3000 m.

Ecology: in dense or more loose mats (rarely also pendulous: e.g. coll. Gradstein \mathcal{E} Weber H454) almost exclusively epiphytic on trunks, stems and twigs of living trees and shrubs; rarely on logs or shaded rocks. Growing in a wide variety of both natural and degraded habitats: tropical rain forest and mountain forest, often degraded and secondary, as well as in mesic to xeric woodlands (e.g. on the Galapagos Islands, GRADSTEIN \mathcal{E} WEBER 1982: 147), on roadside trees, in plantations and in gardens. Recorded epiphyllous in a montane forest in the Kilimanjaro Mountains of Tanzania (BIZOT \mathcal{E} POCS 1979, coll. Pócs 6931/P, the only epiphyllous record of the whole genus!). Often recorded growing together with *Frullania* spp. In Nepal collected between *Frullania arecae* in an *Abies-Rhododendron* forest (GROLLE 1966: 295).

<u>Differentiation</u>: except for some specimens of *F. bahamensis*, *F. tristis* is the only paroecious species of the genus *Frullanoides*. This mode of inflorescence is the main diagnostic character. Additional characters are provided by: 1) the underleaf ears, and 2) the wings on the female bracts, but these are less diagnostic. The underleaf ears, $0.05-0.15 \times 0.05-0.10$ mm, are medium-sized when compared with the very small ears of *F. bahamensis* and *F. corticalis* (consisting of a few cells only or even absent) and the large ears of *F. densifolia* and *F. laciniatiflora* ($0.15-0.35 \times 0.15-0.25$ mm, appressed to the ventral-lateral side of the stem). The female bract wings of *F. tristis*, 450-800 x 100-500 µm, are intermediate in size between *F. bahamensis* and *F. corticalis* (small: $110-320(-600) \times 50-300 \mu$ m) and *F. densifolia* and *F. laciniatiflora* ($1arge: 700-1400 \times 200-600 \mu$ m). Both underleaf ears and female bract wings are ± equal in size to those of *F. liebmanniana* and *F. mexicana*. The latter two species are, however, clearly characterized by their leaf lobules (see under *F. liebmanniana* and *F. mexicana*).

Furthermore, F. densifolia and F. laciniatiflora differ from F. tristis by: 1) their thick-walled ventral cortex (thinwalled in F. tristis; compare PI. XVIII, fig. 5 and PI. XXII, fig. 3 with PI. XVI, figs. 4-5), 2) being dioecious, 3) their generally larger number of cortex and medulla cells: (16-)20-37 and (35-)45-115 respectively (in F. tristis 14-20 cortex and (22-)26-48(-91) medulla cells), and 4) their more slender habitus (compare
habitus figures on Plates XIX, XXII and XVI).

Besides the aforementioned characters F. mexicana, F. liebmanniana and F. corticalis differ from F. tristis by being dioecious and F. bahamensis by being autoecious. The few paroecious specimens of the latter species are easily distinguished by the (nearly) absent underleaf ears, the plane to incurved female bracts (squarrose in F. tristis) and in the small size of the plants, not exceeding $1\frac{1}{2}$ cm in length (F. tristis 2-4 cm).

<u>Variation</u>: morphologically the species is rather stable. Variation is observed in general size, expressed in: 1) the number of medullary cells: 26-48 but occasionally only 22 or up to 91, 2) the size of the underleaf ears, $0.05-0.14 \times 0.03-0.10 \text{ mm}$, 3) the outline of the leaf apex: rounded, blunt or minutely apiculate, and 4) the male bracts with rather indistinct to very pronounced inflated lobules.

Notes:

1. The new delimination of F. tristis is the result of the synonymisation of all the paroecious species, described in (the former) Brachiolejeunea subg. Plicolejeunea: B. chinantlana, B. jackii, B. mohriana and B. parva from Central and South America, B. insularis and B. wrightii from the West Indies. Β. camerunensis, Β. camerunensis var. anaolensis. Β. confertifolia. B. crenata and B. tristis from Africa, and B. poeltii from Nepal. The African species were already reduced to two (B. confertifolia and B. tristis) by ARNELL (1963a), whereas GROLLE (1966: 296) already emphasized the close relationship of B. poeltii and the neotropical B. chinantlana, differing only in the outline of the underleaf. Six of the twelve species have been described by STEPHANI (Species Hepaticarum 5: 112 etc., 1912), frequently based on scanty material. Comparison of their type specimens has revealed no discriminating characters that could have lead to another species concept. This leads to

my conclusion that all these differently described species represent in fact only one single, pantropical species which, in this new delimitation, can be distinguished satisfactorily from the other species in *Frullanoides*.

- 2. A remarkable collection of *F*. tristis is represented by Düll 4/A52a from Mexico. The well-developed plants are very similar to *F*. densifolia because of: a) the number of cortex (32) and medulla (83) cells, b) the ventral merophyte, consisting of 10 cell rows, c) the rather large ears of the underleaves that are \pm appressed to the ventral-lateral side of the stem, and d) the reniform rhizoid discs at the underleaf base. I nevertheless reckon these plants to *F*. tristis because of: 1) the very clear paroecious male bracts: 2-4 series after 1-2 series of vegetative leaves, and 2) the thin-walled ventral cortical cells that would undoubtly have been thick-walled in a comparable specimen of *F*. densifolia. Though this collection indicates that the distinction of vegetative *F*. tristis and *F*. densifolia is not always satisfactorily, the generative distinction is diagnostic.
- 3. The type collection of Brachiolejeunea hildebrandtii var. pluriplicata Gola

must be in TO or TOM, but has unfortunately not been available. The description of GOLA (1916) clearly suggests *F. tristis*.

Specimens examined (F. tristis):

- MEXICO. Huatusco, Mohr 35, 1847 (G 20204), type collection of Brachiolejeunea mohriana Steph.; Chinantla, Liebmann 456b, V.1841 (C, FH-Schiffner, G 20100, S, W (hb. Lindenberg 5957), type collection of Brachiolejeunea chinantlana (Gott.) Schiffn.; Tlapacoyo, Liebmann 563b, V.1841 (C); ibid., Liebmann s.n., V.1841 (G 20158, W), type collection of Brachiolejeunea jackii Steph.; Orizaba, Mohr 35, 1857 (MANCH 14055); Veracruz-Orizaba, near Orizaba, Düll 4/A52a, 16.X.1966 (DUIS, JE); s.loc., Jack s.n. (G 20159); s. loc., s. coll., s.n. (G 20205).
- HONDURAS. Atlantida, Lancetilla Valley near Tela, Standley 56075a (JE), type collection of *Brachiolejeunea parva* Herz.
- COSTA RICA. Cartago, Turrialba, Rio Reventazon, Svihla 47-749 & 47-778, 10-12. X.1947 (WTU).
- PANAMA. Chirique, Hélion 497 (G 20160).
- CUBA. Oriente: Guantánamo La Runicion, Schubert M194, 13.I.1968 (JE);
 Tal Huerto, Schubert M265, 26.I.1968 (JE); Sierra de Boniato, Pócs 9102/F, 14.V.1979 (EGR, HAC, U); Monte Christo, Hadaĉ s.n., 27.I.1968 (JE); Baracoa, El Yunque, Underwood & Earle 1144, III.1903 (YU); Monte Verde, Wright s.n. (BM, BP, U), several collections; ibid., Wright s.n., II.1927 (YU); s.loc., Wright 1186 (G 20375), type collection of Brachiole-jeunea wrightii Steph. & s.n. (MANCH 14053 & 14054).
- JAMAICA. Parish St. James, zwischen Catadupa und Moche, E. & P. Hegewald 8208 & 8220, 8.XI.1973 (hb. Hegewald, U); near Castleton Botanical Garden, Underwood 55, 26-27.I.1903 (YU); Clyde Valley, Evans 260 & 268, 24.VII.1903 (YU); Clyde River, Johnson 51, 28.IV.1906 (YU); Portland, Spring Garden, Orcutt 4761, VII.1928 (BM, hb. Fulford); Troy, Evans 638 & 671, 13-14.IX.1906 (YU); Cinchona Hill, Evans 143d, 15.VII.1903 (YU, U); ibid. Johnson 33, 28.IV.1903 (YU); Cinchona, Evans 407, 28.VIII.1906 (YU); vicinity of Cinchona, Maxon & Killip 865, 8.III.1920 (YU); Cinchona plantation, Underwood 1105, II.1903 (YU); ibid., s.loc., Orcutt 3039 (BM), 3593 (hb. Fulford), 3973 & 3974, 3.VII.1928 (BM, hb. Fulford).
- PUERTO RICO. Carite State Forest, Griffin III s.n., 6.VII.1968 (FLAS, U); Mayaguez, Heller 4463a, 31.1.1900 (YU); mount Morales, near Utado, Howe 465, 15.III.1906 (YU); near Cayey, Evans 97, 23-26.VII.1900 (YU), type collection of *Brachiolejeunea insularis* Evans.

TRINIDAD. s.loc., Wallace s.n. (NY); s.loc., Fendler s.n. (NY).

FRENCH GUIANA. Cayenne, Moen 115 (G 20376).

- SURINAM. Paramaribo, Kegel s.n., I.1845 (FH-Schiffner, G 20358 & 20359, S, U, W (hb. Lindenberg 5968); s.loc., Nonthoper s.n., 1871 (L, U); s.loc., s. coll., s.n. (G 20357, L).
- BRAZIL. Bahia, Lütgelburg 43 (G 20377) & s.n., 1911 (B); Sergipe, Itabaiana, Vital 2869, 29.1.1974 (SP, U).
- VENEZUELA. Mérida, Mucuy, Onraedt 78.V.6540, 5.VII.1978 (hb. Onraedt, JE, U); Mérida, s.coll., s.n. (BM); s.loc., Grossmann s.n., 1906 (JE).
- COLOMBIA. Magdalena, N-Hang des San Lorenzo der Sierra Nevada de Santa Marta, Winkler C192, 7.1.1962 (hb. Winkler); Boyacá, Sácama, Aguirre et al. 2970, 16.VIII.1982 (COL, U); Cundinamarca, route Bogotá-La Calera, Bischler 563, 23.VII.1958 (PC, U); Risaralda, Santa Rosa de Cabal, van Reenen et al. 1857, 25.VII.1980 (COL, U); Meta, Sierra Nevada de Sumapaz, above Minca, Winkler C192, 7.1.1967 (COL, U, hb. Winkler).
- ECUADOR, GALAPAGOS ISLANDS. Floreana: Cruz Farm, Gradstein H153, 24.IV.1976 (U); Cerro Pajas, Gradstein H155, 25.IV.1976 (U); Santa Cruz: old trail to Bella Vista, Gradstein & Weber H5, 11.IV.1976 (COLO, U); ibid., Gradstein & Sipman H341, 16.VI.1976 (U); between Puntudo and Mt. Crocker, Gradstein & Weber H17, 14.IV.1976 (COLO, U); Caseta, van der Werff 1702, 30.VIII.1974 (U); Bella Vista, Weber B-13655, 1964 (COLO, JE); Isabela: rim of volcano Alcedo, Gradstein & Weber H227, 10-12.V.1976 (COLO, U); Cerro Azul, Gradstein & Sipman H373 & H454, 21-24.VI.1976 (U); Vulcan Alcedo, van der Werff 1547b, 25.IX.1974 & 2013, IV.1975 (U); San Cristobal: Tres Palos towards El Junco, Gradstein & Lanier H297b, 22.V.1976 (U); El Progreso, Gradstein & Lanier H327, 24.V.1976 (U).
- PERU. Huanuco, Leoncio Prado, Tingo Maria, E. & P. Hegewald 7885, 23.X.1973 (hb. Hegewald, U); Junín, Tarma, San Ramón, E. & P. Hegewald 8395, 0.VI.1977 (hb. Hegewald, U).
- SIERRA LEONE. Loma Mountains, Biutimane, Jones 1495, 18.111.1971 (hb. Jones).
- NIGERIA. Heiphan, Jones 970/971 p.p., 11.IV.1958 (hb. Jones); Naraguta Forest Reserve, Jones 908B p.p., 26.III.1958 (BM, hb. Jones).
- CAMEROUN. Victoria, Ukile, Jones 404B, 30.111.1948 (BM, hb. Vanden Berghen) & 432, 2.1V.1948 (BR, hb. Vanden Berghen), syntype collections of *Brachiolejeunea camerunensis* E. Jones & Vand. Bergh.

ZAIRE. Kivu, Honda, Marlier 2d, 1949 (hb. Vanden Berghen).

- ANGOLA. Cuanza Sul, Faz. Chipepe, near Cassongue, Degelius s.n., 20.11.1960 (S), type collection of *Brachiolejeunea camerunensis* var. angolensis S. Arnell.
- ETHIOPIA. s.loc., Hampe (?) s.n. (G 739, S, W (hb. Lindenberg 5996), type collection of *Frullanoides tristis* (Steph.) van Slageren.
- TANZANIA. <u>Kilimanjaro</u>: valley of Ghona near Makon, Pócs & Jones 6366/D, 3.1.1971 (EGR, U); above Marangu, Pócs 6363C/Jones 2131 p.p., 2.1.1971 (BM, hb. Jones); between rivers Umbwe and Lonzo, Pócs 6352 p.p./Jones 1813 p.p., 30.XII.1970 (hb. Jones); along Umbwe route, Pócs 6931/P, 1.VII.1976 (EGR); Marangu, Hans Meyer s.n., 1890 (G 740); s.loc., Bishop Harrington s.n. (NY); <u>Mweka Wildlife College garden, Pócs & Jones s.n., 29.XII.1970 (EGR); Arusha National Park, along Ngarenanyuki river, Sharp et al. 9785, 9.VII.1968 (EGR).</u>
- RWANDA. Gisenyi, vallée de la Bikoneko, Gikungu, de Sloover 18511 & 18671, 23-29.VII.1974 (hb. de Sloover, hb. Vanden Berghen).
- BURUNDI. Bugarama, Petit 2395, 13.1.1968 (BR).
- SOUTH AFRICA. <u>Transvaal</u>: Lemonwood spelonken, Sim 9765, III.1918 (PRE), syntype collection of *Brachiolejeunea crenata* Sim; Mariepskop, Vorster 3432, 12.11.1969 (L) & 4776, 6.111.1969 (hb. Jones); near Pilgrim Rest., Schelpe 6134, 1956 (JE, UPS); Zoutpansberg, Pisanghoek, Bosman 204, 3.V.1929 (PRE) & s.n., 1929 (JE, UPS); Zoutpansberg, Rosbach Lemana Estales, Watson 924 & 924a, 12.1.1931 (PRE); <u>Natal</u>: Knoll, Hilton Road, Sim 8298, 1915, & 9771, I.1916, & 9773, IV.1916 (PRE) & above Elandskop, Sim 9770, I.1921 (PRE), syntype collections of *Brachiolejeunea crenata* Sim; Bergville, Cathedral Peak Area, Almborn 9471, 8.XI.1953 (G 20102); <u>Cape Prov</u>.: Steenbras river, Arnell 691, 16.IX.1951 (S); Kaapstad, Kirstenbosch, Vanden Berghen s.n., 4.1.1972 (hb. Vanden Berghen); <u>Transkei</u>: Evelope Valley, Sim 86, 1888 (PRE).
- MADAGASCAR. Betsileo, Villaume s.n. (G 20222), type collection of Brachiolejeunea parviflora Steph.; s.loc., Mathieu s.n. (G 738), type collection of Brachiolejeunea confertifolia Steph.
- INDIA. Nilgiri Mountains, Strachey s.n. (NY, U); Munnar, Udar et al. 5776/82, 23.IX.1982 (LWU).
- NEPAL. Vorhimalaya, near Thodung, Poelt H208/B, 1962 (JE, M, NICH), type collection of *Brachiolejeunea poeltii* Mizut. & Grolle.

EXCLUDENDA

1. Taxa, studied from type material

All taxa listed here were studied from type material. Two categories of names are treated:

- a. names published in *Brachiolejeunea* (starting point for valid combinations = SCHIFFNER sept. 1893);
- b. names published in Lejeunea subg. Brachiolejeunea (Brachiolejeunea combination not available).
- BRACHIOLEJEUNEA AFRICANA Steph. Spec. Hep. 5: 114 (1912) = Mastigolejeunea florea (Mitt.) Steph. (vide VANDEN BERGHEN 1951).

BRACHIOLEJEUNEA ALICULATA Herz., Memoranda Soc. Fauna FI. Fenn. 26:
50 (1951) syn. nov. = Trocholejeunea sandvicensis (Gott.) Mizut.
HERZOG (I.c.) already emphasizes the close relationship of *B. aliculata* Herz. and *B. sandvicensis* (Gott.) Evans (= Trocholejeunea sandvicensis (Gott.) Mizut.), which were supposed to be different in the alate plicae on the perianth of *B. aliculata*. I have observed alate plicae, however, in numerous collections of *B. sandvicensis*. In addition, I have found weakly developed male bracts in the type of *B. aliculata*, which is apparently paroecious as in *B. sandvicensis*, and not dioecious.

BRACHIOLEJEUNEA ALCINA (Aongstr.) Steph., Bull. Herb. Boissier 5: 842 (1897), Spec. Hep. 4: 791 (1912).

Basionym: Lejeunea alcina Aongstr., Ofvers. Förh. Kongl. Svenka Vetensk.-Akad. 29(4): 23 (1872) = Spruceanthus polymorphus.

EVANS (1900: 423) points out that 1) "alcina" in AONGSTROM (1872) is a misprint and that "aliena" is the correct name, and 2) that *B. aliena* is a synonym of *Thysananthus elongatus* (Aust.) Evans. Examination of the label of the type collection reveals "aliena", the spelling that was used by EVANS and subsequent authors. According to VERDOORN (1934a, 1934c) *Thysananthus elongatus* is a synonym of *Spruceanthus polymorphus* (Sande lac.) Verd.

- BRACHIOLEJEUNEA ANDAMANA Steph., Spec. Hep. 5: 130 (1912) = Ptychanthus striatus (Lehm. & Lindenb.) Nees (vide VERDOORN 1933, 1934c).
- BRACHIOLEJEUNEA ASPLUNDII Herz., Svensk Bot. Tidskr. 51: 190 (1957) = Blepharolejeunea securifolia (Steph.) Schust. (vide VAN SLAGEREN & KRUIJT 1985).
- BRACHIOLEJEUNEA ASSIMILIS Steph., in Mildbread, J.M. (ed.): Wiss. Ergebn. Deutsche Z.-Afr. Exped. 2: 129 (1910-11) = Mastigolejeunea nigra

Steph.

VANDEN BERGHEN (1951) suggests the synonymy of *B. assimilis* and *B. nigra* (Steph.) Steph. (= *Mastigolejeunea nigra* Steph.). After examining the type collection I can confirm this.

- BRACHIOLEJEUNEA BIDENS Steph., Spec. Hep. 5: 116 (1912) = Mastigolejeunea carinata (Mitt.) Steph. (vide VANDEN BERGHEN (1951, 1960) = Mastigolejeunea auriculata (Wils.) Schiffn. (cf. GRADSTEIN & INOUE 1980).
- BRACHIOLEJEUNEA BIRMENSIS Steph., Hedwigia 34: 63 (1895a), Spec. Hep. 5: 134 (1912) = Trocholejeunea infuscata (Mitt.) Verd. (vide VERDOORN 1934c).
- BRACHIOLEJEUNEA CHINENSIS Steph., Hedwigia 34: 63 (1895a), Spec. Hep. 5: 136 (1912) = Brachiolejeunea sandvicensis (Gott.) Evans (vide STEPHANI 1912) = Trocholejeunea sandvicensis (Gott.) Mizut. (cf. MIZUTANI 1962).
- BRACHIOLEJEUNEA CLAVULATA (Spruce) Steph., Spec. Hep. 5: 129 (1912).
 Basionym: Lejeunea (subg. Brachiolejeunea) clavulata Spruce, Mem. Torrey
 Bot. Club 1: 121 (1890) syn. nov. = Marchesinia brachiata (Sw.) Schiffn.
- BRACHIOLEJEUNEA CORDISTIPULA Steph., in Herzog, Biblioth. Bot. 87: 251 (1916), Spec. Hep. 6: 381 (1923) syn. nov. = Hygrolejeunea catinulifera (Spruce) Steph.
- BRACHIOLEJEUNEA EAVESIANA (Gott. & Müll.) Steph., Spec. Hep. 5: 140 (1912).
 Basionym: Phragmicoma eavesiana Gott. & Müll., Fragm. Phyt. Austr., suppl. ad Vol. XI: 63 (1880) syn. nov. = Spruceanthus semirepandus (Nees) Verd.
 The type collection of this species was burnt in B in 1945. Isotype material in G, coll. Eaves 495 from Australia (G 20116), contained Spruceanthus semirepandus (Nees) Verd.
- BRACHIOLEJEUNEA ERECTILOBA Steph., Spec. Hep. 5: 138 (1912) syn. <u>nov.</u> = Acrolejeunea pycnoclada (Tayl.) Schiffn. ssp. pycnoclada. According to VERDOORN (1934a) this species was probably a form of Ptychocoleus pynocladus, but later (VERDOORN 1934c) he considered it a synonym of Ptychocoleus aulacophorus. Examination of the type shows that it belongs to A. pycnoclada ssp. pycnoclada.
- BRACHIOLEJEUNEA ETESSEANA Steph., Spec. Hep. 5: 133 (1912) = Phaeolejeunea etesseana (Steph.) Mizut., J. Hattori Bot. Lab. 31: 133 (1968).

- BRACHIOLEJEUNEA FLAVOVIRENS Steph., Bot. Jahrb. Syst. 23: 311 (1896a), Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. KI. 85: 200 (1910), Spec. Hep. 5: 131 (1912); Bonner (1963: 450) = Thysananthus planus Sande Lac. (vide VERDOORN 1934a, 1934b, 1934c; GROLLE & SCHULTZE-MOTEL 1972 and MILLER et al. 1983).
- BRACHIOLEJEUNEA FRAUENFELDII (Reich.) Steph., Bull. Herb. Boissier 5: 847 (1897), Spec. Hep. 5: 131 (1912).
 Basionym: Thysananthus frauenfeldii Reich., in Fenzl, E. (ed.): Reise Osterr. Fregatte Novara, Bot. Theil: 155 (1870) = Mastigolejeunea frauenfeldii (Reich.) Steph. (vide VERDOORN 1934a, 1934c).
- BRACHIOLEJEUNEA GALAPAGONA (Aongstr.) Steph., Spec. Hep. 5: 139
 (1912).
 Basionym: Phragicoma galapagona Aongstr., Ofvers. Förh. Kongl. Svenska
 Vetensk.-Akad. 30(5): 114 (1873) = Marchesinia brachiata [Sw.] Schiffn.
 (vide GRADSTEIN & WEBER 1982).
- BRACHIOLEJEUNEA GIBBOSA (Aongstr.) Steph., Spec. Hep. 5: 132 (1912).
 Basionym: Lejeunea gibbosa Aongstr., Ofvers. Förh. Kongl. Svenska Vetensk.-Akad. 29(4): 23 (1872) = Mastigolejeunea frauenfeldii (Reich.) Steph. (vide VERDOORN 1934a, 1934c).
 MILLER et al. (1983) erroneously place B. gibbosa as a synonym under Lopholejeunea subnuda (Mitt.) Steph.
- BRACHIOLEJEUNEA GOTTSCHEI Schiffn., Hedwigia 33: 186 (1894) = Brachiolejeunea sandvicensis (Gott.) Evans (vide EVANS 1900) = Trocholejeunea sandvicensis (Gott.) Mizut. (cf. MIZUTANI 1962).
- BRACHIOLEJEUNEA GROSSIVITTA Steph., J. & Proc. Roy. Soc. New South Wales 48: 100 (STEPHANI & WATTS 1914); Bonner (1963: 451); Miller et al. (1983: 68) syn. nov. = Thysananthus planus Sande Lac.
- BRACHIOLEJEUNEA HANS-MEYERI Steph., Spec. Hep. 5: 118 (1912) = Blepharolejeunea securifolia (Steph.) Schust. (vide VAN SLAGEREN & KRUIJT 1985).
- BRACHIOLEJEUNEA HEUSSLERI Steph., Spec. Hep. 5: 140 (1912) = Archilejeunea olivacea (Hook. & Tayl.) Steph. (vide VERDOORN 1934a, 1934c).
- BRACHIOLEJEUNEA HILDEBRANDTII Steph., Spec. Hep. 5: 113 (1912) syn. nov. = Mastigolejeunea auriculata (Wils.) Schiffn.
- BRACHIOLEJEUNEA INFUSCATA (Mitt.) Schust., Bryologist 64: 165 (1961). Basionym: Lejeunea infuscata Mitt., J. Proc. Linn. Soc., Bot. 5: 111 (1861) = Trocholejeunea infuscata (Mitt.) Verd. (vide VERDOORN 1934c).

- BRACHIOLEJEUNEA INNOVATA Steph., Hedwigia 34: 63 (1895a) = Brachiolejeunea sandvicensis (Gott.) Evans (vide VERDOORN 1934c) = Trocholejeunea sandvicensis (Gott.) Mizut. (cf. MIZUTANI 1962).
- BRACHIOLEJEUNEA KIRKII Steph., Spec. Hep. 5: 141 (1912) = Archilejeunea scutellata (Hook. & Tayl.) Steph. (vide VERDOORN 1934a, 1934c) = Archilejeunea olivacea (Hook & Tayl.) Steph. (cf. GRADSTEIN & BUSKES 1985).
- BRACHIOLEJEUNEA LACEROSTIPULA Steph., Spec. Hep. 5: 119 (1912) syn. nov. = Marchesinia brachiata (Sw.) Schiffn.
- BRACHIOLEJEUNEA LEVIERI Steph., Spec. Hep. 5: 134 (1912) = Trocholejeunea infuscata (Mitt.) Verd. (vide VERDOORN 1934c). STEPHANI (1912 I.c.) refers for this species erroneously to SCHIFFNER's article in Hedwigia (1894) since the epithet *levieri* is nowhere mentioned there.
- BRACHIOLEJEUNEA LUMAE Herz., Beih. Bot. Centralbl. 60: 15 (1939) = Aureolejeunea lumae (Herz.) van Slageren <u>comb.</u> <u>nov</u>. Type: Chili, Calbuco, Schwabe s.n. (JE holo). The species fits into the genus Aureolejeunea Schust. as circumscribed by SCHUSTER (1978), but it is not conspecific with any one of the species described in the genus so far.
- BRACHIOLEJEUNEA MACROBRACTEOLA Pears., J. Proc. Linn. Soc., Bot. 46: 35 (1922) syn. nov. = Acrolejeunea aulacophora (Mont.) Steph.
- BRACHIOLEJEUNEA MICHOLITZII Steph., Hedwigia 34: 64 (1895a), Spec. Hep. 5: 137 (1912) = Ptychocoleus fertilis (Reinw., Blume & Nees) Trev. (vide VERDOORN 1934c) = Acrolejeunea fertilis (Reinw., Blume & Nees) Schiffn. (cf. GRADSTEIN 1974a, 1975).
- BRACHIOLEJEUNEA MIOKENSIS Steph., Spec. Hep. 5: 132 (1912) = Mastigolejeunea humilis (Gott.) Schiffn. (vide VERDOORN 1934a-c).
- BRACHIOLEJEUNEA MIYAKEANA Steph., Spec. Hep. 5: 130 (1912) = Archilejeunea mariana (Gott.) Steph. (vide VERDOORN 1934c).
- BRACHIOLEJEUNEA MOLUKKENSIS Steph., Spec. Hep. 5: 133 (1912) =
 Mastigolejeunea humilis (Gott.) Schiffn. (vide VERDOORN 1934c).
- BRACHIOLEJEUNEA NATALENSIS Sim, Trans. Roy. Soc. South Africa 15: 55 (1926) syn. nov. = Dicranolejeunea chrysophylla (Lehm.) Grolle.
- BRACHIOLEJEUNEA NIGRA (Steph.) Steph., Spec. Hep. 5: 115 (1912) = Mastigolejeunea nigra Steph., Bot. Jahr. Syst. 20: 319 (1895b) (vide

JONES 1957).

- BRACHIOLEJEUNEA NITIDIUSCULA (Gott.) Schiffn., Hedwigia 33: 186 (1894).
 Basionym: Phragmicoma nitidiuscula Gott., Ann. Sci. Nat., Ser. 5(1): 145 (1864) = Blepharolejeunea incongrua (Lindenb. & Gott.) van Slageren & Kruijt (vide VAN SLAGEREN & KRUIJT 1985).
- BRACHIOLEJEUNEA PAPILIONACEA Steph., Hedwigia 34: 64 (1895a) = Phaeolejeunea latistipula (Steph.) Mizut. (vide MIZUTANI 1968).
- BRACHIOLEJEUNEA PARAMICOLA Herz., Hedwigia 74: 95 (1934) = Omphalanthus paramicola (Herz.) Gradst., J. Hattori Bot. Lab. 50: 244 (1981).
- BRACHIOLEJEUNEA PLAGIOCHILOIDES Steph. & Spruce ex Steph., Hedwigia 28: 167 (1889), Spec. Hep. 5: 141 (1912).

Type: Australia, New South Wales, W. Watts 49 (G 20224 holo, B, BM). According to the ICBN ed. 1983 art. 42.1 note 1 the genus *Brachiolejeunea* is validly published in 1889 by STEPHANI with *B. plagiochiloides* as the type species. According to various authors (e.g. VERDOORN 1934a) the type collection of *B. plagiochiloides* is a specimen of *Archilejeunea scutellata* (Hook & Tayl.) Steph., but I consider it a form of *Spruceanthus semirepandus* (Nees) Verd. with almost entire leaves and female bracts. The genus *Brachiolejeunea* (Spruce) Schiffner 1893 needs to be conserved against *Brachiolejeunea* sensu Steph. & Spruce 1889, since otherwise the generic name *Brachiolejeunea* would become a heterotypic synonym of *Spruceanthus* Verd. (see History & Nomenclature).

- BRACHIOLEJEUNEA PLURIPLICATA Steph., Spec. Hep. 5: 135 (1912) = Spruceanthus pluriplicatus (Steph.) Gradst. in HIEPKO & SCHULTZE-MO-TEL (1981: 14).
- BRACHIOLEJEUNEA POLYGONA (Mitt.) Steph., Bull. Herb. Boissier 5: 79 (1897), Spec. Hep. 5: 138 (1912).
 Basionym: Phragmicoma polygona Mitt., Trans. Linn. Soc. London, Bot. 3: 204 (1891) = Brachiolejeunea sandvicensis (Gott.) Evans (vide VERDOORN 1934c) = Trocholejeunea sandvicensis (Gott.) Mizut. (cf. MIZUTANI 1962).
- BRACHIOLEJEUNEA RECONDITA (Steph.) Steph., Spec. Hep. 5: 134 (1912). Basionym: Ptycholejeunea recondita Steph., Hedwigia 35: 122 (1896a) = Mastigolejeunea recondita (Steph.) Mizut., J. Hattori Bot. Lab. 32: 134 (1969b).
- BRACHIOLEJEUNEA RECURVIDENTATA Chen & Wu, Acta Phytotax. Sin. 9: 225 (1964) nom. inval.

According to the ICBN art. 37.1 (VOSS et al. 1983) this species is invalidly published since no holotype is indicated. The collections on which the species is based are specimens of *Caudalejeunea reniloba* (Gott.) Steph.

- BRACHIOLEJEUNEA RETUSA Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot.: 258 (1934) = Ptychocoleus hasskarlianus (Gott.) Steph. (vide AMAKAWA 1960) = Schiffneriolejeunea tumida (Nees) Gradst. (cf. GRADSTEIN & TERKEN 1981).
- BRACHIOLEJEUNEA RHODESICA Vand. Bergh., Bull. Jard. Bot. Etat 21: 94 (1951) = Mastigolejeunea rhodesica (Vand. Bergh.) E. Jones, Trans. Brit. Bryol. Soc. 3: 196 (1957).
- BRACHIOLEJEUNEA ROBUSTA Steph., Spec. Hep. 5: 141 (1912) = Archilejeunea robusta (Steph.) Verd., Blumea 1: 222 (1934a).
- BRACHIOLEJEUNEA SANDVICENSIS (Gott.) Evans, Trans. Connecticut Acad. Arts. 10: 419 (1900). Basionym: Phragmicoma sandvicensis Gott., Ann. Sci. Nat. Bot. 4 (8): 344 (1857) = Trocholejeunea sandvicensis (Gott.) Mizut., Misc. Bryol. Lichenol. 2(12): 169 (1962).
- BRACHIOLEJEUNEA SECURIFOLIA Steph., Spec. Hep. 5: 128 (1912) = Blepharolejeunea securifolia (Steph.) Schust., Phytologia 45: 424 (1980a).
- BRACHIOLEJEUNEA SEXPLICATA Steph., Spec. Hep. 5: 136 (1912) = Brachiolejeunea sandvicensis (Gott.) Evans (vide VERDOORN 1934a, 1934c) = Trocholejeunea sandvicensis (Gott.) Mizut. (cf. MIZUTANI 1962).
- BRACHIOLEJEUNEA TORTIFOLIA Steph., Spec. Hep. 5: 135 (1912) = Ptychocoleus fertilis (Reinw., Blume & Nees) Trev. (vide VERDOORN 1934b, 1934c) = Acrolejeunea fertilis (Reinw., Blume & Nees) Schiffn. (cf. GRADSTEIN 1975).
- BRACHIOLEJEUNEA TYLIMANTHOIDES Steph., Spec. Hep. 5: 129 (1912); Miller et al. (1983: 69) = Mastigolejeunea repleta (Tayl.) Evans (vide VERDOORN 1934c).
- BRACHIOLEJEUNEA USAMBARENSIS Steph., Spec. Hep. 5: 115 (1912) = Brachiolejeunea nigra (Steph.) Steph. (vide VANDEN BERGHEN 1951) = Mastigolejeunea nigra Steph.
- LEJEUNEA (subg. BRACHIOLEJEUNEA) USTULATA (Tayl.) Steph., Hedwigia 29: 134 (1890). Basionym: Phragmicoma ustulata Tayl., Lond. J. Bot. 5: 388 (1846) = Acrolejeunea fertilis (Reinw., Blume & Nees) Schiffn. (vide GRADSTEIN 1975).
- BRACHIOLEJEUNEA WARDIANA (Mitt.) Steph., Spec. Hep. 5: 129 (1912). Basionym: Lejeunea wardiana Mitt., J. Proc. Linn. Soc., Bot. 5: 109 (1861) = Mastigolejeunea repleta (Tayl.) Evans (vide VERDOORN 1934c).

II. Taxa, not studied from type material

For various reasons, the type collection has not been available for the taxa listed here. Three categories of names are treated:

- a. names published in Brachiolejeunea (starting point for valid combinations = SCHIFFNER sept. 1893);
- b. names published in Lejeunea subg. Brachiolejeunea (Brachiolejeunea combination not available);
- c. hitherto unrevised names published in *Phragmicoma* (*Brachiolejeunea* combination not available).

BRACHIOLEJEUNEA ACUTA Winkler, Rev. Bryol. Lichénol. 35: 316 (1968). Type: El Salvador, Dep. Santa Ana, Cerro Miramundo, Winkler B/6/c/8, 23.V.1962.

The type material was unfortunately not sent on loan. Judging from the original description this species should be excluded from *Brachiolejeunea*.

BRACHIOLEJEUNEA APICULATA Steph., Bull. Herb. Boissier 5: 846 (1897). Type: Hawai, Oahu, Heller 2111 (NY-hb. Underwood (?) holo).

EVANS (1900) points out that the type of this species is inaccessible since no collection of Heller in the Underwood herbarium in NY is to be found, designated as type by Stephani. EVANS (I.c.) judged, from the drawings of the plant by Stephani, that "the plant is very close to *Thysananthus elongatus* and may be a form of it". According to VERDOORN (1934c) *Thysananthus elongatus* (Aust.) Evans (and its probably heterotypic synonym *B. apiculata*) is a synonym of *Spruceanthus polymorphus* (Sande Lac.) Verd.

BRACHIOLEJEUNEA BROTHERI Steph. ex Bonner, Index Hep. 3: 447 (1963) nom. nud.

This herbarium name was unfortunately published by BONNER. The collection in the Stephani herbarium on which the name is based (Australia, Queensland, Brotherus 867; G 20098) is a specimen of *Spruceanthus semirepandus* (Nees) Verd.

LEJEUNEA (subg. BRACHIOLEJEUNEA) CALEDONICA Steph., Hedwigia 28: 167 (1889) nom. nud.

This undescribed species is only present in a list of "Brachiolejeunea" species by STEPHANI, by that time still to be considered as a subgenus of *Lejeunea* in the Sprucean sense, as is recently advocated by ZIJLSTRA (1982) and GRADSTEIN et al. (1982).

BRACHIOLEJEUNEA JAPONICA Gott. ex Steph., Bull. Herb. Boissier 5: 842 (1897) nom nud.

Basionym: *Phragmicoma japonica* Gott. in sched., Hedwigia 28: 257 (1889). The basionym is present in a list of *"Mastigolejeunea"* species by STEPHANI (1889). SCHIFFNER (1894: 186) points out that Stephani was erroneous in placing the name P. *japonica* in *Mastigolejeunea* and makes it a synonym of his newly described *B. gottschei* Schiffn. According to the ICBN art. 32.1(c) (VOSS et al. 1983) the combination in *Brachiolejeunea* is invalid.

According to EVANS (1900) *B. japonica* is a synonym of *Brachiolejeunea* sandvicensis (Gott.) Evans (= *Trocholejeunea* sandvicensis (Gott.) Mizut. cf. MIZUTANI 1962).

BRACHIOLEJEUNEA OCEANICA (Mitt.) Mill., Whitt. & Whitt., Bryophyt. Biblioth. 25: 69 (1983).
Basionym: Lejeunea oceanica Mitt., in Seemann, B.: Flora Vitiensis: 414 (1865-73) = Ceratolejeunea oceanica (Mitt.) Steph.

BRACHIOLEJEUNEA PARVA (Steph.) S. Arnell, Svensk Bot. Tidskr. 57: 192 (1963b), non Herzog 1951, comb. illeg. Basionym: Ptychocoleus parvus Steph., Spec. Hep. 5: 50 (1912). Ptychocoleus parvus is a synonym of Acrolejeunea securifolia (Endl.) Watts ex Steph. ssp. securifolia (vide GRADSTEIN 1975).

BRACHIOLEJEUNEA PARVISTIPULA Steph. ex Bonner, Index. Hep. 3: 457 (1963) nom. nud.

This herbarium name was unfortunately published by BONNER. The collection in the Stephani herbarium on which the name is based (India, Udipi, Pfeiderer 29, 1913; G 20223) is a specimen of *Archilejeunea mariana* (Gott.) Steph.

BRACHIOLEJEUNEA POLYMORPHA (Sande Lac.) Mill., Whitt. & Whitt., Bryophyt. Biblioth. 25: 69 (1983).

Basionym: *Phragmicoma polymorpha* Sande Lac., Ned. Kruidk. Archief 3: 420 (1855).

Lejeunea (subg. Brachiolejeunea) polymorpha (Sande Lac.) Steph., Hedwigia 28: 168 (1889) = Spruceanthus polymorphus (Sande Lac.) Verd., Ann. Bryol. Suppl. 4: 155 (1934c).

PHRAGMICOMA QUADRICRENATA Gott. ex Steph., Hedwigia 28: 168 (1889) nom. nud.

The name is published in a list of "*Brachiolejeunea*" species by STEPHANI. Type material and description are nowhere mentioned.

BRACHIOLEJEUNEA SCHWABEI Herz., Rev. Bryol. Lichénol. 23: 60 (1954), Solari (1983): 526.

Type: Chile, Fray Jorge, im Kammwald, Schwabe 194 p.p. (not seen). = Blepharolejeunea securifolia (Steph.) Schust. (vide VAN SLAGEREN & KRUIJT 1985). BRACHIOLEJEUNEA THOZETIANA (Gott. & Müll.) Steph., Spec. Hep. 5: 142 (1912).

Basionym: *Phragmicoma thozetiana* Gott. & Müll., Fragm. Phyt. Austr., suppl. ad Vol. XI: 63 (1880).

Type: Australia, near Keppel's Bay, Thozet s.n.

VERDOORN (1934a, 1934c) type material was "nicht aufzufinden". If it had been in B, it was destroyed in 1945. Judging from the original description this is probably a species of *Thysananthus*.

BRACHIOLEJEUNEA WATTSIANA Steph. ex Verd., Blumea 1: 222 (1934a) nom. nud.

According to VERDOORN (1934a, 1934c) this species is synonym with *Mastigolejeunea phaea* Gott. ex Steph., but a description and a type collection are nowhere mentioned.

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Plate I. Stem transverse section of *Brachiolejeunea*, *Frullanoides* and related genera.

Fig. 1. Acrolejeunea fertilis. Fig. 2. Acrolejeunea torulosa. Fia. 3. Dicranolejeunea aberrans. Fig. 4. Trocholejeunea sandvicensis. Fia. 5. Blepharolejeunea securifolia. Fig. 6. Dicranolejeunea axillaris. Fia. 7. Frullanoides liebmanniana. Fig. 8. Frullanoides corticalis, showing origin of Lejeunea-type branch. Fig. 9. Brachiolejeunea fernandeziana. Fig. 10. Brachioleieunea laxifolia. Fig. 11. Mastigolejeunea humilis. Fig. 12. Mastigolejeunea nigra. Fig. 13. Lindigianthus cipaconeus.

Fig. 1 from Sipman 6883, Singapore. Fig. 2 from Prance et al. 11729b, Brazil. Fig. 3 from Eggers & Frahm 32, Mexico. Fig. 4 from Faurie 240, Hawaii. Fig. 5 from Philippi P-253, Peru. Fig. 6 from Sipman 11935, Costa Rica. Fig. 7 from Liebmann 197, Mexico. Fig. 8 from Spellman & Stoddart B128b, Belize. Fig. 9 from Kunkel H298, Chili. Fig. 10 from Cleef 1170, Colombia. Fig. 11 from Gradstein et al. 3833, Papua New Guinea. Fig. 12 from van Meel s.n., Tanzania. Fig. 13 from Aguirre 1520, Colombia.

D = dorsal; la = lamella; Lb = Lejeunea-type branch initial cell; lbr = leaf brace-cells; V = ventral.



Plate II. Stem longitudinal section and underleaf attachment in Brachiolejeunea, Frullanoides and related genera.

Fig. 1. Acrolejeunea fertilis. Fig. 2. Trocholejeunea infuscata. Fig. 3. Dicranolejeunea aberrans. Fig. 4. **Frullanoides** mexicana. Fig. 5. Fig. 6. Dicranolejeunea axillaris. Blepharolejeunea securifolia. Fig. 7. Blepharolejeunea Mastigoleieunea nigra. Fig. 8. securifolia. Fia. 9. Brachiolejeunea Frullanoides tristis. Fia. 10. leiboldiana . Fia. 11. Brachiolejeunea fernandeziana, Fig. 12. Blepharolejeunea incongrua, Fig. 13. Brachiolejeunea leiboldiana, Fig. 14. Lindigianthus cipaconeus.

Fig. 1 from Sipman 6883, Singapore. Fig. 2 from Sureil s.n., Sikkim. Fig. 3 from Eggers & Frahm 32, Mexico. Fig. 4 from Eggers & Frahm MX 22.7, Mexico. Fig. 5 from Cleef 942a, Colombia. Fig. 6 from Sipman 11935, Costa Rica. Fig. 7 from van Meel s.n., Tanzania. Fig. 8 from Bischler 2795, Colombia. Fig. 9 from Liebmann 456b, Mexico. Fig. 10 from Leibold s.n., Mexico. Fig. 11 from Kunkel H298, Chili. Fig. 12 from Aguirre & Gradstein 1326, Colombia. Fig. 13 from Schiffner 1521, Brazil. Fig. 14 from Spruce s.n., Ecuador.

i = inferior central cell; i.l. = intermediate cell layer; mc = modified cortex cell; r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate III. Frullania-type branch appendages in Brachiolejeunea, Frullanoides and related genera.

Figs. 1-2. First branch underleaf. Fig. 3. Dorsal stem half-leaf. Figs. 4-6. First branch acroscopic leaf (Figs. 1-6 Acrolejeunea emergens). Figs. 7-8. First branch underleaf. Fig. 9. Dorsal stem half-leaf. Figs. 10-13. First branch acroscopic leaf (Figs. 7, 9, 12-13 Trocholejeunea infuscata; Figs. 8, 10-11 Trocholejeunea sandvicensis), Figs, 14-16, First branch underleaf, Figs, 17-18, Dorsal stem half-leaf, Figs, 19-20, First branch acroscopic leaf (Figs. 14, 16-17, 20 Frullanoides densifolia; Figs. 15, 18-19 Frullanoides bahamensis). Fig. 21. First branch underleaf. Fig. 22. Dorsal stem half-leaf. 23-24. First branch acroscopic leaf (Figs. 21-24 Brachiolejeunea Figs. laxifolia). Figs. 25-27. First branch underleaf. Fig. 28. Dorsal stem half-leaf. Figs. 29-32. First branch acroscopic leaf (Figs. 25, 29 Dicranolejeunea phyllorhiza; Figs. 26-28, 30-32 Dicranolejeunea axillaris). Figs. 33, 35, 41. Dorsal stem half-leaf. Figs. 34, 36, 39-40. First branch underleaf. Figs. 37-38, 42-43. First branch acroscopic leaf (Figs. 33-34, 37 Blepharolejeunea saccata; Figs. 35-36, 38 Blepharolejeunea fuegiana; Figs. 39-43 Blepharolejeunea securifolia). Fig. 44. First branch underleaf. Fig. 45. First branch acroscopic leaf (Figs. 44-45 Lindigianthus cipaconeus).

Figs. 1, 4 from Vital 2647, Brazil. Figs. 2-3, 5-6 from Vital 6424, Brazil. Figs. 7, 13 from Kitagawa T 12176, Thailand. Figs. 8, 10-11 from Tagawa & Kitagawa T 1344, Thailand. Figs. 9, 12 from Sureil s.n., Sikkim. Figs. 14, 16-17, 20 from Weberbauer 736, Peru. Figs. 15, 18-19 from Small 7557, U.S.A. Figs. 21-24 from Cleef 1170, Colombia. Figs. 25, 29 from Claziou 7404, Brazil. Figs. 26-28, 30-32 from Sipman 11935, Costa Rica. Figs. 33-34, 37 from Reyes 967, Cuba. Figs. 35-36, 38 from Hooker s.n., Chili. Figs. 39-43 from Cleef 1990, Colombia. Figs. 44-45 from Aguirre 1520, Colombia.



Plate IV. Gynoecia and sporophyte in *Brachiolejeunea*, *Frullanoides* and *Trocholejeunea*.

Fig. 1. Archegonium and archegonial neck. Fig. 2. Juvenile perianth and protruding archegonial neck. Fig. 3. Juvenile perianth and archegonium *in situ*, showing also female bracts and remnants of the subgynoecial underleaf (bracteole removed). Fig. 4. Antheridium and antheridial stalk. Fig. 5. Male bract with two antheridia. Figs. 6-7. Theca longitudinal section. Figs. 8-9. Young seta cross section (calyptra partially drawn). Fig. 10. Seta cross section of *Trocholejeunea infuscata*, showing irregular arrangement of the cells of the inner and outer layer. Fig. 11. Seta cross section of *Trocholejeunea sandvicensis*.

Figs. 1-2 from Frullanoides densifolia, Onraedt 83.A.10317, Colombia. Fig. 3 from Frullanoides densifolia, Frahm et al. 507, Peru. Figs. 4-5 from Frullanoides densifolia, Aguirre et al. 6363, Colombia. Figs. 6, 8 from Frullanoides tristis, E. & P. Hegewald 7885, Peru. Fig. 7 from Brachiolejeunea laxifolia, Aguirre & Gradstein 1630, Colombia. Fig. 9 from Brachiolejeunea laxifolia, Cleef 1170, Colombia. Fig. 10 from Trocholejeunea infuscata, Sureil s.n., Sikkim. Fig. 11 from Trocholejeunea sandvicensis, Pócs 4574, Vietnam.

a = archegonial neck; b = beak; br = bract; ca = calyptra; p = perianth; sgu = (remnants of) subgynoecial underleaf; tli = theca layer: inner; tlo = theca layer: outer; w = (bract) wing.



Plate V. Sporophyte in Brachiolejeunea and Frullanoides.

Fig. 1. General aspect of a young sporophyte, attached to the stem. Fig. 2. Detailed aspect of the attachment of a sporophyte to the stem, showing a thickened base of the perianth and a short calyptral foot. Fig. 3. Detailed aspect of a closed, young sporophyte. Fig. 4. Detailed aspect of the apical part of the calyptra and the young sporophyte, showing archegonial neck and theca layers.

Fig. 1 from F. tristis, E. & P. Hegewald 7885, Peru. Fig. 2 from B. laxifolia, Aguirre & Gradstein 1630, Colombia. Figs. 3-4 from B. laxifolia, Frahm et al. 1248, Peru.

a = archegonial neck; b = beak; br = bract; bra = bracteole; c = cortex; ca = calyptra; cs = calyptral stalk; e = (location of) elater; f = foot of sporophyte; l = leaf; la = (dorsal) lamella; m = medulla; p = perianth; pb = perianth base; r = rhizoid; s = superior central cell; se = seta; sgl = subgynoecial leaf; sgu = subgynoecial underleaf; sp = spores; t = theca; tli = theca layer: inner; tlo = theca layer: outer; u = lowermost underleaf lamina cell; un = underleaf.

All figures are longitudinal sections; black area between calyptra and sporophyte in Fig. 2 due to preparation.



Plate VI. Sporeling development in Brachiolejeunea and Frullanoides.

Fig. 1. Germinating spore, showing young sporeling (\pm 7 days). Fig. 2. Germinating spore, showing sporeling and rhizoid development (\pm 7 days). Fig. 3. Sporeling, showing three primary leaves and one juvenile leaf (\pm 19 days). Fig. 4. Sporeling, showing three primary leaves, two juvenile leaves and first underleaf (\pm 30 days). Note well developed hyaline papillae (hp). Fig. 5. (major part of) Sporeling, showing primary and juvenile leaves as well as several series of adult leaves. Note spiral segmentation of the adult leaves (\pm 90 days). Figs. 6-7. Sporeling, showing five primary leaves.

Figs. 1-4 from *Brachiolejeunea leiboldiana*, Aguirre et al 2956, Colombia. Fig. 5 from *Brachiolejeunea leiboldiana*, Aguirre & Gradstein s.n., Colombia. Figs. 6-7 from *Frullanoides tristis*, van der Werff 1702, Galapagos Islands.

hp = hyaline papilla; ju = juvenile leaf; pr = primary leaf; r = rhizoid.

Figs. 1-5: Lejeunea-type sporeling; Figs. 6-7: Lopholejeunea-type sporeling.



Plate VII. Brachiolejeunea fernandeziana S. Arn.

Fig. 1a. Habitus with male bracts, perianths and a *Lejeunea*-type branch. Fig. 1b. Habitus with *Frullania*-type branch. Fig. 2. Mid leaf cells. Fig. 3. Stem transverse section, showing tendency towards a dorsal lamella (arrow). Fig. 4. Stem transverse section with underleaf attachment and offspring of a *Frullania-Bleparolejeunea*-type branch. Fig. 5. Male bract and lobule in detail. Fig. 6. Underleaf. Fig. 7. Leaf with lobule in detail. Fig. 8. Inner view of leaf lobule at apical tooth, showing hyaline papilla.

Figs. 1a, 2-8 from Kunkel H298, Chili, type collection of *B. fernandeziana*. Fig. 1b from Sparre H 54, Chili.

a = apical tooth; Lb = Lejeunea-type branch; r = rhizoid; s = superior central cell; u = underleaf.


Plate VIII. Figs. 1-2 Brachiolejeunea fernandeziana S. Arn. Figs. 3-7 Brachiolejeunea laxifolia (Tayl.) Schiffn.

Fig. 1. Female bracts and bracteole. Fig. 2. Stem longitudinal section. Fig. 3. Stem longitudinal section, showing dorsal lamellae. Fig. 4. Dorsal aspect of the leafy appendages at a *Frullania*-type branch (dorsal stem half-leaf removed except the insertion). Fig. 5. Underleaf, ventral aspect. Fig. 6. Underleaf, dorsal aspect. Fig. 7. Detailed aspect of dorsal lamella.

Figs. 1-2 from Kunkel H298, Chili, type collection of *B. fernandeziana*. Fig. 3 from Aguirre & Gradstein 1630, Colombia. Figs. 4, 7 from Bischler 1723, Colombia. Figs. 5-6 from Cleef 1170, Colombia.

a = lower lamella cell; al = first branch acroscopic leaf; c = cortex; dli = dorsal leaf insertion; la = lamella; lo = lobe; r = rhizoid; s = superior central cell; u = underleaf lamina cell; ul = first branch underleaf.



Plate IX. Brachiolejeunea laxifolia (Tayl.) Schiffn.

Fig. 1a. Stem transverse section, showing several thickened outer layers. Fig. 1b. Detailed aspect of section of fig. 1a, showing layered structure of the wall thickenings. Fig. 2. Stem transverse section with underleaf attachment. Fig. 3. Male bract. Fig. 4. Leaf with lobule in detail. Fig. 5. Mid leaf cells with *Massula*-type oil bodies. Fig. 6. Transverse sections of the perianth through upper 1/3 (left) and \pm midway (right). Fig. 7. Habitus; arrow pointing at perianth with only one innovation Fig. 8. Ventral stem cortex, showing thickened walls and very small oil bodies.

Fig. 1a-b from Mandon 796, Bolivia. Figs. 2, 5, 8 from Gradstein & Aguirre 3642a, Colombia. Fig. 3 from Cleef 1170, Colombia. Figs. 4, 6 from Bischler 2312, Colombia. Fig. 7 from Frahm et al. 1248, Peru.

a = apical tooth; la = lower lamella cell; r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate X. Figs. 1-5 Brachiolejeunea laxifolia (Tayl.) Schiffn. Figs. 6-10 Brachiolejeunea leiboldiana (Gott. & Lindenb.) Schiffn.

Fig. 1. Stem transverse section, showing eight ventral merophyte cells (u = underleaf). Fig. 2. Dorsal aspect of female bracts and perianth, showing insertion of the bract wings on the dorsal-lateral side of the stem (arrows). Fig. 3. Female bracteole. Fig. 4. Female bract. Fig. 5. *Frullania*-type branch appendages: 5a dorsal stem half-leaf; 5b first branch acroscopic leaf; 5c first branch underleaf. Fig. 6. Female bracts at two innovations. Fig. 7. Female bract and modified stem leaf at one innovation. Fig. 8. Female bracteole. Fig. 9. Female bract. Fig. 10. Underleaf.

Figs. 1-4 from Cleef 1170, Colombia. Fig. 5 from Hermann 24701, Bolivia. Figs. 6, 9 from Leibold s.n., Mexico. Figs. 7-8, 10 from Aguirre et al. 2956, Colombia.



Plate XI. Brachiolejeunea leiboldiana (Gott. & Lindenb.) Schiffn.

Fig. 1. Habitus, showing frequent occurrence of only one innovation. Fig. 2. Stem transverse section with underleaf attachment and one cell high lamella. Fig. 3. Stem transverse section. Fig. 4. Apical part of perianth, showing sulcate ventral plica. Fig. 5. Leaf with lobule in detail. Fig. 6. Inner aspect of leaf lobule, showing hyaline papilla.

Fig. 1 from Aguirre et al. 2956, Colombia. Figs. 2, 4 from Leibold s.n., Mexico. Figs. 3, 6 from Liebmann 191, Mexico. Fig. 5 from Leibold s.n., Mexico, type collection of *B. leiboldiana*.

a = apical tooth; hp = hyaline papilla; la = lamella; s = superior central cell.



Plate XII. Figs. 1-5 Brachiolejeunea spruceana (Mass.) Schiffn. Figs. 6-10 Brachiolejeunea leiboldiana (Gott. & Lindenb.) Schiffn.

Fig. 1. Leaf with lobule in detail. Fig. 2. Female bracteole. Fig. 3. Female bract. Fig. 4. *Frullania*-type branch appendages: 4a first branch underleaf; 4b dorsal stem half-leaf; 4c first branch acroscopic leaf. Fig. 5. Male bract with lobule in detail. Figs. 6-7. Stem longitudinal sections, showing underleaf attachments. Fig. 8. Apical part of perianth. Fig. 9. Transverse section of perianth in upper 1/3. Fig. 10. Mid leaf cells.

Figs. 1, 5 from Cunningham s.n., Chili. Figs. 2-3 from Hosseus 524 p.p., Chili. Fig. 4 from Schwabe 74 p.p., Chili. Fig. 6 from Schiffner 1591, Brazil. Figs. 7, 10 Leibold s.n., Mexico, type collection of *B. leiboldiana*. Figs. 8-9 from Liebmann 191, Mexico.

a = apical tooth; D = dorsal; dli = dorsal leaf insertion; la = lamella; r = rhizoid; s = superior central cell; u = underleaf lamina cell; V = ventral.



Plate XIII. Brachiolejeunea spruceana (Mass.) Schiffn.

Fig. 1. Habitus. Fig. 2. Stem transverse section with underleaf attachment and tendency towards a dorsal lamella (arrow). Fig. 3. Stem transverse section, showing tendency towards a dorsal lamella (arrow). Fig. 4. Mid leaf cell. Fig. 5. Stem longitudinal section. Fig. 6. Underleaf.

Figs. 1-2 from Dusén 466, Chili. Fig. 3 from Bachman s.n., Chili. Figs. 4-6 from Cunningham s.n., Chili. Fig. 5 from Dusén s.n., Chili.

r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate XIV. Frullanoides bahamensis (Evans) van Slageren.

Fig. 1. Habitus, showing *Lejeunea*-type branches. Fig. 2. Stem transverse section with underleaf attachment. Fig. 3. Mid leaf cells. Fig. 4. Underleaf (detailed outline of basis present on Pl. XV, fig. 4). Fig. 5. Female bracts, female bracteole and perianth. Fig. 6. Stem longitudinal section. Fig. 7. Stem transverse section. Fig. 8. Leaf with lobule in detail. Fig. 9. Male bract with lobule in detail.

Figs. 1-5, 8-9 from Britton 584 p.p., Bahamas. Figs. 6-7 from Small 7557, U.S.A.

a = apical tooth; Lb = Lejeunea-type branch; r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate XV. Figs. 1-5 Frullanoides bahamensis (Evans) van Slageren. Figs. 6-14 Frullanoides tristis (Steph.) van Slageren.

Fig. 1. Leaves and underleaf. Fig. 2. Female bract and bracteole. Fig. 3. Female bract. Fig. 4. Detailed aspect of the base of an underleaf; note the absence of auricles (arrows). Fig. 5. Subgynoecial underleaf. Fig. 6. Male bract. Fig. 7. Underleaf (detailed outline of the basis with auricles on Pl. XVI, fig. 6). Fig. 8. Leaf with lobule in detail (a = apical tooth). Fig. 9. Leaf lobule (a = apical tooth). Fig. 10. Apical part of perianth. Fig. 11. Female bract and juvenile perianth. Fig. 12. Female bracteole. Fig. 13. Subgynoecial underleaf. Fig. 14. Female bract. Note the insertion of the lobule.

Figs. 1-2 from Britton 562, Bahamas. Figs. 3-5 from Britton 584 p.p., Bahamas. Figs. 6-8, 11-14 from Bosman s.n., South Africa. Fig. 9 from E. & P. Hegewald 7885, Peru. Fig. 10 from an unknown collector, Surinam.



Plate XVI. Frullanoides tristis (Steph.) van Slageren.

Fig. 1. Habitus. Fig. 2. Transverse section through the upper part of the perianth. Fig. 3. Mid leaf cells. Figs. 4-5. Stem transverse section with underleaf attachment. Fig. 6. Detailed aspect of underleaf basis with auricles and rhizoid disc. Fig. 7. Stem longitudinal section.

Figs. 1, 5 from E. & P. Hegewald 7885, Peru. Figs. 2, 7 from Liebmann 456b, Mexico. Figs. 3, 6 from Bosman s.n., South Africa. Fig. 4 from Sim 9773, South Africa.

D = dorsal; r = rhizoid; s = superior central cell; u = underleaf lamina cell; V = ventral.



Plate XVII. Frullanoides corticalis (Lehm. & Lindenb.) van Slageren.

Fig. 1a. Habitus of female plants. Fig. 1b. Habitus of male plants. Fig. 2. Female bract and subgynoecial leaf. Fig. 3. Female bracteole. Fig. 4. Subgynoecial underleaf. Fig. 5. *Frullania*-type branch appendages: 5a first branch underleaf; 5b first branch acroscopic leaf; 5c dorsal stem half-leaf. Fig. 6. Underleaf. Fig. 7. Transverse section of the perianth through the upper 1/3 (7a) and \pm midway (7b). Fig. 8. All male bracts of a single spike, showing variation in outline of the lobule and in size of the lobe. Fig. 9. Stem transverse section with *Lejeunea*-type branch.

Figs. 1, 7-9 from Spellman & Stoddart B128b, Belize. Figs. 2-6 from Leprieur 273, French Guyana.

Lb = Lejeunea-type branch initial cell; lbr = leaf brace cells.



Plate XVIII. Figs. 1-3 Frullanoides corticalis (Lehm. & Lindenb.) van Slageren. Figs. 4-7 Frullanoides densifolia Raddi.

Fig. 1. Stem longitudinal section. Fig. 2. Mid leaf cells. Fig. 3. Leaf with lobule in detail. Fig. 4. Stem longitudinal section. Fig. 5. Stem transverse section, showing 14 ventral merophyte cells. Figs. 6-7. Thickenings of ventral cortical cell walls.

Fig. 1 from Spellman & Stoddart B128b, Belize. Figs. 2-3 from Evans 337, Jamaica. Fig. 4 from Herzog 5857, Bolivia. Fig. 5 from Spruce s.n., Ecuador. Fig. 6 from Puiggari s.n., Brazil. Fig. 7 from Frahm et al. 1148, Peru.

a = apical tooth; r = rhizoid; s = superior central cell; u = underleaf lamina cell; ul = underleaf.



Plate XIX. Frullanoides densifolia Raddi.

Fig. 1. Habitus of male plant. Fig. 2. *Frullania*-type branch appendages: 2a first branch underleaf; 2b dorsal stem half-leaf; 2c first branch acroscopic leaf. Fig. 3. Female bract. Fig. 4. Female bracteole. Fig. 5. Subgynoecial underleaf. Fig. 6. Stem longitudinal section. Fig. 7. Underleaf. Fig. 8. Stem transverse section with underleaf attachment.

Fig. 1 from Puiggari s.n., Brazil. Fig. 2 from Weberbauer 736, Peru. Figs. 3-5 from Frahm et al. 1148, Peru. Fig. 6 from Herzog 3365, Bolivia. Fig. 7 from Herzog 5857, Bolivia. Fig. 8 from Sipman 11941, Costa Rica.

r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate XX. Frullanoides densifolia Raddi: Figs. 1-4 ssp. densifolia. Figs. 5-10 ssp. grandidentata (Clark) van Slageren.

Fig. 1. Male bract. Fig. 2. Leaf with lobule in detail. Figs. 3-4. Underleaves. Fig. 5. Male bract. Fig. 6. Leaf with lobule in detail. Fig. 7. Underleaf. Fig. 8. Inner aspect of the leaf lobule, showing hyaline papilla. Fig. 9. Habitus. Fig. 10. Detailed outline of the underleaf base of fig. 7, showing small auricles (arrows).

Figs. 1-2 from Puiggari s.n., Brazil. Fig. 3 from Sipman 11941, Costa Rica. Fig. 4 from Frahm et al. 1148, Peru. Figs. 5-8, 10 from Gradstein & Weber H11, Galapagos Islands. Fig. 9 from Gradstein & Weber H485, Galapagos Islands.

a = apical tooth; hp = hyaline papilla.



Plate XXI. Figs. 1-3 Frullanoides densifolia Raddi. Figs. 4-9 Frullanoides laciniatiflora (Loitl.) van Slageren.

Fig. 1. Habitus of female plant. Fig. 2. Mid leaf cells. Fig. 3. Transverse section of perianth. Fig. 4. Underleaf. Figs. 5-6. Female bracteoles. Fig. 7. Female bract. Fig. 8. Subgynoecial underleaf showing variation in dentation of the apical region (8a-b). Fig. 9. Female bract.

Fig. 1 from Frahm et al. 1148, Peru. Fig. 2 from Puiggari s.n., Brazil. Fig. 3 from van Reenen et al. 1559, Colombia. Figs. 4, 8a from Killip & Smith 22229, Peru. Figs. 5, 7, 8b from Frahm et al. 744, Peru. Figs. 6, 9 from Jelski 535, Peru.



Plate XXII. Frullanoides laciniatiflora (Loitl.) van Slageren.

Fig. 1. Habitus of female plant. Fig. 1b. Habitus of male plant. Fig. 2. Mid leaf cells. Fig. 3. Stem transverse section, showing 14 ventral merophyte cells and the insertion of the underleaf auricles. Fig. 4. Stem longitudinal section. Fig. 5. Male bract. Fig. 6. Thickenings of the ventral cortical cell walls. Fig. 7a. Leaf with lobule in detail. Fig. 7b. Apex of leaf of Fig. 7a. Fig. 8. Apical part of leaf margin, showing dentation.

Figs. 1a-b, 4, 7a-b from Jelski 536, Peru, type collection of *F. laciniati-flora*. Figs. 2, 5 from Jelski 535, Peru. Figs. 3, 6 from Killip & Smith 22229, Peru. Fig. 8 from Frahm et al. 744, Peru.

a = apical tooth; r = rhizoid; s = superior central cell; u = underleaf lamina cell; ue = underleaf ears.



Plate XXIII. Frullanoides liebmanniana (Lindenb. & Gott.) van Slageren.

Fig. 1a. Habitus of female plant. Fig. 1b. Habitus of male plant. Fig. 2. Stem transverse section with underleaf attachment. Fig. 3. *Frullania*-type branch appendages: 3a first branch underleaf; 3b dorsal stem half-leaf; 3c first branch acroscopic leaf. Fig. 4. Leaf with lobule in detail. Fig. 5. Inner aspect of leaf lobule, showing location of hyaline papilla. Fig. 6. Male bract. Fig. 7. Mid leaf cells. Fig. 8. Stem transverse section.

Fig. 1a from Weir s.n., Colombia. Figs. 1b-4, 6-8 from Schiffner 2231, Brazil. Fig. 5 from Liebmann 197, Mexico, type collection of *F. liebmanniana*.

a = apical tooth; r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate XXIV. Figs. 1-7 Frullanoides liebmanniana (Lindenb. & Gott.) van Slageren. Figs. 8-11 Frullanoides mexicana van Slageren.

Fig. 1. Detailed aspect of the underleaf base, showing relatively small auricles (underleaf of Fig. 5) Figs. 2-3 Female bracts. Fig. 4. Transverse section of perianth. Fig. 5. Underleaf. Fig. 6 Subgynoecial underleaf. Fig. 7. Female bracteole. Fig. 8. Stem longitudinal section Fig. 9. Mid leaf cells. Fig. 10. Stem transverse section with underleaf attachment. Fig. 11. Stem transverse section.

Figs. 1-2, 5-7 from Fendler s.n., Trinidad. Fig. 3. from Micholitz s.n., Colombia. Fig. 4. from Weir s.n., Colombia. Figs. 8-11 from Eggers & Frahm 792229, Mexico, type collection of *F. mexicana*.

r = rhizoid; s = superior central cell; u = underleaf.



Plate XXV. Frullanoides mexicana van Slageren.

Fig. 1. Habitus of male plant. Fig. 2. *Frullania*-type branch appendages: 2a first branch underleaf; 2b dorsal stem half-leaf; 2c first branch acroscopic leaf. Fig. 3. Male bract. Fig. 4. Subgynoecial underleaf. Fig. 5. Underleaf. Fig. 6. Detailed aspect of the underleaf base of Fig. 5, showing small auricles (arrows).

Figs. 1-6 from Eggers & Frahm 792229, Mexico, type collection of *F. mexi-cana*.


Plate XXVI. Frullanoides mexicana van Slageren.

Fig. 1. Habitus of female plant. Fig. 2. Apex of perianth. Fig. 3. Young seta with irregular arrangement of the outer cell rows and part of the calyptra base. Fig. 4. Female bracteole. Fig. 5. Leaf with lobule in detail. Figs. 6-7. Female bracts. Fig. 8. Inner aspect of leaf lobule, showing hyaline papilla. Fig. 9. Transverse section of perianth.

Figs. 1, 3-8 from Eggers & Frahm 792625, Mexico, Figs. 2, 9 from Standley 54526, Honduras.

a = apical tooth; c = calyptra; s = seta.





- 1. 🔵 = B. leiboldiana.
- 2.
 = B. laxifolia (doubtful West African record not shown).
- B. spruceana.
 B. fernandeziana.

XXVII



Plate XXVIII. Distribution of Frullanoides Raddi.

- 1. = F. corticalis. = F. laciniatiflora.
- 2. = F. liebmanniana. ■ = F. mexicana.

XXVIII



Plate XXIX. Distribution of Frullanoides Raddi.

- F. densifolia ssp. densifolia.
 ▲ = F. densifolia ssp. grandidentata.
 = F. bahamensis.
- 2. = F. tristis.

XXIX



Plate XXX. Sporophyte of Brachiolejeunea.

Fig. 1. Two values outer surface, showing elaters and articulate seta. Note small areas with evenly distributed cell wall thickenings (arrow) (bar = 200 μ m). Fig. 2. Apical part of value outer surface (bar = 40 μ m). Figs. 3-4. Value inner surface, showing marginal elaters (m.e.) and additional elaters (a.e.) (bar = 100 μ m). Fig. 5. Value lateral margin, showing theca outer layer (wrinkled surface), inner layer (open) and elater attachment (bar = 10 μ m). Fig. 6. Lateral part of a longitudinal section of a closed capsule (bar = 40 μ m).

Figs. 1, 4-5 from Aguirre & Gradstein 1630, Colombia. Fig. 2 from Dusén s.n., Chili. Fig. 6 from Gradstein et al. 3389, Ecuador.

Figs. 1, 3-6 = B. laxifolia; Fig. 2 = B. spruceana.

XXX



Plate XXXI. Sporophyte of Brachiolejeunea.

Fig. 1. Capsule longitudinal section (bar = 100 μ m). Fig. 2. Detail from central part of a longitudinal section of a capsule, showing spore storage (bar = 20 μ m). Fig. 3. Capsule transverse section, showing elater arrangement (bar = 200 μ m). Fig. 4. Detail of Fig. 3, showing marginal elaters (m.e.) and additional elaters (a.e.). Note attachment location (a.l.) of spores (bar = 100 μ m). Figs. 5-6. Spore ornamentation, showing tendency towards rosette formation in *B. spruceana* (Fig. 5: bar = 2 μ m; Fig. 6: bar = 4 μ m).

Fig. 1 from Aguirre & Gradstein 1630, Colombia. Fig. 2 from Gradstein et al. 3389, Ecuador. Figs. 3-4 from Frahm et al. 1248, Peru. Fig. 5 from Gradstein & Aguirre 3570a, Colombia. Fig. 6 from Dusén 466, Chili.

Figs. 1-5 = B. laxifolia; Fig. 6 = B. spruceana.

XXXI



Plate XXXII. Sporophyte of Frullanoides and Spruceanthus.

Fig. 1. Two valves outer surface. Note small areas with evenly distributed cell wall thickenings (arrow) (bar = 200 μ m). Fig. 2. Apical part of valve outer surface (bar = 40 μ m). Fig. 3. Valve inner surface (bar = 100 μ m). Fig. 4. Apical part of valve inner surface, showing elater attachment (e.a.) (bar = 40 μ m). Fig. 5. Central and basal part of valve inner surface, showing longitudinal ridges (l.r.) (bar = 100 μ m). Fig. 6. Basal part of capsule, showing longitudinal ridges (l.r.), protruding into the capsule base, and a smooth surface of the capsule base with "footprints" of elaters (bar = 40 μ m).

Figs. 1, 4 from E. & P. Hegewald 7885, Peru. Fig. 2 from Schiffner 1552, Brazil. Fig. 3 from Pócs 9056/J, Cuba. Fig. 5 from Reyes 732, Cuba. Fig. 6 from Gradstein 3811, Papua New Guinea.

Figs. 1, 4 = F. tristis; Fig. 2 = F. densifolia; Fig. 3 = F. bahamensis; Fig. 5 = F. corticalis; Fig. 6 = Spruceanthus polymorphus.

XXXII



Plate XXXIII. Sporophyte of Frullanoides.

Fig. 1. Capsule longitudinal section (bar = 40 μ m). Fig. 2. Part of capsule longitudinal section, showing regular arrangement of spores and elaters (bar = 40 μ m). Fig. 3. Detail of Fig. 2, showing three spores of a tetrad and their attachment location (a.l.) (bar = 20 μ m). Fig. 4. Base of capsule, showing regular arrangement of elaters, similar to "footprints" of Plate XXXII, fig. 6 (bar = 40 μ m). Fig. 5. Valve lateral margin, showing fenestrate inner valve thickenings and elater arrangement (bar = 10 μ m). Fig. 6. Detail of elater, showing well developed spiral and ornamentation with punctae and small pores (bar = 10 μ m).

Figs. 1-3 from Reyes 732, Cuba. Figs. 4-5 from E. & P. Hegewald 7885, Peru. Fig. 6 from Schiffner 1522, Brazil.

Figs. 1-3 = F. corticalis; Figs. 4-5 = F. tristis; Fig. 6 = F. densifolia.

XXXIII



Plate XXXIV. Spore ornamentation of Frullanoides, Acrolejeunea, Trocholejeunea and Mastigolejeunea.

Fig. 1. Ornamentation of three spores, showing rosette and attachment points (bar = 4 μ m). Fig. 2. Spore ornamentation, showing granulose surface, weakly developed rosette and attachment point (bar = 4 μ m). Fig. 3. Three facets of a spore, showing one rosette per facet (bar = 10 μ m). Figs. 4-5. Variable development of rosettes within a single species (bar = 4 μ m). Fig. 6. Well developed rosette, showing gradual increase in size of surface spinulae and rosette spinae (bar = 4 μ m). Fig. 7. Spore ornamentation, showing sharp distinction between clusters of spinulae/baculae on the surface and rosette spinae (bar = 4 μ m).

Fig. 1 from Weir s.n., Colombia. Fig. 2 from Lorentz s.n., Argentina. Fig. 3 from Reyes 732, Cuba. Figs. 4-5 from Dahlan 35, Riau Archipel. Fig. 6 from Inoue 15, Japan. Fig. 7 from Gradstein 3833, Papua New Guinea.

Fig. 1 = Frullanoides liebmanniana; Fig. 2 = F. densifolia; Fig. 3 = F. corticalis; Figs. 4-5 = Acrolejeunea fertilis; Fig. 6 = Trocholejeunea sandvicensis; Fig. 7 = Mastigolejeunea humilis.

XXXIV



Plate XXXV. Oil body-types in *Brachiolejeunea*, *Frullanoides* and related genera.

Fig. 1. Brachiolejeunea laxifolia. Note desintegrating oil bodies (arrow). Fig. 2. Frullanoides densifolia. Fig. 3. Blepharolejeunea incongrua. Fig. 4. Dicranolejeunea axillaris. Fig. 5. Lindigianthus cipaconeus (cells of leaf base). Fig. 6. Omphalanthus sp. (oil body type similar to Mastigolejeunea).

Fig. 1 from Aguirre & Gradstein 4617, Colombia. Fig. 2 from Aguirre et al. 6223, Colombia. Fig. 3 from Gradstein & Aguirre 4236, Colombia/v. Zanten & Gradstein 440, Colombia. Fig. 4 from Aguirre et al. 6221, Colombia. Fig. 5 from Aguirre et al. 6503, Colombia. Fig. 6 from Aguirre & Gradstein s.n., Colombia.

Figs. 1-2, 5 Massula-type; Figs. 3-4 Jungermannia-type; Fig. 6 Calypogeia-type.

XXXV





A review of the genus Blepharolejeunea S. Arnell



Adapted from: van Slageren, M.W. & Kruijt, R.Ch. (1985). A review of the genus *Blepharolejeunea* S. Arn. - Beih. Nova Hedwigia 80: 113-154.

II A review of the genus Blepharolejeunea S. Arnell

INTRODUCTION

The genus Blepharolejeunea was founded by S. ARNELL in 1962 as a monotypic genus, based on a small collection of a new species of Lejeuneaceae from Ecuador with strongly dentate-ciliate leaves, B. harlingii s. Arnell. SCHUSTER (1980a, 1980b) added Brachiolejeunea securifolia Steph. to the genus, based mainly on the leaf lobule structure, which differs from that of the genus Brachiolejeunea (delimited as in Chapter I, i.e. comprising only the former subgenus Brachiolejeunea) in the right 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), with Oreolejeunea securifolia (Steph.) Schust. Oreolejeunea Schust. was based on a) edentate female bract lobes, b) suborbicular (?) female bracts, which are rotundate in their distal part, c) large trigones in the leaf cells and d) "clear" male bracts (1980a: 424), all of them different from B. harlingii S. Arnell where obovate-triangular female bract lobes, which are dentate in their apical region, are present and in which male bracts have not vet been found.

In the present paper, Blepharolejeunea is emended, as a result of monographic studies of the genera Brachiolejeunea (Chapter 1) and Dicranolejeunea (KRUIJT 1985 and in prep.). The study of Brachiolejeunea revealed, besides B. securifolia, one further species, B. nitidiuscula (Gott.) Schiffn., with a similar lobule. The revision of Dicranolejeunea revealed two such species: D. incongrug (Lindenb. 3 Gott.) Steph. (= Brachiolejeunea nitidiuscula) and D. saccata Steph. (= Blepharolejeunea harlingii). In addition, two further species proved to possess a similar lobule: Archilejeunea fuegiana (Besch. & Mass.) Steph. (GRADSTEIN & BUSKES 1985) and a newly discovered species from Venezuela, Blepharolejeunea chimantaensis van Slageren & Kruijt. Blepharolejeunea is related both to Brachiolejeunea and Dicranolejeunea. Differences are shown in Table 1.

The main characteristic features of the genus *Blepharolejeunea* are: 1) the shape and dentation of the leaf lobule, and 2) the variation of trigone shapes in the cells of the leaves, underleaves, bracts and perianth. The lobule form

and dentation differs from both *Brachiolejeunea* and *Dicranolejeunea* in the right 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 right apex of the lobule, consists of a straight (to weakly curved) and sharp point, and is never inflexed (e.g. PI. II, figs. 5-6). Moreover, areolation in all species of *Blepharolejeunea* varies from elongate cells with cordate trigones to isodiametric cells 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* possesses only species with clearly cordate trigones and elongate 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, the oil bodies and the sporophyte morphology.

Underleaf attachment is tristratose in B, fuegiana (Pl. 11) and B, saccata and bistratose in B. chimantaensis and B. incongrug (Pls, I, III). B. securifolia is most remarkable in this respect by its possession of both the bi- and tristratose attachment (Chapter I: Pl. II, figs. 5, 8); the bistratose attachment may be short, 40-70 µm, as in B. incongrug, or elongated, 90-190 um, with additional cells between the superior central cell and the lowermost underleaf lamina cell. Accordingly, the length of the underleaf attachment in B. securifolia varies considerably: 40-190 µm. This variation does not seem to other characters investigated, although correlate with 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 has been suggested by GRADSTEIN (1979).

Several authors recently have paid attention to the morphology of the first leaf cycle at the base of a Frullania-type branch (CRANDALL 1969, MIZUTANI 1970. GRADSTEIN 1979). MIZUTANI (1970) recognized three different subtypes of the Frullania branch, of which the Frullania-Ptychanthus-subtype is present in B. chimantaensis and B. fuegiana (PIs, I-II). VAN SLAGEREN & KRUIJT (1985) described the Frullania-Blepharolejeunea subtype, which is present in B. inconqua, B. saccata and B. securifolia (Table 2). In this subtype the outline of the first branch appendage varies from suborbicular and bilobed in B. securifolia (Pl. V, fig. 7b) and B. saccata to very asymmetrically bilobed and reduced to a scale in B. incongrua. The second leafy appendage is also reduced in size and has no lobule. Its shape varies from suborbicular-bilobed in B. securifolia (Pl. V, fig. 7c) and B. saccata to an asymmetrically bilobed scale in B. incongrua.

Besides Frullania-type branches, all species of Blepharolejeunea have Lejeunea-type branches, which form the majority of the branches present in B. saccata (Table 2). 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, and the third is an acroscopic leaf (MIZUTANI

genus character	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 height to ventral
paraphyllia	lamellate on dorsal stem (weak in B. spruceana)	lacking	cortical cells
leaf cells	elongate with cordate trigones	elongate with tri- gones cordate to iso- diametric with tri- gones	elongate with tri- gones cordate to isodiametric with trigones
oil bodies	homogeneous, <i>Massula</i> - type	simple triangular homogeneous, <i>Massula</i> - type	simple triangular segmented, <i>Junger-</i> <i>mannia</i> -type (or homogeneous <i>Massula</i> -type?)
leaf lobule	not reducing	not reducing	reducing
leaf lobule free	weakly curved, no	rectangular with sharp	curved with variable
margin	sharp angle	angle at 2nd tooth (90-130°)	angle at 1st tooth (130-150°), except in strongly reduced lobules
leaf lobule	(2-)3(-4) similar,	dissimilær: first	2(-3) similar, in-
teeth	inflexed teeth	(apical) tooth blunt, inflexed, 2nd tooth straight and sharp	flexed teeth (but lst tooth sometimes larger)
underleaf	apical margin re~ curved, lateral margins incurved	plane	margins narrowly recurved or plane
underleaf -	tri-stratose	bi- or tri-stratose	tri-stratose
base anatomy		(in <i>B. securifolia</i> bi- and tri-stratose	
male bract lobe	not reduced in size when compared with leaves	not reduced in size when compared with leaves	strongly 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

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

1970). This innovation type is also found in the genera related to Blepharolejeunea.

Table 2. Branching and innovations in Blepharolejeunea.

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

species	B. chimant	B. fuegiana	B. incongru	a B. saccat	a B. securifolia
branching-type					
Frullania-Ptychanthus	+	±			
Frullania-Blepharolejeunea			+	-	+
Lejeunea	-	±	-	+	-
Radula-Jubula	-	-	-	-	·

Recently Dr. S.R. Gradstein was able to study oil bodies in fresh material of *Blepharolejeunea incongrua* and *B. securifolia* and found *Jungermannia*-type oil bodies in both species. In *B. incongrua* 15-30 oil bodies were present in each median leaf cell (Table 1; see also Chapter 1: Pl. XXXV, fig. 3), each oil body faintly segmented in 3-8 globules. In *B. securifolia* 15-30 very small and narrow ellipsoid to subglobose oil bodies were present, each oil body made up of 4-10 granules. The presence of *Jungermannia*-type oil bodies indicates an affinity to *Dicranolejeunea*, where this type of oil bodies has also been found, rather than to *Brachiolejeunea*, which possesses only *Massula*-type oil bodies.

In the course of a comprehensive analysis of the sporophyte in the Ptychanthoideae (Chapter III), scanning electron microscopic (SEM) analysis of various details of the sporophyte generation was carried out in B. incongrua and B. securifolia, the only two species of Blepharolejeunea in which this generation is known. It appears that the sporophyte is of the nodular-type, characterised amongst others by thickenings of the inner cell layer of the capsule valves consisting of nodules in the angles and on the intermediate, radial cell walls, which are located inside the cells. Consequently these thickenings are only visible with the light microscope and not with the SEM, which shows a smooth inner valve surface (Pl. VI, figs. 4, 6). The outer layer has nodular thickenings only on the angles of the cells (Pl. VI, figs. 3, 5). This valve morphology is characteristic for the sporophyte type of the subfam. Lejeuneoideae; within the Ptychanthoideae it has also been found in genera Brachiolejeunea and the related Dicranolejeunea (GEISSLER 3 GRADSTEIN 1982) as well as in Neurolejeunea, Odontolejeunea, Stictolejeunea and Symbiezidium (GRADSTEIN & VAN BEEK 1985). The majority of the genera of Ptychanthoideae produce capsules with fenestrate, sheetlike thickenings on the inner valve surface.

It thus appears that *Blepharolejeunea* is part of a group of genera which, in 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 (see Chapter III).

In transverse section of a closed capsule (PI. VI, fig. 2), 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 (PI. VI, fig. 2: m.e.). This has already been described for *Dicranolejeunea axillaris* (STOTLER & CRANDALL 1969) and *Brachiolejeunea laxifolia* (FULFORD 1961). These authors do not mention the *in situ* presence and location of additional elaters on the inner valve surface (PI. VI, figs. 2, 4: a.e.). These elaters intersect the four sectors filled with spores at more or less regular distances from each other, and moreover, remain attached at both ends to the valve inner surface (PI. VI, figs. 4, 6).

The spore shape is basically more or less rectangular (Pl. VII, fig. 2). In longitudinal sections of the capsule the spores appear rather brick-like (Pl. VI, fig. 2) but a transverse section shows more elongate as well as trapezoid forms (Pl. VI, fig. 2). The ultrastructure of the sporoderm shows the following differences, at the specific level between B, securifolia and B. incongrua. In B. securifolia the sporoderm is covered with minute granulae c. 0.1-0.2 µm in diam. At irregular intervals larger verrucae, 1.0-2.5 µm in diam., are present, These verrucae are in addition covered with small, wartlike processes, appearing as "whitish" punctae on a SEM micrograph (Pl. VII, fig. 3). 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, 1.0-2.5 µm in diam. and covered with small, wartlike processes, as well as 6-11 rosettes, consisting of 7-9 radially oriented spinae. The diameter of the rosettes is 8-10 μ m; the length of the spines is 2.5-5.0 um. The spines become somewhat baculate in well developed rosettes (Pl. VII, fig. 6). The rate of development of the rosettes varies considerably: from ± indistinct to well defined (Pl. VII, figs. 4-6).

The five species of Blepharolejeunea occur in cool habitats in Latin American regions (Pl. VIII). B. chimantaensis, B. incongrua, B. saccata and B. securifolia are tropical-montane, usually occurring above 1800 m in the parámo 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 the distribution of *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. However, its 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) seem to be more of a relict nature. The altitude on the Antilles is estimated to be lower than on the continent (ca. 1000-1800 m), which might be due to the compression of altitudinal zonation on islands. Precise figures of altitude are,

however, usually lacking and for the Antilles given only for one collection on Cuba (1800 m). For *B. fuegiana* altitudinal data are lacking but they are reckoned to be from 0-500 m. Temperature conditions at the localities of *B. fuegiana* may thus be similar to those 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 Chile (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 extreme as that shown by e.g. *Eopleurozia paradoxa* (HASSEL DE MENENDEZ & GREENE 1980), *Dendrocryphaea* (GRIFFIN III et al. 1982), *Andreaea wilsonii* (DUSEN 1903) or *Colura patagonica* (SOLARI 1976), but represents a pattern, at the generic level, which is apparently frequently found in neotropical-montane mosses and hepatics.

BLEPHAROLEJEUNEA S. Arnell

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

Lectotype: Blepharolejeunea harlingii S. Arnell (= Blepharolejeunea saccata (Steph.) van Slageren & Kruijt).

Heterotypic synonym:

Oreolejeunea Schust., Hep. Anth. N. America 4: 762 (1980b).
Type: Oreolejeunea securifolia (Steph.) Schust. (= Blepharolejeunea securifolia (Steph.) Schust.).

Plants dioecious (?) or paroecious, 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*-type and *Lejeunea*-type. The gynoecia with two *Radula-Jubula*-type innovations that may be repeatedly floriferous, giving parts of the shoots a dichotomous appearance.

Stems flaccid or rigid (*B. chimantaensis*), 0.09-0.19 mm in diam., ventral merophyte 2-4 cell rows wide; dorsal cortical cells arranged in straight longitudinal rows, the lateral merophytes interlocking dorsally; stem in transverse section with 9-14 thick-walled cortical cells surrounding 15-32 thin-walled 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, subcrect-convoluted to rather widely spreading when dry, when moist widely spreading and erecto-patent. Lobe (ob)ovate-falcate to broadly so to suborbicular, inserted along 1/4-1/2 of the length of the lateral merophyte, the dorsal base straight, 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, when spread out forming an angle of 90-135°(-180°) with the keel, 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 $(15-)21-47 \times$ (11-)15-36 µm, slightly larger at the leaf base, towards the margins becoming gradually smaller, at the margins rectangular to subguadrate, (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, involucrum, perianth and stem cortex, Jungerman *nia*-type, in the leaf lobe 10-30 per cell, finely granulose, each oil body build up of c. 4-10 granules, ellipsoid to globose, up to 8 um long, upon degeneration becoming septate and subsequently desintegrating into minute granula (obs. S.R. Gradstein).

Lobule 0.4-0.6 x the length of the lobe, <u>never reduced</u>, <u>rotundate-rec-tangular</u> or <u>short rectangular</u>, inflated along the keel and with a plane to concave distal part, the free margin plane, truncate, <u>straight from the keel</u> to the second tooth with the <u>blunt</u>, inflexed apical tooth situated midway, the <u>second tooth a sharp point</u>, <u>not inflexed</u>, 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 x the width of the stem, suborbicular, plane, the apex widely rounded, the margins entire, the bases rounded and shortly decurrent, the line of insertion cuneate or subtransverse, 60-145µm deep; the underleaf base with four superior central cells, 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 1-4 series of vegetative leaves below the gynoecium; 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, <u>epistatic</u>, the free margin similar to the vegetative leaves but the second tooth not always developed, the lobule enveloping <u>one</u> globose antheridium subtended by a curved, uniseriate stalk; the bracteoles similar to underleaves, present throughout the male spike.

Gynoecium terminating long or short stems, *Frullania*-type or *Lejeunea*-type branches, the bracts and bracteole in one series; the bract lobe plane or concave, broadly (ob)ovate, spathulate or obovate-triangular, the apical region entire or ciliate, the apex rounded, blunt or minutely apiculate, the keel a sharp or wide angle, a narrow linear to more elliptic wing usually developed at the keel but sometimes reduced to absent, the 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 when mature, obovoid to obovoid-oblong or cuneiform to pyriform, frequently stalked, \pm 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 thin-walled 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 of which the two outer cell layers are identical to the cells of the upper part, the 1-5 inner layers consisting of much smaller and \pm iso-diametrical cells, the calyptral stalk very short.

Mature sporophyte exserted up to 1.5 mm above the perianth, the foot consisting of a few bulging cells in three layers, the seta articulate, with 16 evenly tiered longitudinal rows of outer cells and 4 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, alternatively with five marginal elaters - one apical and four marginal - or six marginal elaters, the elaters thus forming a series of six at each interlocking of two valves in a closed capsule, each valve in addition bearing three 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, weaker at the extreme base, the inner cells smooth on their outside surface and with irregular nodulose thickenings on their radial, inner cell walls, the capsule base 3-4 stratose, consisting of thin-walled cells; elaters 2x5 + 2x6 +4x3 = 34 per capsule, 140-370 µm long: along the margin of the valves 290-370 μ m, the lowermost lateral ones 140-160 μ m, on the inner surface of the value one central elater of 195-250 μm and two lateral elaters of 145-180 μm are present, all elaters 14-23 um wide, with one yellowish-brown, c. 4 µm wide spiral that is often incompletely developed (wall thickenings only); spores with precocious germination, the outline inside the capsule rectangular to trapezoid, 54-95 µm long, irregularly angular when dry, the outer surface covered with numerous irregular arranged verrucae and (in B. incongrua only) 6-11 rosettes of radially oriented spinae 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 (PI. VIII): CENTRAL and SOUTH 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 dense or loose mats on stems and branches of living trees and shrubs in mountain forests and in páramo regions; often together with other Lejeuneaceae (e.g. *Brachiolejeunea laxifolia*), *Frullania* or, more rarely, with mosses; at higher altitudes (3400-4600 m) also growing epilithic or terrestric and then sometimes in rather dense cushions; not epiphyllous; once found pendulous.

Differentiation: important diagnostic characters are underlined in the description.

KEY TO STERILE PLANTS

1.	Leaf lobes dentate to ciliate; ventral merophyte 2 cell rows wide
1.	Leaf lobes entire; ventral merophyte 2-4 cell rows wide
	2. Leaf lobule first tooth consisting of one cell that is part of the lobule
	margin; stems rigid 1. <i>B. chimantaensis</i>
	2. Leaf lobule first tooth consisting of one or more cells superimposed on
	the lobule margin; stems flaccid
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 of $1-3(-4)$ 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 <i>B. securifolia</i>); plants from tropical America
	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
	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

KEY TO FERTILE PLANTS

1.	Female	bracte	eole a	as lai	rge as	the	bra	cts,	strong	ly cor	icave;	female	bract
	lobe e	ntirely	conca	ave,	strong	gly so	o in	the	apical	regior	n; stem	n <mark>s ri</mark> gio	l with
	strong	ly thic	kened	cort	ical ce	lls .		• •		. 1.	B. chin	nantaen	sis

- 1. Female bracteole distinctly smaller than the bracts, plane, apical region sometimes concave; female bract lobe plane to (weakly) concave, mainly in 2. Female bract lobe broadly obovate or ovate-falcate, margins entire . 3 2. Female bract lobe spathulate or obovate-triangular, margins entire or 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 x the length of the bract lobe 3. Perianth obovoid to obovoid-oblong with 3 smooth, rounded plicae; female bract ovate-falcate, the keel rounded, the lobule large, 0.55-0.65 x 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. Female bract lobe spathulate, apical margin entire; perianth obovoid to

1. BLEPHAROLEJEUNEA CHIMANTAENSIS van Slageren & Kruijt (Plate I)

Beih. Nova Hedwigia 80: 126 (1985).

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

Description: Beih. Nova Hedwigia 80: 126-128 (1985).

Distribution: Venezuela.

2. BLEPHAROLEJEUNEA FUEGIANA (Besch. & Mass.) Gradst. (Plate II)

Beih. Nova Hedwigia 80: 108 (1985); van Slageren & Kruijt (1985: 130). Lejeunea fuegiana Besch. & Mass., Bull. Mens. Soc. Linn. Paris 80: 638 (1886); 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: Chile, 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., s.n. (Vanadis Expedition) (G 20790 holo).

Description: Beih. Nova Hedwigia 80: 130-133 (1985).

Distribution: Southern Chile ((Tierra del Fuego region).

3. BLEPHAROLEJEUNEA INCONGRUA (Lindenb. & Gott.) van Slageren & Kruijt (Plate III)

Beih. Nova Hedwigia 80: 133 (1985).

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

Heterotypic synonym:

Brachiolejeunea nitidiuscula (Gott.) Schiffn., Hedwigia 33: 186 (1894); Stephani (1912: 124); Gradstein et al. (1977: 390).
Phragmicoma nitidiuscula Gott., Ann. Sci. Nat. Bot. 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).

Description: Beih. Nova Hedwigia 80: 133-138 (1985).

- Distribution: Tropical Andean South America (Bolivia to Colombia) and Central America (Mexico, Costa Rica).
- 4. BLEPHAROLEJEUNEA SACCATA (Steph.) van Slageren & Kruijt (Plate IV)

Beih. Nova Hedwigia 80: 138 (1985). Dicranolejeunea saccata Steph., Hedwigia 35: 78 (1896); Stephani (1912: 168). Type: Cuba, Wright 1074 (G holo).

Heterotypic synonym:

Blepharolejeunea harlingii S. Arnell, Svensk Bot. Tidskr. 56: 335 (1962). Type: Ecuador, Napo-Pastaza, Harling 3364 p.p. (S holo).

Description: Beih. Nova Hedwigia 80: 138-142 (1985).

Distribution: Central America, West Indies, Andean South America. Only known from scattered locations on Caribbean islands, Costa Rica and Ecuador. 5. BLEPHAROLEJEUNEA SECURIFOLIA (Steph.) Schust. (Plate V)

Phytologia 45: 424 (1980a); van Slageren & Kruijt (1985: 142).

Brachiolejeunea securifolia Steph., Spec. Hep. 5: 128 (1912); Schuster (1963: 104), (1980b: 762); Gradstein et al. (1981: 239).

- Lejeunea (subg. Brachiolejeunea) securifolia Spruce, Trans & Proc. Bot. Soc. Edinburgh 15: 131 (1884) nom. illeg. non Gottsche 1882; Stephani (1889: 168).
- Oreolejeunea securifolia (Steph.) Schust., Hep. Anth. N. America 4: 762 (1980b).

<u>Type</u>: 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). 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). Lectotype: 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).
 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 (1980b) comb. inval.

Description: Beih. Nova Hedwigia 80: 142-150.

Distribution: Tropical Andean South America (N. Peru, Ecuador, Colombia), Central America and Southeastern Brazil.

SPECIMENS EXAMINED: Beih. Nova Hedwigia 80: 150-151.

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Plate I. Blepharolejeunea chimantaensis Van Slageren & Kruijt.

Fig. 1. Habitus ventral. Figs. 2-3. Stem transverse section (3) and with underleaf attachment (2). Fig. 4. *Frullania-Ptychanthus*-type branch appendages: 4a dorsal stem half-leaf; 4b first branch underleaf; 4c first branch acroscopic leaf. Fig. 5. Stem longitudinal section with underleaf attachment. Fig. 6. Mid leaf cells.

Figs. 1-6 from Steyermark et al. 128593, Venezuela.

r = rhizoid disc initial cell; s = superior central cell; u = underleaf lamina cell.



Plate II. Blepharolejeunea fuegiana (Besch. & Mass.) Gradst.

Fig. 1. Habitus. Fig. 2. Stem transverse section. Fig. 3. Stem longitudinal section with underleaf attachment. Fig. 4. Leaf. Figs. 5-6 Leaf lobule margin outer view (5) and inner view with inflexed apical tooth (6). Figs. 7-8 Mid leaf cells. Note confluent trigones (t). Fig. 9. Underleaf. Fig. 10. Male bract. Fig. 11. *Frullania-Ptychanthus*-branch appendages: 11a dorsal stem half-leaf; 11b first branch underleaf; 11c first branch acroscopic leaf.

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

r = rhizoid; s = superior central cell; t = confluent trigones; u = underleaf lamina cell.



Plate III. Blepharolejeunea incongrua (Lindenb. ε Gott.) van Slageren ε Kruijt.

Fig. 1. Habitus ventral. Fig. 2a-d. Leaves, showing different outline of the lobule. Fig. 3. Mid leaf cells. Fig. 4. Leaf lobule with large marginal cells. Fig. 5. Stem transverse section. Fig. 6. Stem longitudinal section with underleaf attachment.

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

r = rhizoid; s = superior central cell; u = underleaf lamina cell.



Plate IV. Blepharolejeunea saccata (Steph.) van Slageren & Kruijt.

Fig. 1. Habitus ventral. Fig. 2a-e. Leaves, showing variable dentation. Fig. 3. Mid leaf cells. Fig. 4a-b. Leaf lobe margin, showing variable dentation. Fig. 5. Leaf lobule.

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



Plate V. Blepharolejeunea securifolia (Steph.) Schust.

Fig. 1. Habitus ventral, with sporophyte. Figs. 2-3. Stem transverse section with antheridial stalk (2) and with underleaf attachment (3). Fig. 4. Perianth and involucrum. Fig. 5. Female bract. Fig. 6. Female bracteole. Fig. 7. *Frullania-Blepharolejeunea*-type branch appendages: 7a dorsal stem halfleaf; 7b first branch underleaf; 7c first branch acroscopic leaf.

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

r = rhizoid disc initial cell; s = superior central cell; u = underleaf lamina cell.



Plate VI. Sporophyte capsule and elaters of Blepharolejeunea S. Arnell.

Fig. 1. Capsule length section, showing marginal elaters and spore storage in situ (bar = 100 μ m). Fig. 2. Capsule transverse section, showing marginal elaters (m.e.) in 2 axes meeting at right angles in the centre and additional elaters (a.e.) intersecting the four sectors filled with spores (bar = 100 μ m). Fig. 3. Valve outer surface, showing nodular thickening (bar = 100 μ m). Fig. 4. Valve inner surface, showing marginal elaters (m.e.) and additional elaters (a.e.) (bar = 100 μ m). Fig. 5. Capsule outer surface and articulate seta (bar = 100 μ m). Fig. 6. Two valves inner surface, showing marginal and additional elaters (bar = 100 μ m).

Figs. 1-2 from Cleef 1990, Colombia. Fig. 3 from Cleef 2291, Colombia. Fig. 4 from Lukas s.n., Peru. Fig. 5 from Griffin et al. 435, Costa Rica. Fig. 6 from Gradstein et al. 3372, Ecuador.

Figs. 1-4 = B. securifolia (Steph.) Schust.; Figs. 5-6 = B. incongrua (Lindenb. & Gott.) van Slageren & Kruijt.

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Plate VII. Spores of Blepharolejeunea S. Arnell.

Fig. 1. Part of length section, showing marginal elaters and spore storage in situ (bar = 40 μ m). Fig. 2. Spores with elaborate, compound verrucae (bar = 10 μ m). Fig. 3. Sporoderm, showing verrucate ornamentation with additional wratlike processes (bar = 4 μ m). Fig. 4. Sporoderm, showing verrucae and a tendency towards rosette formation (bar = 4 μ m). Fig. 5. Sporoderm, showing verrucae and a distinct rosette (bar = 4 μ m). Fig. 6. Sporoderm, showing ver rucae and a very distinct rosette (bar = 4 μ m).

Figs. 1, 4 from Griffin et al. 435, Costa Rica. Fig. 2 from Cleef 1990, Colombia. Fig. 3 from Lukas s.n., Peru. Fig. 5 from Aguirre & Gradstein 1326, Colombia. Fig. 6 from Gradstein et al. 3372, Ecuador.

Figs. 1, 4-6 = B. incongrua (Lindenb. & Gott) van Slageren & Kruijt; Figs. 2-3 = B. securifolia (Steph.) Schust. VII



Plate VIII. Distribution of Blepharolejeunea S. Arneli.

- = B. incongrua.
 = B. chimantaensis.
 2. = B. securifolia.
 = B. saccata.
- 3. $\blacktriangle = B$. fuegiana.

VIII





A scanning electron microscopic analysis of the sporophyte in the Ptychanthoideae



By M.W. van Slageren & W. Berendsen

III A scanning electron microscopic analysis of the sporophyte in the Ptychanthoideae

1. INTRODUCTION

The taxonomy of the Lejeuneaceae is mainly based on characters of the gametophyte. Characters of the sporophyte have been used only occasionally, although their importance was emphasized by e.g. MULLER (1948), GRADSTEIN (1975, 1979) and SCHUSTER (1980). The first important application of sporophyte characters in the Lejeuneaceae was in MIZUTANI's (1961) treatment of the Japanese members of the group, in which the subfamilial delineation was based primarily on seta and capsule characters. Several recent, detailed studies of individual genera and species have revealed important sporophyte characters (e.g. CRANDALL 1967, STOTLER & CRANDALL 1969, GEISSLER & GRADSTEIN 1981, CRANDALL-STOTLER & GEISSLER 1983). In spite of this, sporophytes are still unknown for many taxa in the family. As to Ptychanthoideae, GRADSTEIN (1975) arranged the genera of this subfamily on gametophytic characters but called attention to the importance of the sporophyte, at that time known only in 9 of the 22 genera of this subfamily. GEISSLER & GRADSTEIN (1982) briefly reviewed our knowledge of the sporophyte of the Ptychanthoideae and called attention to the existence of two types within this subfamily: 1) with a sheet-like, fenestrate type of thickening on the inner surface of the capsule valves (present in most of the genera), and 2) with irregular, nodular type thickenings on the walls of the inner cells of the capsule valves (present in e.g. Brachiolejeunea and Dicranolejeunea). This latter type is more or less similar to the type which occurs in the subfam. Lejeuneoideae. Based on sporoderm ornamentation they distinguished two spore types: 1) with rosettes, and 2) without rosettes. This was also the first study using scanning electron microscopy for a larger group of taxa of Lejeuneaceae.

The use of scanning electron microscopy (SEM) in the taxonomy of mosses and liverworts has expanded rapidly over the last ten years. This type of ultrastructural analysis has been widely applied, especially in mosses, where important systematic characters such as peristome teeth, leaf surface and spore ornamentation are well suited to examination by means of SEM (MAGILL & HORTON 1982). With few exceptions (e.g. TAYLOR et al. 1974) the use of SEM in liverworts has been more casual and applied mainly in the study of sporophyte characters, of which many are difficult to study and illustrate with light microscopy (LM). Through its higher resolution power (magnification up to 20.000 times) and its effectiveness in revealing complex, threedimentional structures, SEM has become an important aid to interpretation and character analysis.

In the present study sporophyte characters such as capsule wall thickenings, sporoderm ornamentation and three-diamentional structures in 22 of the 25 genera of Ptychanthoideae are analysed with SEM, with the purpose of establishing the distribution of the sporophyte types, recorded within the subfamily by GEISSLER & GRADSTEIN (1982). The presence of the two types of sporophytes within the genus *Brachiolejeunea*, as traditionally circumscribed, has initiated the present study, which is completed in several cases with LM and literature data. The results are shown in Table 2.

In order to obtain a broad view, the monogeneric subfam. Bryopteroideae, some representatives of the subfam. Lejeuneoideae and a species of *Frullania*, a genus in the related fam. Jubulaceae, are also taken into account. It should be noted that differences in sporophyte characters between these groups were already discussed in some detail by SPRUCE (1884: 69-70) but were ignored by later authors.

2. MATERIALS AND METHODS

2.1 Materials

Species	Collector	Location	Herbarium
Fam. Lejeuneaceae Casares Gil			
Subfam. Ptychanthoideae Mizut.			-
Acrolejeunea emergens (Mitt.) Steph. var. emergens	Reese 12976	Bolivia, Guayara- mérín	NY, U
A. fertilis (Reinw., Blume & Nees) Schiffn.	Dahlan 35 & 36	Riau, Dapur Tiga	G, GRO, L
A. mollis (Hook. & Tayl.) Schiffn.	Hodgson s.n.	New Zealand, Wairoa	F, U
A. pycnoclada (Tayl.) Schiffn.	Sipman 6991	Indonesia, Java,	hb. Sipman,
		Mt. Ardjuno	U
A. Securifolia (Nees) Watts ssp.	Hürlimann	Tahiti, Hitiaa	hb. Hürli-
pallida (Aongstr.) Gradst.	T 1137		mann, U
A. torulosa (Lehm. & Lindenb.)	Vital 2846	Brazil, Espirito	SP, U
Schiffn.		Santo	
Archilejeunea olivacea (Hook. &	Child 2202	New Zealand, Auck-	BM
Tayl.) Steph.		land, Waitakene	

Table 1. Enumeration of examined species.(1) = only light microscopical observations.

A. parviflora (Nees) Steph.	Vital 6688	Brazil, Sao Paulo	SP, U	
A. porelloides (Spruce) Schiffn.	Griffin et al.	Brazil, Amazonas,	FLAS, SP, U	
	418	Rio Lages		
Blepharolejeunea incongrua (Lin-	Lindig s.n.	Colombia, Choachi	G 20219	
denb. & Gott.) van Slageren &	Gradstein et	Gradstein et Ecuador, Otavala U		
Kruijt	al. 3372			
	Griffin & Eakin	Costa Rica, Cartago	FLAS, U	
	435			
	Aguirre &	Colombia, Risaralda	COL, U	
	Gradstein 1326			
	Troll 2180a	Colombia	JE	
B. securifolia (Steph.) Schust.	Cleef 1990 & 2291	Colombia, Boyacá	COL, U	
	Gradstein et al.	Ecuador, Carchi	COLO, U	
	3457			
	Lukas s.n.	Peru	JE	
	Schwab s.n.	Mexico	U 👞	
Brachiolejeunea laxifolia (Tayl.)	Aguirre & Grad-	Colombia, Tolima	COL, U	
Schiffn.	stein 1630			
	Gradstein 3570a	Colombia, Risaralda	COL, U	
	Gradstein et al.	Ecuador, Carchi	COLO, U	
	3389			
	Frahm et al. 1248	Peru, San Martin	B, G, U	
B. spruceana (Mass.) Schiffn.	Dusèn 466	Chili	G 16171	
	s. coll.	Argentina	YU	
Caudalejeunea hanningtonii (Mitt.)	Pócs & Crosby	Tanzania, Morogoro	HAC, U	
Steph.	6856/1			
Dicranolejeunea aberrans (Lindenb.	Underwood	Jamaica, Cinchona	NY	
& Gott.) Steph.	1126c	plantation		
D. axillaris (Nees & Mont.) Schiffn.	Griffin & Eakin	Costa Rica, Cartago	FLAS, U	
	247			
D. johnsoniana (Mitt.) Grolle	Bornmüller 158	Madeira, Pico Grande	S	
D. madegascariensis Steph.	Onraedt	Mauritius, La Lande	hb. Onraedt	
	71.Ma.257/a	de Pétrin	JE	
D.phyllorhiza (Nees) Schiffn.	Mosén Hl	Brazil	S	
	Pringle 10690	Mexico, Canada	YU	
Frullanoides bahamensis (Evans)	Рбсв 9056/1	Cuba, Oriënte,	HAC	
van Slageren		Sierra Maestra		
F. corticalis (Lehm. & Lindenb.)	Reyes 732	Cuba, Guantánamo	HAC	
van Slageren				
F. densifolia Raddi	Lorentz. s.n.	Argentina, San	G 20088	
		Andrès		
	Moritz s.n.	Venezuela, Mérida	G 20079	

	Pearce s.n.	Bolivia, Unduavi	G 20070
	Schiffner 1522.	Brazil, Sao Paulo	s, w
F. liebmanniana (Lindenb. & Gott)	Vital 6148 Brazil, Goiás		SP, U
van Slageren	Weir s.n.	eir s.n. Colombia	
F. tristis (Steph.) van Slageren	Hegewald 7885	Peru, Huanuco	hb. Hege-
			wald, U
Lopholejeunea muelleriana (Gott.)	Rapp. s.n.	USA, Florida,	υ
Schiffn.		Sanford	
Mastigolejeunea auriculata (Wils.)	Mosén Hh	Brazil, Sao Paulo	G 20076
Schiffn.			
M. humilis (Gott.) Schiffn.	Gradstein 3833	Papua New Guinea,	U, UPNG
		Wau	
M. nigra Steph.	Pócs 6086/BD	Tanzania, Usambara	EGR, HAC,
Neurolejeunea breutelii (Gott.)	Reyes 607 & 631	Cuba	HAC
Evans (1)			
Odontolejeunea sieberiana (Gott.)	Vital 2791c	Brazil, Sao Paulo	ŚP, U
Steph.			
0. tortuosa (Lehm. & Lindenb.) Evans	Früs et al. B 146	Ethiopia, Bonga	c, U
Ptychanthus striatus (Lehm. & Lin-	Schofield 53812	Japan, Miyazaki	U, UBC
denb.) Nees (1)			
Schiffneriolejeunea occulta (Steph.)	Assel 1023	Congo-Brazzaville	EGR, U
Gradst.			
S. pappeana (Nees) Gradst.	Onraedt	Madagascar, Tana	hb. Onraedt
	74.R.8079		U
S. tumida var. haskarliana (Gott.)	Hürlimann	New Caledonia	hb. Hürli-
Gradst. & Terken	2269a		mann, U
Spruceanthus polymorphus (Sande	Gradstein 3811	stein 3811 Papua New Guinea,	
Lac.) Verd.		Wau	
S. semirepandus (Nees) Verd.	Inoue 4632	Japan, Kochi, Mt.	TNS, U
		Kudarukawa	
Stictolejeunea squamata (Web.)	Sellow s.n.	Brazil	STR
Schiffn. (1)			
Symbiezidium barbiflorum (Lindenb.	Pócs & Borhi-	Cuba, Sierra de Es-	EGR, HAC, U
& Gott.) Evans	di 9004/A	cambray	
	Pócs & Reyes	Cuba, Holguin	EGR, HAC, U
	9055/BD	ł	
S. transversale (Sw.) Trev. var.	Frahm et al. 1396	Peru, San Martin	B, G, U
hookeriana (Nees) Gradst. & van			
Beek			
Thysananthus pterobryoides (Spruce)	Mägdefrau 1501	Colombia, Quibdo	hb. Mägde-
Schiffn.			frau. U

Trocholejeunea infuscata (Mitt.) Verd.	Sureil s.n.	Sikkim	G 20189	
T. sandvicensis (Gott.) Mizut.	Inoue 15	Japan, Sakawe-Mura	G 20134	
	Foreau s.n.	India	JE	
Subfam. Lejeuneoideae Mass.				
Cyclolejeunea convexistipa (Lehm. &	Bekker	Suriname, Kabalebo	BBS, U	
Lindenb.) Evans				
Omphalanthus filiformis (Sw.) Nees	Duss 612.	Martinique	NY	
Fam. Jubulaceae Klinggr.				
Frullania ericoides Nees	van Reenen 2513	Colombia	COL, U	

2.2 Light Microscopy (LM)

Light microscopical examination was carried out with the aid of an Olympus dissecting microscope and with an Olympus FH microscope. Drawings were made with the aid of a Wild drawing apparatus.

2.3 Scanning Electron Micrsocopy (SEM)

For this study only dry herbarium material was used. Though field-fixed capsules are likely to yield the most true to nature images, it is our experience that extensive resoaking of herbarium material, together with a careful preparation provides satisfactory results as well.

As a result of a pilot study two preparation methods have been applied.

- Direct mounting and coating. This method proved adequate for examination of elater morphology, spore shape, and sporoderm ornamentation, as well as the storage of the spores inside the capsule. Preparation included: 1) longitudinal and transverse sectioning of dry capsules, and 2) mounting of the cleaved capsules on aluminium stubs.
- Fixation and critical point drying, prior to mounting and coating. This method proved most effective for the examination of seta morphology and of the inner, outer and lateral surfaces of the capsule valves, including the elater attachment. Preparation included: 1) overnight hydration, after isolation, of the dry setae and capsule valves, 2) fixation in 2.5 % glutaric aldehyde, buffered in 0.1 Mol K-Na-phosphate buffer for 2.5 hours, 3) rinsing in the same buffer, 4) post fixation in 1% Os04, buffered in 0.1 Mol K-Na-phosphate buffer for 2.5 hours, 3) rinsing in the same buffer for 45 minutes, 5) rinsing in the same buffer, 6) dehydration through a graded series of ethanol, up to 100%, 7) critical point drying (c.p.d.), and 8) mounting on aluminium stubs.

Glutaric aldehyde was used for the fixation of cell wall material, and OsO4 for fixation of surface elements, attached to the cell wall. Dehydration and replacement by ethanol caused overall shrinkage of the objects but only to an extent whereby the outline of the valves remained more or less unaltered.

Critical point drying caused partial collapse of the outer cell walls, revealing the outline of the trigones and the intermediate wall thickenings of the outer valve layer (e.g. Pl. I, fig.4). In order to prevent charging of the objects, evaporation of carbon was applied to enhance conduct under SEM examination. This treatment was particularly important for the half-globose, cleaved capsules and for the sometimes strongly curved capsule valves since they were attached to the stubs by only a small part of their total surface.

Mounting on the stubs with Scotch double sided adhesive tape was followed by double rotating evaporation of carbon at an angle of \pm 45° in a vacuum of 10° Torr, and by gold evaporation under the same conditions. Carbon and gold evaporation was carried out in a modified Edwards high vacuum apparatus. In some of the experiments the material was covered with only a thin gold layer by sputtering . Examination was carried out with a Cambridge Stereoscan 600M at 7.5 KV accelaration voltage.

GEISSLER & GRADSTEIN (1982) showed a difference in outline of the capsule valves when they were critical point dried as compared with air dried. Air dried material was distorted to such an extent that a precise interpretation of the examined characters proved impossible. Much better and almost true to life results were obtained following fixation and c.p.d. This latter preparation method could also have been applied in the study of cleaved capsules but, unlike results with the capsule valves, a pilot study showed no significant difference when compared with preparation involving only mounting and coating of air dried material.

3. GLOSSARY

Anisopolar: having the proximal and distal part of the spore dissimilar (MIYOSHI 1966).

Anticlinal: see radial.

Aperture: persisting spore dehiscence fissure, which is trilete or deformed trilete in outline (MIYOSHI 1966; ERDTMAN 1965); also visible on the dehiscence through the thin or absent exine (CLARKE 1979).

Apolar: proximal and distal surface of the spore not differentiated (MIYOSHI 1966).

Areolation (of cells): spatial arrangement.

Articulate: a seta is articulate when, of each tier, all cells are arranged on the same level after elongation; the seta is thus entirely and regularly segmented transversally (GRADSTEIN 1975).

Atreme: having no aperture or trema (ERDTMAN 1965).

Capsule dehiscence: process of opening of the mature capsule.

- Dispersal (of spores): spreading of the spores after capsule dehiscence, effected by wind, water etc.
- Distal part (of the spore): often somewhat convex part of the spore, which faces outwards when the spore is still associated in the tetrad.
- Exine: the main, outer, usually resistant layer of a sporoderm (MIYOSHI 1966).

General type (of seta): the seta is formed by a large, more or less indefinite number of similar rows of cells (DOUIN 1908; SCHUSTER 1966).

Intine: innermost wall layer of the spore (ERDTMAN 1952).

LM: Light Microscopy.

Mamilla: outward fold of the cell wall which containts a part of the cell lumen. Monofenestrate (thickening): incomplete sheet-like thickening, covering the

- tangential wall of the inner layer of the capsule valve and leaving one large "window" or fenestra where no thickening is present (SCHUSTER 1966). This type of thickening shows intergradation to the plurifenstrate type of thickening.
- Nodular (thickening): knot-like thickenings present in the angles and on the intermediate walls of the cells of the capsule valve outer layer. In several genera of Lejeuneaceae subfam. Ptychanthoideae also present in the cells of the inner valve layer (in the so called "nodular-type" capsules).
- Non-articulate: a seta is non articulate when the cells after elongation are arranged on different vertical levels (GRADSTEIN 1975).
- Ornamentation: the total of processes and their configuration on the outer surface of the spore.

Papilla: outward fold of the cell wall, consisting only of wall material.

Periclinal: see tangential.

Perine: outermost wall layer of the spore; mainly present in the order Marchantiales (MIYOSHI 1966).

- Plurifenestrate (thickening): incomplete sheet-like thickening, covering the tangential wall of the capsule valve inner layer, leaving several (4-12) small "windows" or fenestrae where no thickening is present (SCHUSTER 1966). Present in most genera of Lejeuneaceae subfam. Ptychanthoideae (in the so called "fenestrate-type" capsules).
- *Precocious germination* (of spores): germination of spores before capsule dehiscence in which the sporecoat stretches to accommodate the developing sporeling.

Processes/Projections: two types of descriptive terminology exist: a)

for the projections (BOROS & JARAI-KOMLODI 1975), and b) for the resulting arrangement of the projections over the spore surface (MIYOSHI 1966). In our description of the sporoderm surfaces we have decided to follow the terminology of BOROS & JARAI-KOMLODI (1975):

- bacula: small rod, not thickened at the top or end, height larger than the greatest diameter (PI. VIII, figs. 1-2).
- granula: minute (0.1-0.3 μm in diam.) and \pm globose projection, broadest at the base (e.g. Pl. VII, figs. 1-6).
- spina: narrow triangular projection, widest at the base, length at least 1½ times the average length of the spinula, forming stellate rosettes (e.g. Pl. VII, figs. 1-6).
- spinula: narrow triangular projection, widest at the base, scattered over the spore surface, smaller than spina (Pl. VII, figs. 1-5).
- verruca: ± globose projection, broadest at the base, at least 1 µm in diam. (PI. VII, fig. 6). This is termed "granula" by MIYOSHI (1966). Both verrucae and baculae may also be present in compound clusters or rows (PI. IX, figs. 1-2, 5-6).
- *Proximal part* (of the spore): part of the spore that was turned inward when the spore was still associated in the tetrad and that usually bears the

tetrad scar (MIYOSHI 1966).

Radial: perpendicular to the surface (FAHN 1974).

- Reticulate (thickening): a mesh or network of local thickenings on the radial walls of the cells of the inner valve layer (SCHUSTER 1966). When extending over the inner tangential wall of the inner cell layer this thickening type changes to monofenestrate.
- *Rosette*: stellate sporoderm ornamentation, consisting of spirally or subconcentric arranged spinae.

SEM: Scanning Electron Microscopy.

- Specialized type (of seta): the cells of the seta are arranged in distinct inner and outer rings, e.g. 16 outer cells and 4 inner cells ("Brachiolejeuneatype") or 12 outer and 4 inner ("Lejeunea-type") (SCHUSTER 1966).
- Sporeling: All stages in the development of the young plant from the time of the first division of the spore to the formation of leaves of the adult type (FULFORD 1956).

Tangential: parallel to the surface (FAHN 1974).

TEM: Transmission Electron Microscopy.

4. DESCRIPTIONS AND CONCLUSIONS

4.1 Introduction

Table 2 summarises the sporophyte characters examined in this study. The genera are arranged according to their seta type, from the large, general seta type of the Bryopteroideae and *Frullania* to the small and reduced, specialised seta type of the Lejeuneoideae (DOUIN 1908; SCHUSTER 1966), and to capsule valve morphology, elater arrangement and spore shape.

For the sake of completeness, several genera are included that have not been studied with SEM. Data on these are extracted from the literature (*Cephalolejeunea*: MIZUTANI 1979b; *Marchesinia*: GEISSLER & GRADSTEIN 1982; *Ptychanthus*: MIZUTANI 1961; *Stictolejeunea*: GEISSLER & GRADSTEIN 1981; *Verdoornianthus*: GRADSTEIN 1977) or from light microscopical observations (*Neurolejeunea*, *Ptychanthus*, *Stictolejeunea*). Two genera of Ptychanthoideae, in which the sporophyte generation is unknown up to now (*Phaeolejeunea* Mizut., cf. MIZUTANI 1968; *Tuzibeanthus* Hatt., cf. MIZUTANI 1961) are not included. The list of genera of Ptychanthoideae follows GRADSTEIN (1975), with the addition of the more recently established or emended genera *Blepharolejeunea* (VAN SLAGEREN & KRUIJT 1985), *Brachiolejeunea* and *Frullanoides* (this publication), *Cephalolejeunea* (MIZUTANI 1979b), *Lindigianthus* (KRUIJT & GRADSTEIN 1985), and *Verdoornianthus* (GRADSTEIN 1977).

Bryopteris (Bryopteroideae), Cyclolejeunea and Omphalanthus (Lejeuneoideae) and Frullania (Jubulaceae) are added to demonstrate the sporophyte characters in taxonomically allied groups. Cyclolejeunea and Omphalanthus are two genera that formerly were considered to be in the Ptychanthoideae: Cyclolejeunea was erected for a group of species, previously in Odontolejeunea (EVANS 1904) and Omphalanthus was considered a true member of the Holostipae (sensu SPRUCE, now replaced for the major part by the Ptychanthoideae) until GRADSTEIN (1975: 138) reported the presence of a Lejeunea-type seta as in the Lejeuneoideae. The sporophyte morphology of the latter two genera has not yet been described in detail and a light microscopic analysis of the valves and elaters is presented here for the first time (see 4.5.3 and 4.5.4), together with a SEM analysis of the spore surface (*Omphalanthus* only). It should be noted that these two genera are <u>not</u> representative of the subfam. Lejeuneoideae as a whole since considerable differences in the sporophytes are present in this subfamily (MIZUTANI 1979a). In most genera (notable exceptions are Acrolejeunea, Brachiolejeunea and Frullanoides) only one or a few species have been examined and the data in Table 2 are thus in part preliminary. Future monographic treatments may modify these results (see e.g. the variation in the seta of Acrolejeunea presented by GRADSTEIN 1975).

4.2 Fenestrate-type capsules in the subfam. Ptychanthoideae (Plates I-III)

Present in: Acrolejeunea, Caudalejeunea, Cephalolejeunea, Frullanoides, Lopholejeunea, Marchesinia, Mastigolejeunea, Ptychanthus, Schiffneriolejeunea, Spruceanthus, Thysananthus, Trocholejeunea, Verdoornianthus.

In this capsule type the upper half of the valves curves outward after capsule dehiscence (PI. I, fig. 1), while the basal half remains more or less convex. The whole capsule thus opens widely, allowing the spores to disperse (the spores are actually hurled out by the movement of the elaters, see 4.4). The valves are two cell layers thick in the upper half, 3-5 layers in the lower half. The outer cell layer of the valve is considerably wider (up to about three times) than the inner layer(s).

4.2.1 Valve outer surface

The outer cells of the valves are arranged radially. In the basal-central part of the valve the cells are rather small (20-35 x 15-25 μ m) and elongate-hexagonal, whereas in the apical part they are larger (35-70 x 30-40 μ m) and hexagonal to rhombic to rectangular (Pl. 1, figs. 3-4). Each valve is bordered by a single row of small (20-45 x 10-35 μ m), narrow rectangular cells. At the extreme basal-lateral part of the valve, at the lateral end of the capsule dehiscence lines, a few cells with ± equally thickened walls are present (Pl. 1, fig. 3). A light microscopic diagram of this area has been presented by MIZUTANI (1979a) for Lopholejeunea subfusca.

Cells of the outer valve layer possess sinuose-nodulose thickenings in the angles as well as on the intermediate walls (Pl. I, fig. 4). Contrary to the nodular-type capsules, the thickenings are uniformily developed throughout and do not become confluent in the central part of the valve.

4.2.2 Valve inner surface and capsule base

The cells of the inner valve layer are smaller than those of the outer layer. In the central part the areolation is longitudinal, in the apical part it is

PART OF CAPSULE	SETA		THECA		ELATERS	SPORE		SPORELING
GENUS	not articulate (+) articulate (-)	number cells in diam.	reticulate (r) monofenestrate (m) plurifenestrate (p) nodular (n)	nodular (1/2)	number in capsule	isodiametric (+) rectangular (-)	with rosettes (+) without rosettes (-)	Fruillania-type (F) Lopholejeunea-type (Lo Lejeunea-type (Le)
Fam. Jubulaceae Klinggr.								
Frullania Raddi (see 4.5)	+	54 - 106	r, n	1	35 - 144	+	+	F
Fam. Lejeuneaceae Casares Gil								
Subfam. Bryopteroidese (Stotl.) Gradst.								
Bryopteris (Nees) Lindenb. (see 4.5)	- (?)	30 - 100	r, m (-p)	1	60 - 80	+	+	F
Subfam. Ptychanthoideae Mizut.								
Trocholejeunea Schiffn.	+ (16	-32)+(8-16)	р	1	72	Γ + -	+	Lo, F (?)
Archilejeunea (Spruce) Schiffn.	+	16+4	P	1	72	+	+	Lo
Caudalejeunea (Steph.) Schiffn.	+	16+4	р	1	72	:+	+	Lo
Cephalolejeunea Mizut.	+	16+4	p	1	2	1 ?	+	Lo
Marchesinia S.F. Gray	+ 16(-17)+4(-9)	P	1	72	+	+	Loi
Mastigolejeunea (Spruce) Schiffn.	+	16+4	P	1	72	į +	+	Lo
Ptychanthus (Nees)	+	16+4	P	1	72	i +	+	Lo
Spruceanthus Verd.	+	16+4	P	1	72	+	+	Lo
Thysananthus Lindenb.	+	16+4	P	1	72	+	+	Lo
Verdoornianthus Gradst.	?	16+4	P	ì	?	1 ?	+	Lo
Acrolejeunea (Spruce) Schiffn.	_ + _ (14	-)16+4(-8)	P	1	30 - 38	i +	+	Lo
Frullanoides Raddi	- 16(-17)+4(-6)	P	1	30 - 68	i +	+	Lo
Lopholejeunea (Spruce) Schiffn.		1 6+ 4	P	1	30	i +	+/-	Lo
Schiffneriolejeunea Verd.	الا ال 16(-17)+4	P	1	30	<u>_?</u> _	±	<u>Lo</u>
Blepharolejeunea S. Arnell	-	16+4	n	2	34		+/-	Le
Brachiolejeunea (Spruce) Schiffn.	-	1 6+ 4	n	2	34	-	-	Le
Dicranolejeunea (Spruce) Schiffn.	- (15	-)16+4	l n	2	34	-	+	Lei
Lindigianthus Kruijt & Gradst.	-	16+4		2	34	-	+	Le
Neurolejeunea (Spruce) Schiffn.	-	16+4	l n	2	34	-	+	Le
Odontolejeunea (Spruce) Schiffn.	-	16+4	1 0	2	34	-	-	Le
Stictolejeunea (Spruce) Schiffn.	+ (?)	16+4		2	34	-	+	Le
Symplezidium Trev.	-	16+4	L	2_			±	Le
Subfam. Lejeuneoideae Mass.					L	ļ		
Cyclolejeunea Evans (see 4.5)	-	12+4	n	2	26	-	+	Le
Omphalanthus Lindenb. (see 4.5)	-	12+4	n	2	22	-	+	Le

Table 2. Conspectus of sporophyte characters.

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radial. Cells in the central part are subquadrate to rectangular, in the apical part rectangular to rhombic (PI. I, figs. 5-6). Except for the smooth base of the capsule the inner tangential walls of the cells are covered with yellow-brown, sheet-like thickenings, except for 4-12 pitted regions ("fenestrae"), which appear as depressed areas in SEM micrographs (PI. II, figs. 3-5). CRANDALL-STOTLER & CEISSLER (1983) showed, both by SEM surface examination and by LM transverse sections, that these fenestrae are holes in the cell walls of mature valves. The fenestrae are circular to oblong in shape. The thickened cells are normally plurifenestrate, but in the apical part the number of fenestrae is usually lower (4-6 versus 6-12) and occasionally reduced to only one ("monofenestrate").

In the central part of the valve 5-7 ridges are present, consisting of narrow-rectangular cells which protrude from the valve surface (PI. II, figs. 4-5). Five ridges are present in type "2" of the fenestrate capsules (characterized by the presence of 30-38 elaters, see 4.2.4); seven ridges are found in type "1" capsules (with 72 elaters, see under 4.2.4). Both apical and basal ends of the ridges are formed by tapering cells. In the capsule base they are short and blunt and protrude shortly into the smooth capsule base (PI. II, fig. 5); in the apical part of the valve they are long and narrow and protrude into the radially arranged cells (PI. II, fig.4). In a closed capsule the ridges separate the vertically arranged piles of spores that are adjacent to the inner surface of the valve (see 4.2.6.).

4.2.3. Valve lateral margin

In lateral view the cells of the outer valve layer appear to be covered with a wrinkled surface and have a narrow linear pit. The inner valve layer is very thin ans SEM examination shows hardly more than the margin of the plurifenestrate thickenings of the inner tangential wall. Elater attachment is seemingly only on to the surface of the thickening layer (PI. II, fig. 6).

4.2.4 Elaters (Plates I-III, XI)

Elaters in the fenestrate-type capsules are regularly distributed over the inner surface of the apical region. In a closed capsule they are in a vertical position and attached by their broadly dilated bases to the smooth inner capsule base (PI. III, fig. 3). The elaters, at equal distances from each other, are arranged regularly as is clearly reflected in the attachment pattern on the capsule base (PI. I, fig. 5). As to the number of elaters per capsule, two types exist.

In type "1" of fenestrate capsules the valves have alternately 16 (1+3+5+7) elaters or 20 (2+4+6+8) elaters, totalling 72 elaters per capsule (PI. XI, fig. 1). This capsule type is found in most genera of Ptychanthoideae (Tab. 2), but in *Frullanoides* only 68 elaters (valves with 16 (1+3+5+7) or 18 (2+4+6+6) elaters) and 56 elaters (valves with (1+3+5+7) or (2+4+6) elaters) have been found. We assume that these lower numbers are due to the loss of elaters during capsule dehiscence and spore dispersal.

In type "2" of fenestrate capsules in the Ptychanthoideae the valves have alternately 9 (1+3+5) or 6 (2+4) elaters, totalling 30 elaters per capsule (Pl.

XI, fig. 2). This arrangement is normally present in Acrolejeunea (except A. fertilis), Lopholejeunea, Schiffneriolejeunea, and in Frullanoides bahamensis and F. corticalis (see also Chapter I: Pl. XXXII, fig. 3). In Acrolejeunea fertilis the valves have 9 (1+3+5) or 10 (2+4+4) elaters, thus totalling not 30 but 38 elaters.

The length of the elaters is correlated with the place of attachment, hence a considerable variation observed: $260-550 \mu m$. The elaters are $(15-)18-20-(-25) \mu m$ wide, and monospiralled by a well developed, yellow-brown thickening band, which is c. 4 μm wide. The thickening band encircles the free, flattened, suborbicular basis of the elater and extends to just below the apical attachment at the valve (PI. II, fig. 6). Close examination of elaters shows ornamentation with very small, randomly scattered punctae on the spiral band and small, pit-like depressions in the elater wall just adjacent to the spiral (PI. III, fig. 4). These punctae are reported for *Frullanoides densifolia* (Chapter I), *Spruceanthus marianus* (CRANDALL-STOTLER & GEISSLER 1983) and *Marchesinia brachiata* (GEISSLER & GRADSTEIN 1982).

4.2.5 Spores (Plates VII-VIII)

The mature spores undergo precocious germination; consequently they are green and relatively large, $38-65 \mu m$ in diam. Within the capsule the spores are isodiametric and possess a ± regular, polyhedral shape with eight pentagonal or hexagonal facets. Upon sporeling development spores turn globose. The distal facet of the spore is always somewhat larger than the proximal facets (PI. III, figs. 2-3). The spore surface is ornamented in various ways (see below at) and includes one "rosette" per facet, hence a total of eight rosettes per spore. The regular shape of the spores of fenestrate capsules greatly contrasts with the irregular spore shape in the nodular-type capsules (see below at 4.7.3).

Spore ornamentation is developed prior to tetrad separation, as has been shown for *Spruceanthus marianus* by CRANDALL-STOTLER & GEISSLER (1983).

4.2.6 Spore storage and elater arrangement in a closed capsule (Plate III)

Spore storage and elater arrangement have been studied by means of longitudinal and transverse sections of a closed capsule. Longitudinal sections were taken along the valve dehiscence lines, since this plane of sectioning provides the most regular view of the inner capsule. Both sections show a very regular arrangement of the elaters, which intersect the spore mass at equal distances from each other. The spore mass is made up of square vertical columns, with an elater on each corner, in which the individual spores are piled in tetrads (Pl. III, figs. 5-6). Tetrads are made up of two perpendicularly arranged pairs of spores. The spores of each pair are parallel to one another. The attachment of the spores in the tetrads is located in the centre of each column. Transverse sections of the capsule show that the orientation of the spores in adjacent columns is alternate (Pl. III, fig. 6). This configuration is sometimes blurred by the oblique orientation of spores after the division of the spore mother cell (Pl. III, fig. 6: arrow). Spores of adjacent columns have their distal facets facing each other.

4.2.7 <u>Sporeling</u> (Lopholejeunea-type and Frullania-type (Chapter I: Plate VI, figs. 6-7)

A "Lopholejeunea-type" sporeling has been found in the following genera with fenestrate-type capsules: Lopholejeunea, Archilejeunea, Mastigolejeunea (FULFORD 1942a-c), Thysananthus (FULFORD 1956), Trocholejeunea (INOUE 1958, sub Brachiolejeunea), Ptychanthus (NEHIRA 1966), Spruceanthus (NEHIRA 1966) and Acrolejeunea (GRADSTEIN 1975).

In the Lopholejeunea-type sporeling endogenous germination leads to an increase in size of the spores, the spore wall stretching to accommodate this increase. In this sporeling type the number of cells in the enlarged spore varies from 4 to 20 before the development of the leafy shoot starts. Cermination is precocious, i.e. it takes place inside the capsule. The shape of the spore changes from isodiametric with eight facets to more or less sphaerical. The ornamentation of the exine is still visible during this enlargement and forms an even covering (FULFORD 1942b), although the rosettes become less clear. The development of the Frullania-type sporeling, reported in Frullania (e.g. INOUE 1958; NEHIRA 1966) and Bryopteris (STOTLER & CRANDALL-STOTLER 1974), is identical but starts with a larger number of protonemal cells (20-50; SCHUSTER 1966). The number of cells in the enlarged spore of the Lopholejeunea-type thus overlaps slightly with that in the Frullania-type: 4-20 versus 20-50. When ± 20 cells are counted in the enlarged spore it may become difficult to determine the sporeling type, as has been found in Trocholejeunea sandvicensis where both types are reported (INOUE 1958, sub Brachiolejeunea; NEHIRA 1966, 1974, 1983, sub Brachioleieunea).

After emergence of the mature protonema 3(-5) primary leaves are formed, which are small, plane and ovate (FULFORD 1942a-c). Each new primary leaf is larger than its predecessor. The sporeling at this stage is rather compact. Usually the third primary leaf is followed by the juvenile leaves, which are much larger in size and saccate-inflated with the lobule nearly as large as the lobe. The first, narrow lanceolate underleaf is formed at the same time as the first juvenile leaf.

4.3 Nodular-type capsules in the subfam. Ptychanthoideae (Plates IV-V)

Present in: Blepharolejeunea, Brachiolejeunea, Dicranolejeunea, Lindigianthus, Neurolejeunea, Odontolejeunea, Stictolejeunea, Symbiezidium.

In this capsule-type the valves remain suberect after dehiscence: the central part remains concave and the lateral parts become \pm plane (Pl. IV, fig 1), allowing the spores to disperse through relatively narrow slits (see 4.4). The valves are two cell layers thick in the upper half, and 3-4 layers thick in the lower half. Lateral view shows the outer and inner valve layers to be \pm equally thick.

4.3.1 Valve outer surface

The outer cells of the valves are arranged radially. The cells are rather small (30-45 x 15-35 μm) and elongate-hexagonal in the centro-basal part of the valve; much larger (35-65 x 30-55 μm) and quadrate to rhombic in the apical part. The valves are bordered by a single row of small (15-30 x 10-25 μm), quadrate-rectangular cells. In the extreme basal-lateral part of the valve, at the lateral end of the valve dehiscence line, a few cells with \pm equally thickened walls are present.

Cells of the outer valve layer possess yellowish, sinuose-nodulose thickenings in the angles but not on the intermediate walls. The trigones tend to become confluent in the basal and central part, but in the apical part the narrowly tapering and twisted ends of the thickenings end seemingly parallel to each other (PI. IV, fig. 4). The centro-basal part of the valve is characterised by the presence of small cells with thickenings that are more strongly developed than elsewhere. This valve portion is therefore rather inflexible. The valve border cells have enlarged trigones along the valve margin, where they form a continuous line of more or less triangular elements. The trigones in the opposite angles are smaller and confluent with the trigones of the adjacent cells (PI. IV, fig. 4).

4.3.2 Valve inner surface and capsule base

SEM examination shows that the inner valve layer and the capsule base have a smooth surface (PI. IV, figs. 5-6). The outline of the nodules in the inner valve layer thus cannot be studied with SEM. LM analysis shows roundish, nodular thickenings present in the angles and on the intermediate, radiate walls of all cells except those in the base of the capsule (above the seta attachment) and in the basal-lateral part of the valves at the lateral end of the dehiscence lines. Where they are present, the yellowish, nodular thickenings are uniformily developed throughout. In *Stictolejeunea*, the thickenings may become rather elaborate and coalescent; the resulting pattern then superfically resembles a plurifenestrate thickening layer (PI. X, fig. 1).

4.3.3 Valve lateral margin

In lateral view the cells of the outer valve layer appear to be covered with a wrinkled surface and have a narrow linear pit. Whether the surface of the outer cells is wrinkled in reality or if this is due to SEM preparation could not be established. The cells of the inner layer show a smooth radial wall with, in addition, a large, rounded to elliptic pit. Frequently the whole cell wall has disappeared and the nodules inside the cells of this layer are only indistinctly visible (Pl. V, fig. 4). The elaters are attached only to the surface of the inner tangential wall.

4.3.4 Elaters (Plates IV-V, XI)

Two types of elaters are distinguished in the nodular-type capsules: marginal elaters, which are attached to the apical part of the valve margin and to the capsule base, and "additional" elaters, which are attached with both ends to the inner valve surface (PI. IV, figs. 5-6).

Opposite valves have five marginal elaters (one apical and four lateral), or six marginal elaters (Pl. IV, fig. 5). The length of the elaters is correllated with the place of attachment: the apical ones are $325-470 \ \mu m$ long, the lower-most lateral ones only $220-340 \ \mu m$. The apical end of the marginal elaters is only slightly dilated, but the basal end is dilated into a wide, suborbicular plane (Pl. IV, fig. 6).

The "additional" elaters are located on the central and lateral parts of the valve (Pl. IV, fig. 6). These elaters differ from the marginal elaters in their narrowly tapered ends. Unlike the marginal elaters the "additional" elaters remain attached by both ends to the valve at capsule dehiscence. One central elater, 280-400 μ m long, and two lateral elaters, 145-270 μ m long, are present on each valve. The total number of elaters in a nodular-type capsule is 2x(1+4) + 2x6 + 4x3 = 34.

Both marginal and additional elaters are c. 16-20 μ m wide. They are monospiralled by a c. 4 μ m wide thickening band. The thickenings are pale yellow to almost colourless and often incompletely developed, consisting of wall thickenings only (PI. V, fig. 3).

4.3.5 Spores (Plates V, VIII-IX)

The mature spores undergo precocious germination; consequently they are green and relatively large, 45-120 μ m in length. Within the capsule the shape of the spores is variable. In a longitudinal section the spores are quadrate to rectangular (PI. V, fig. 2), becoming somewhat irregular near the valves, whereas in a transverse section they are ± rectangular to trapezoid (PI. V, fig. 5-6).

4.3.6 Spore storage and elater arrangement in a closed capsule (Plate V)

Spore storage and elater arrangement have been studied by means of longitudinal and transverse sections of a closed capsule. Longitudinal sections were taken through the valve dehiscence lines, since this plane provides the most regular view of the inner capsule.

A transverse section shows the marginal elaters to be concentrated along two axes, meeting at right angles in the centre of the capsule and dividing the capsule into four compartments. The alternate location of the elaters on adjacent valves causes the oblique zig-zag pattern in the axes (Pl. V, fig. 6: m.e.). Each compartment in the capsule contains a mass of spores, arranged in tetrads. In each compartment this spore mass is intersected only by the three additional elaters (Pl. V, fig. 6: a.e.).

In longitudinal section the spores are piled up like paired bricks, each spore pair alternating with the pairs above and below (PI. V, fig. 2).

The attachment of the four spores in a tetrad becomes visible when one or two spores are removed (Pl. V, fig. 6: arrow).

4.3.7 Sporeling (Lejeunea-type) (Chapter 1: Plate VI, figs. 1-5)

A "Stictolejeunea-type" sporeling has been found in the following genera with nodular-type capsules: Stictolejeunea (FULFORD 1942a), Symbiezidium and Dicranolejeunea (FULFORD 1956) and Blepharolejeunea (VAN SLAGEREN &

In the *Stictolejeunea*-type sporeling endogenous germination leads to an increase in size of the spores which is accommodated by stretching of the wall. In this sporeling type an eight-celled protonema is formed (two rows of four cells; FULFORD 1956) before the development of the leafy shoot starts. Germination is precocious, i.e. taking place inside the capsule. The shape of the spore changes from rectangular-trapezoid to more roundish-rectangular (Chapter I: Pl. VI, figs. 1-2). The ornamentation of the exine is still visible but less dense. The sporeling is initiated on one of the ends of the enlarged spore and three plane, ovate and increasingly large primary leaves are formed, followed by the first juvenile leaf and its accompanying underleaf, as well as by its large, saccate-inflated appearance, the third primary leaf may also be more or less saccate-inflated (Pl. VI, fig. 4). The first underleaf is ovate-lanceolate in outline and the ventral merophyte is only two cell rows wide here.

The Stictolejeunea-type sporeling is supposedly different from the Lejeunea-type in that it should "not grow by means of an apical cell" (NEHIRA 1974), whereas the Lejeunea-type sporeling should have an apical cell with three cutting faces. Recently NEHIRA (1983) reported a break-down of this distinction and united both types in a more broadly defined Lejeunea-type.

4.4 Discussion: a comparison of the fenestrate-type and the nodular-type sporophyte

The two sporophyte types in the Ptychanthoideae show similarities as well as clear differences in a number of characters. Based on the observed structural differences, some hypotheses may be formulated with respect to a possible mechanism of spore dispersal.

As to structural features, similarities between the fenestrate-type and the nodular-type sporophyte are as follows: 1) the presence of nodular thickenings in the cells of the outer layer of the valves, and 2) the number of cell layers of the valves in cross section: 2 in the upper half, 3-4(-5) in the lower half.

The structural difference between the capsule types, as described above, are much more distinct and include: 1) the distribution and development of the nodules in the cells of the upper valve layer, 2) the thickenings of the cell layer of the inner valve, 3) the width of the outer layer as compared to the inner layer(s) in cross section of the valve, 4) the number of elaters per capsule as well as the development of the elater spiral, 5) the arrangement of the elaters on the valve, 6) the shape of the spores, 7) the arrangement of the spore ornamentation a further difference between the capsule types is observed in the presence and number of rosettes: always present and a fixed number of eight in the nodular-type capsule (see 4.7). In addition, a conspi-
cuous difference in the shape of the valves after capsule dehiscence is seen. In the fenestrate-type capsules the upper half of the valve curves outward, while the basal half remains more or less convex; in the nodular-type capsule the entire valve remains suberect and more or less convex (compare Pl. I, fig. 1 and Pl. IV, fig. 1).

In their valve shape and thickenings (as well as in the shape and ornamentation of the spores, see 4.7), the two sporophyte types of the Ptychanthoideae show very different affinities. The fenestrate-type capsule resembles the capsules of *Bryopteris* and *Frullania*; the nodular-type capsule those of the subfam. Lejeuneoideae (see Table 2).

Based on the different valve shapes after dehiscence and the presence or absence of elater spirals the following hypotheses regarding spore dispersal mechanisms may be formulated.

As to fenestrate-type capsules, which are very similar to those of Frullania in several important aspects, we assume that spore dispersal is likely to be similarly achieved, though detailed observations, in support of this assumption, are unfortunately lacking. Spore dispersal in Frullania has been described by GOEBEL (1895), KAMERLING (1898) and in greater detail by INGOLD (1939), and is known as "spiral-spring-mechanism". In this mechanism evapora tion causes contraction in the cells of the outer layer of the valves, up to the point where the created tensions lead to an outward bending of the valves along the four predetermined lines. Through this movement the elaters become stretched. The attachment of the dilated ends of the elaters to the capsule base is less strong than to the apical part of the valves and, almost simultaneously, the elaters break free and the stretched spirals return to their original shape. During this movement the spore mass is lifted from the capsule and hurled away. The stiff, inner thickening layer of the valves probably causes the characteristic shape of the dehisced capsule valves, which remain \pm convex in the central and basal part and plane to concave in the apical part. This dissemination mechanism, in which the elaters act as spiral springs, allows the spores to spread easily from the widely opened capsule.

Regarding the nodular-type capsules, in which the valves remain erect after capsule dehiscence and the elaters have reduced spirals, we assume that, as in fenestrate-type capsules, evaporation may cause contraction in the cells of the outer valve layer, up to the point where the valves split along the four predetermined lines and move upwards. Since the nodular thickenings are more strongly developed in the central part of the valve and weaker in the lateral and apical parts (see 4.3.1), the tensions may also be unequal. Probably the greatest tensions will be developed in the lateral and apical parts and may force the convex valve to become flattened, whereas the nodules of the central part may prevent such a movement. The movement of the valve may thus be very limited notwithstanding the weak thickening of the inner valve layer, which might more easily give way (unlike the inner layer of the fenestrate-type capsule). Furthermore, taking into account the characteristic form and arrangement of the marginal elaters, capsule dehiscence may initially cause only a loosening of the compact spore mass. The three "additional" elaters, present on each of the four valves, may, in fact, be more effective as spore dispersal agents than the marginal elaters since they intersect the spore mass of each of the four compartments. Since upward movement of the valves may be repeated under subsequent dry and damp conditions, dissemination of the entire spore mass may eventually result. The process is presumably much more slow than in the fenestrate capsules.

4.5 Sporophyte of Bryopteris, Frullania, Cyclolejeunea and Omphalanthus

4.5.1 Bryopteris

The sporophyte of *Bryopteris*, which was described in detail by CRANDALL (1967) and STOTLER & CRANDALL-STOTLER (1974), shows both overall similarities and marked differences to the fenestrate-type sporophyte in the Pty-chanthoideae. Differences are: 1) the seta is of DOUIN's general type and consists of 30-100 cells in transverse section, 2) the elaters are irregularly distributed over the apical part of the valve (1974: fig. 85), and their number is not fixed: 60-80, 3) the sporeling is of the *Frullania*-type, and 4) the thickenings of the inner valve layer are reticulate to monofenestrate, which tend to become plurifenestrate in *B. trinitensis* (1974: fig. 77). In the Ptychanthoideae the thickenings of the inner valve layer are plurifenestrate and tend to become monofenestrate in the apical part only (see 4.2.2), so the state of this character in *Bryopteris* is only gradually different. In general, the sporophyte illustrates the intermediate position of *Bryopteris* between *Frullania* and the Ptychanthoideae (see Table 2).

4.5.2 Frullania (Plates VI, figs. 5-6; XI, fig. 3)

Only one species of this large genus (F. ericoides) has been examined with SEM. In general form the sporophyte is similar to the fenestrate-type sporophytes of the Ptychanthoideae, for example in its non-articulate seta, the location of the thickenings in the outer valve layer, the regular arrangement of the elaters on the apical part of the valves. The sporophyte differs, however, in the following characters: 1) the seta is of DOUIN's general type and within the genus considerable variation in the number of cells in cross section is reported to occur (SCHUSTER 1966, STOTLER 1969), 2) the innermost rows of elaters on the valve are oft incomplete (Pl. VI, fig. 5: elater arrangement 2+4+6+8+10+4; a similar valve in the Ptychanthoideae has 2+4+6+8 elaters), 3) the variation in the number of elaters is considerable within the genus: SCHUSTER (1966: fig. 64-2) reports 35 elaters for F. asagayana, VANDEN BERGHEN (1976) reports a variation between 48 (F. lindenbergii) and c. 100 (F. arecae) elaters per capsule, and SPRUCE (1884) reports 30-36 elaters per valve, hence 120-144 per capsule, 4) the inner valve layer possesses, as in Bryopteris, reticulate to monofenestrate thickenings, which never become plurifenestrate, and 5) the sporeling is of the Frullania-type.

4.5.3 Cyclolejeunea (Plates VI, figs. 3-4; XI, fig. 5)

Data on the sporophyte of *Cyclolejeunea* are presented here for the first time (LM analysis of *C. convexistipa* only). In general form the sporophyte is simi-

lar to the nodular-type sporophytes of the Ptychanthoideae: e.g. in the articulate seta, the outline of the valves after capsule dehiscence, the thickenings of the outer and inner valve layers, and the shape of the elaters and spores. The sporophyte differs, however, in the following characters: 1) the seta is of the *Lejeunea*-type, consisting of 12+4 cells in cross section, 2) the closed capsule is considerably smaller in diameter: c. 0.25 mm (in the Ptychanthoideae c. 0.5 mm), 3) the elaters are smaller, only (115-)180-215 μ m long and 10-12 μ m wide, 4) the valves bear alternately four or five marginal elaters (Pl. VI., fig. 3) of which the most lateral ones differ in their acute basal ends, which remain attached to the valves at capsule dehiscence, and 5) each valve possesses only two additional elaters on the inner surface, which are 120-130 μ m long. The total number of elaters is thus 2x(1+4) + 2x4 + 4x2 = 26.

4.5.4 Omphalanthus (Plates VI, figs. 1-2; X, fig. 2; XI, fig. 6)

In general form the sporophyte of Omphalanthus is similar to the nodular-type sporophyte of the Ptychanthoideae: e.g. in the articulate seta, the shape of the valves after capsule dehiscence, the thickenings in the outer and inner valve layers, the shape of the spores, and the number of (marginal) elaters: 22 (= 2x5 + 2x6). Differences are observed in a number of characters: 1) the seta is of the Lejeunea-type, 2) the closed capsule is considerably smaller in diameter than in the Ptychanthoideae: 0.35 mm versus 0.5 mm, 3) the elaters possess 1-2 brownish spirals that are c. 5 µm wide and sometimes incompletely developed, 4) the inner surface of the valves is smooth but in the central part eight parallel "ridges" are found, which together occupy a more or less hexagonal area (Pl. VI, fig. 1; X, fig. 2). The central ridge is 325-360 µm long, the lateral ridges are gradually shorter, up to only 180-200 µm in length. These ridges are indistinctly seen in the SEM micrograph of 0. platycoleus (GEISSLER & GRADSTEIN 1982; fig. 6). Maybe the ridges represent elaters, but at present their origin and function is still unclear. SEM analysis of transverse sections of closed capsules may provide more insight in this character of the capsules of Omphalanthus.

4.6 The seta

The two large genera of the fam. Jubulaceae show a remarkable difference in the seta. The seta of *Frullania* is large and of the general type, and a considerable variation in the number of cells in cross section is reported: 54-106 (SCHUSTER 1966, STOTLER 1969). The seta of *Jubula* is of the specialized "*Brachiolejeunea*-type" with 16 outer and 4 inner cells in cross section. Since this organisation is also present in several subfamilies of the Lejeuneaceae, MIZUTANI (1961) accordingly has considered *Jubula* to be a member of that family.

Within the three considered subfamilies of Lejeuneaceae a tendency towards reduction and organisation is observed from the Bryopteroideae to the Lejeuneoideae (Table 2). As in *Frullania*, the seta of *Bryopteris* is of the general type and the number of the cells is not fixed. Unlike *Frullania* and most Pty-

chanthoideae with a fenestrate-type capsule, the seta of *Bryopteris* is reported to be "articulate" by CRANDALL (1967) and STOTLER & CRANDALL-STOTLER (1974), which is somewhat surprising since the seta of the taxonomically allied groups is invariably non-articulate. Moreover, the indication "articulate" in their publications seems to be based on examination of only young setae, prior to elongation. Our examination of young setae in the majority of genera of Ptychanthoideae shows that in all genera the seta is articulate at this stage of development, including those genera in which the seta is non-articulate. We would therefore emphasize that the seta-type is to be established in elongated setae only.

In the Ptychanthoideae with fenestrate-type capsules the most common type of seta is the non-articulate seta, but in several genera an articulate seta is found (Table 2). After elongation the outer cells of these articulate setae are short rectangular and $(60-)95-130 \mu m \log n$.

MIZUTANI (1961) has reported an articulate seta in *Thysananthus*, but we found only non-articulate setae in this and related genera (see Table 2). The sporophyte of *Verdoornianthus* was described by GRADSTEIN (1977). Unfortunately the type of seta could not be established since only immature setae were present in the specimens examined.

The setae of genera in the Ptychanthoideae with nodular-type capsules are articulate (Table 2). After elongation the outer cells are rectangular and 140-200 μ m long; these setae are therefore more slender than the articulate setae of genera with a fenestrate-type capsule (see above). The seta of *Stictolejeunea* is reported as (presumably) non-articulate (GEISSLER & GRADSTEIN 1981; GRADSTEIN 1985), which would be unique within this group of Ptychanthoid genera; however the observations were derived from immature setae. Mature and elongated setae are needed before a definite conclusion can be drawn.

In cross section the seta of the Ptychanthoideae normally consists of an outer row of 16 cells surrounding an inner row of 4 cells. Considerable variation is reported, however (Table 2). A larger number of both inner and outer cell rows, known from *Trocholejeunea sandvicensis* (MIZUTANI 1961, GROLLE 1982), is now also reported for *T. infuscata* (Chapter I: Plate VI, figs. 10-11). Apparently, this seta structure is characteristic for the entire genus. Morphologically, the seta of *Trocholejeunea* is similar to the seta of *Bryopteris trinitensis* and thus bridges between the Ptychanthoideae and the Bryopteroideae, as has been pointed out by GRADSTEIN (1975).

In the subfam. Lejeuneoideae the seta is of the specialized *Lejeunea*-type and is organized in an outer row of 12 cells, surrounding an inner row of 4 cells.

4.7 A conspectus of sporoderm ornamentation

4.7.1 Introduction

Several reviews have been published on spore morphology of liverworts and various types of spores and ornamentation have been described. ERDTMAN

(1957, 1965), ONO (1966), MIYOSHI (1966), SCHUSTER (1966) and BOROS & JARAI-KOMLODI (1975) based their reviews on LM observations; TAYLOR et al. (1974) based their review on SEM observations.

The results are based on SEM observation of most genera, but from several genera data are obtained from LM observations (*Ptychanthus, Cyclolejeunea*) or are partly extracted from the literature (*Lopholejeunea*: SCHUSTER 1980; *Marchesinia*: GEISSLER & GRADSTEIN 1982; *Ptychanthus: MIZUTANI* 1961, ONO 1966, MIYOSHI 1966; Schiffneriolejeunea: GRADSTEIN & TERKEN 1981, UDAR & AWASHTI 1982, 1983; *Verdoornianthus*: GRADSTEIN 1977; *Lindigianthus*: KRUIJT & GRADSTEIN 1985; *Neurolejeunea*: GRADSTEIN 1985; *Stictolejeunea*: GEISSLER & GRADSTEIN 1981, GRADSTEIN 1985).

4.7.1.1 General outline of the spores

The spore wall in liverworts consist of three layers: 1) the intine, which is relatively structureless (CLARKE 1979), 2) the exine, which is strong and consists of highly resistant material (sporopollenin, TAYLOR et al. 1974), and 3) the perine, which may be present as outermost sculptures. In liverworts the perine is mainly present in the order of the Marchantiales (MIYOSHI 1966). Since the perine is absent in the Lejeuneaceae and Jubulaceae (SCHUSTER 1966) the examined, sculptured sporoderm is the exine layer.

After division of the spore mothercell the formation of four spores, which are associated in a tetrad, is established. At least in the initial stage all spores have polarity: the proximal pole points towards the centre of the tetrad while the opposite, distal pole is not in contact with the other spores. In addition, the proximal pole, which is the attachment point of the spores in the tetrad, is visible by its irregular granular surface whereupon the characteristic ornamentation lacks (e.g. Pl. VIII, figs. 3-4). An aperture or trema is often present on the proximal pole of the spore and consists of persistent monolete, trilete or deformed trilete fissures (MIYOSHI 1966: spore type 1 and 2).

Based on the presence or absence of a persisting trema or tetrad scar, SCHUSTER (1966) distinguished between apolar, cryptopolar and polar spores. The apolar spores are subdivided in indehiscent spores (present in a.o. *Frullania* and Lejeuneaceae) and irregularly dehiscing spores. MIYOSHI (1966) recognized five basic types of spores, using characters of the tetrad scar, polarity and cell stage: 1) trilete, 2) deformed trilete, 3) cryptopolar (1-4 all unicellular), and 5) multicellular. The spores of *Ptychanthus, Spruceanthus* and *Trocholejeunea* (Lejeuneaceae) were reckoned to type 4 (i.e. apolar, unicellular and lacking a tetrad scar) and *Frullania* was placed in type 5 (i.e. apolar, lacking a tetrad scar but always multicellular in a mature capsule). Spores of Lejeuneaceae are thus atreme, i.e. without distinct aperture or trema (ERDTMAN 1957, 1965).

4.7.1.2 Sculpture/ornamentation

Differences in the sculpture or ornamentation of the exine are the most impor-

tant features for the identification of spores and spore types. A great many terms have been proposed for the description of this ornamentation. Two types of descriptive terms are distinguished: 1) terms for the ornamentation processes themselves (BOROS & JARAI-KOMLODI 1975: verruca, bacula etc.), and 2) terms for the resulting configurations (MIYOSHI 1966: verrucate, baculate etc.).

ONO (1966) recognized four basic spore types in the order Jungermanniales: 1) irregular reticulate, 2) papillate, 3) echinulate, and 4) granulate with rosettes.

Since spore ornamentation patterns are often complex and difficult to describe adequately we have adopted the above mentioned terminology of BOROS & JARAI-KOMLODI (1975).

The terms "mamillae" (KAMIMURA 1972) and "papillae" (e.g. GRADSTEIN 1975; CRANDALL-STOTLER & GEISSLER 1983), sometimes used in spore descriptions, can better be avoided since they only indicate the ontogeny of the ornamentation (TAN 1979).

4.7.2 Spores of fenestrate-type capsules in the Ptychanthoideae

All genera of Ptychanthoideae with fenestrate-type capsules possess spores with a granular surface on which scattered processes and rosettes are produced. Three types of sporoderm ornamentation are found.

1. "Spinulate" spore type (Plate VII, figs. 1-5)

Present in: Acrolejeunea, Frullanoides, Lopholejeunea, Marchesinia, Ptychanthus, Schiffneriolejeunea, Spruceanthus, Trocholejeunea, Thysananthus.

Spore size: (28-)35-50 µm.

Ornamentation: basal surface granulae: 0.1-0.3 μm in diam.; length surface spinulae: 1.0-2.0 μm; number rosettes: 8; diameter rosettes: (4-)6-11(-13) μm; length rosette spinae: (1.5-)2.5-6.5 μm; number rosette spinae: (4-)8-10(-17).

This type is present in the majority of Ptychanthoid genera with fenestrate capsules. Considerable variation is observed with respect to the diameter of the rosettes and the length of the rosette spinae. The spore surface is densely covered with very small, globose granules. Scattered over this surface are spinulae, covered by wartlike processes and topped with a small head with several angles (PI. VII, fig. 1), and orientated parallel to or somewhat curved towards the spore surface. In a SEM micrograph the angular heads appear as "whitish". In addition, a rosette is present on each facet of the spore, consisting of 1-2 subregular circles of spinae around depressions or foramina (KAMIMURA 1972) in the surface. According to CRANDALL-STOTLER & GEISSLER (1983) the foramen is a thin area in the spore wall, with a possible function in water uptake and conservation of internal water. The inward

projecting spinae form a stellate pattern. The spinae of the rosettes and the surface spinulae are of the same basal outline and only differing in size, those of the rosettes being at least $1\frac{1}{2}$ times as long. With malformed rosettes the depression is sometimes obsolete (observed in *Frullanoides densifolia* and *Acrolejeunea fertilis*: Pl. VII, figs. 3-4).

2. "Verrucate" spore type (Plate VII, fig. 6)

Present in: Archilejeunea.

Spore size: (27-)35-45 µm.

Ornamentation: basal surface granulae: 0.1-0.2 μm in diam.; surface verrucae: 1.5-2.5 x 0.6-0.8 μm; number rosettes: 8; diameter rosettes: 6-12 μm; length rosette spinae: (1.6-)2.5-5.0 μm; number rosette spinae: 6-14.

This type differs from the spinulate type by the presence of verrucate instead of spinulate processes. The rosettes, formed by spinae, are clearly defined.

3. "Baculate-spinulate" spore type (Plate VIII, figs. 1-2)

Present in: Caudalejeunea, Mastigolejeunea.

Spore size: 33-40 µm.

Ornamentation: basal surface granulae: 0.1 μ m in diam.; surface clusters: 1.5-3.0 x 1.0-1.5 μ m; number rosettes: 8; diameter rosettes: 7-11 μ m; length rosette spinae: 2-5 μ m; number rosette spinae: 8-15.

This ornamentation is observed in *Caudalejeunea hanningtonii* and in *Mastigolejeunea auriculata* and *M. humilis*. The surface is covered with minute granulae, similar to the spinate and verrucate spore type. Scattered over the spore surface are clusters of spinulate to baculate processes, which are tipped with irregular, knob-like heads, appearing "whitish" in SEM micrographs. The rosettes are clearly defined, the spinae are tipped with similarly shaped knobs.

4.7.3. Spores of nodular-type capsules in the Ptychanthoideae

Spore ornamentation in this group is highly variable and serves to distinguish genera or even (*Blepharolejeunea*) species.

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1. Blepharolejeunea (Plate VIII, figs. 3-4, 6)
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Spore size: 35-60 x 15-25 μ m.

Ornamentation: basal surface granulae: 0.1-0.2 μm in diam.; sporoderm verrucae: 1.0-2.5(-7.0) x 1.0-2.5 μm; number rosettes (in B. incongrua only): ± 8; diameter rosettes: 8-10 μm; length rosette spinae: 2.5-5.0 μm;

number rosette spinae: 7-9.

B. incongrue differs from B. securifolie by the presence of rosettes. The rosettes vary considerably in outline: from \pm indistinct to very pronounced (Chapter II: Pl. VII, figs. 4-6). The rosette spinae are ornamented with small, wartlike processes.

2. Brachiolejeunea (Plate IX, figs. 1-2)

Spore size: $40-75(-105) \times 20-30 \ \mu$ m. Ornamentation: basal surface granulae: 0.1-0.2 μ m in diam.; sporoderm verrucae: 1.0-8.0 x 0.5-2.5 μ m.

The compound vertucae are covering the spore surface and their upper surface is ornamented with small punctae. In *B. laxifolia* the vertucae are regularly covering the sporoderm, but in *B. spruceana* some of the vertucae are more or less arranged in a rosette-like configuration (Pl. IX, fig. 2).

3. Dicranolejeunea/Odontolejeunea (Plate IX, figs. 3-4)

Spore size: $40-55(-110) \times 15-20(-40) \mu m$.

Ornamentation: spore surface: smooth; sporoderm verrucae: 1.0-6.0 x 0.5-1.0 μm; number rosettes: ± 10; diameter rosettes: 4-7 μm; length rosette spinae: 1.5-3.5 μm; number rosette spinae: 7-11.

The sporoderm verrucae are irregular vermiform in outline. The spinae of the rosettes and the verrucae are covered with small, wartlike processes. The stellate configuration of the rosette spinae is rather irregular. UDAR & AWASTHI (1983) present SEM micrographs of two *Dicranolejeunea* species. Their description is generally similar to ours, except for the low number of rosettes (1-2 in *D. gilva*; 3-6 in *D. yoshinagana*). These are probably based on examination of only a part of the spore surface. The difference in granular ornamentation of the "papillae" (i.e. the verrucae) between the two species, reported by them, is unlikely since these granular ornamentations on the different surface processes are observed in all species of Ptychanthoideae with nodular-type sporophytes. STOTLER & CRANDALL (1969) erroneously report the absence of rosettes in *D. axillaris* (R.Ch. Kruijt, pers. comm.).

4. Neurolejeunea

Spore size: 45-70 \times 20-35 μm .

LM observation of *N. breutelii* spores shows the absence of rosettes and a sporoderm, which is ornamented by vermiform processes, resembling those of Brachiolejeunea laxifolia. 5. Stictolejeunea

Spore size: 40-50 x 15-25 µm.

SEM micrographs have been published by GEISSLER & GRADSTEIN (1981). There spore showed a smooth surface, ornamented by scattered verrucae and weakly developed rosettes (1981: Plate 5a). Our LM observations indicate the presence of 7-10 rosettes of c. 5 μ m in diameter.

6. Symbiezidium (Plate IX, figs. 5-6)

Spore size: $30-70 \times 10-25 \ \mu\text{m}$.

Ornamentation: spore surface: smooth; sporoderm verrucae: 1.0-6.5 x 0.5-1.0 μm; spore baculae (compound in strings): 6.0-25.0 x 0.5-2.0 μm; number rosettes: ± 8; diameter rosettes: 3.5-6.5 μm; length rosette spinae: 1.5-3.0 μm; number rosette spinae: 4-11.

On a smooth spore surface the following ornamentation is present: 1) verrucae, which are clustered into compound, vermiform processes (Pl. IX, fig. 5: v), 2) baculae, which are clustered into long strings, appearing as undulate ridges (Pl. IX, fig. 5: b), and 3) rosettes, consisting of rather small spinae, which are ornamented with wartlike projections (Pl. IX, fig. 5: r). The complex ornamentation, which is unique in the Ptychanthoideae, is similarly observed in the two species, currently recognized in this genus (S. barbiflorum and S. transversale, cf. GRADSTEIN & VAN BEEK 1985).

4.7.4. Spores of Bryopteris, Frullania, Cyclolejeunea and Omphalanthus

The spores of *Bryopteris* are isodiametric and 20-35 μ m in diam. The exine is thin and ornamented with verrucae and 6-10 rosettes '(CRANDALL 1967, STOTLER & CRANDALL-STOTLER 1974). The outline thus resembles at most the verrucate spore type of the fenestrate sporophytes of the Ptychanthoideae (see 4.7.2.).

The spores of *Frullania* are globose and 25-40 μ m in diam. The exine ornamentation is verruculose and there are numerous rosettes present (STOTLER 1969). The outline thus resembles *Bryopteris*.

The spores of Cyclolejeunea are irregular rectangular and 15-30 x 7-15 μm in size. The sporoderm is covered by vertucae of 1-2 μm in diam. and by a few (± five) clearly defined rosettes, which are c. 5 μm in diam. (unpublished SEM observations).

The spores of Omphalanthus are much larger than of Cyclolejeunea, narrow elliptical to oblong to \pm rectangular in outline and 55-80(-120) x 15-25(-40) μ m in size. The sporoderm is covered by irregular vertucae of 1-2 um in diam. and by numerous rosettes (up to 35!), which are clearly defined and c. 7-10

µm in diam. (SEM observation: Pl. VIII, fig. 5)

4.8 Concluding remarks

With respect to intrafamilial evolution of the Lejeuneaceae, MIZUTANI (1961) and SCHUSTER (1963) have independently listed primitive and advanced character states, and SCHUSTER (1980: 709) has hypothesised in more detail on major evolutionary trends within the family. In general, it is assumed that primitive members of Lejeuneaceae possess a massive axis and seta, are dioecious and lack asexual reproduction. Advanced members of the family show progressive reduction, especially of stem and seta, combined with more frequent presence of asexual reproduction and presence of autoecious inflorescences. As to sporophyte characters, both MIZUTANI (1961) and SCHUSTER (1963) assume a non-articulate seta with 16 outer cells rows. brown and thick capsule valves, and elaters with well developed, brownish spirals to be more primitive, and an articulate seta with 12 outer cell rows, colourless and thin capsule valves, and elaters with colourless and often incomplete spirals to be more advanced. Based on this concept, the genera of Ptychanthoideae fall into two distinct groups: 1) those with fenestrate-type capsules, and 2) those with nodular-type capsules. In the light of this difference generic relationships of these two groups may now be considered. since the sporophyte types have different affinities.

As is shown in Table 2, a fenestrate-type sporophyte is also present in *Bryopteris* and *Frullania*, which differ from the Ptychanthoideae, however, in their sporeling type (*Frullania*-type instead of *Lopholejeunea*-type) and in the thickenings of the inner valve layer (reticulate instead of fenestrate). It must be noted, however, that the *Lopholejeunea*-type differs from the *Frullania*-type sporeling only in the number of cells of the protonema before development of the leafy shoot (see 4.2.7) and that monofenestrate and plurifenestrate thickenings may be seen as extensions (over the tangential cell walls) of the reticulate-type of thickening (restricted to the radial cell walls) as has been hypothesised by SCHUSTER (1966). The differences thus seem only gradually. The difference in seta structure may seem more fundamental (general-type versus specialised-type), but it has been shown that the seta of *Trocho-lejeunea* bridges the two types (see 4.6).

Within the fenestrate-type sporophytes of the Ptychanthoideae two trends are observed: 1) a reduction in the number of elaters, and 2) seta articulate/non-articulate. The majority of the capsules have 72 elaters, but a reduction to 30 elaters is observed in *Acrolejeunea*, *Frullanoides*, *Lopholejeunea* and *Schiffneriolejeunea*. With the exception of *Acrolejeunea*, the genera with fewer elaters have an articulate seta instead of the non-articulate seta present in the majority of genera.

The differences between the fenestrate-type and the nodular-type sporophytes in the Ptychanthoideae are discussed above (see 4.4). The nodulartype sporophytes are in many respects similar to sporophytes found in the Lejeuneoideae (see 4.5), and the most important difference is only the further reduction of the seta in the Lejeuneoideae (only 12 cells in the outer row). The difference in the number of marginal and additional elaters, of which a considerable variation is expected due to variation in outline of the valves (e.g. MIZUTANI 1979a and PI. VI, figs. 1-4) seems less fundamental.

From the foregoing it appears that the genera of the Ptychanthoideae with nodular-type sporophytes are different to such an extent that a separate taxonomic status is needed to accomodate them. We therefore propose the creation of a tribe in the Ptychanthoideae, which unites all genera with nodular-type sporophytes:

Tribus Brachiolejeuneae van Slageren & Berendsen trib. nov.

Folia caulina in sicco suberecto-convolutiva vel late patula; cellulae loborum elongatae vel isodiametrae; trigonae cordatae vel simplices triangulares vel radiatae. Valva interior sporophyti cellulis nodulosis; sporae rectangulares-elongatae, germinatio modo Lejeuneae.

Stem leaves when dry suberect-convoluted to widely spreading; lobe cells elongated to isodiametric; trigones cordate to simple triangular to radiate. Inner layer of the sporophyte valve with nodules; spores rectangular-elongated, sporeling *Lejeunea*-type.

Within the tribe Brachiolejeuneae the following generic complexes are distinguished:

- Brachiolejeunea-Dicranolejeunea complex (including Brachiolejeunea, Blepharolejeunea, Dicranolejeunea, Odontolejeunea, Lindigianthus).
 As has been shown by GRADSTEIN (1975), the genera Dicranolejeunea and Odontolejeunea are closely related and a complex of these two genera has been established accordingly (1975: 146). The genus Blepharolejeunea was recently emended by VAN SLAGEREN & KRUIJT (1985; see also Chapter II), and unites several species, formerly placed in Brachiolejeunea and Dicranolejeunea. The relationship of Blepharolejeunea and Dicranolejeunea (e.g. in stem anatomy, oil body type) and that of Blepharolejeunea and Brachiolejeunea (e.g. branch- and innovation morphology) have been evaluated above (Chapter I: generic relationships; Chapter II: Table 1).
- 2. Symbiezidium complex.

This genus has been placed in the *Lopholejeunea*-complex (GRADSTEIN 1975) and in a generic complex of its own (SCHUSTER 1963, GRADSTEIN & VAN BEEK 1985). The genus stands somewhat isolated within the subfamily because of: 1) its unique, complex spore ornamentation (Pl. IX, figs. 5-6), and 2) its massive gametophyte (stem!), which is considered more primitive, and nodular-type sporophyte, considered more advanced.

3. Stictolejeunea-Neurolejeunea complex.

These two genera have been placed in one generic complex by SCHUSTER (1963) and GRADSTEIN (1975), based on gametophytic characters (evenly

thickened cell walls, ocelli). For a discussion of the relationships of this complex to the *Symbiezidium*-complex, already suggested by SPRUCE (1884), we may refer to GRADSTEIN (1985).

In this subdivision of the Ptychanthoideae, based on sporophyte types, the creation of a tribe, which contains all genera with a nodular-type sporophyte, evokes the creation of a tribe, containing all genera with the other, fene-strate-type of sporophyte. This second tribe is established by emending GRADSTEIN's (1975) tribe Ptychantheae:

Tribus Ptychantheae Bischler emend. van Slageren & Berendsen

Valva interior sporophyti cellulis plurifenestratis; sporae isodiametrae, germination modo Lopholejeuneae.

Cells of the inner layer of the sporophyte valve with plurifenestrate thickening layer; spores isodiametric, sporeling *Lopholejeunea*-type.

The following genera are included in this subtribe: Acrolejeunea, Trocholejeunea, Frullanoides, Ptychanthus, Thysananthus, Mastigolejeunea, Schiffneriolejeunea, Caudalejeunea (all with elongated lobe cells, cordate trigones and suberect-convoluted dry leaves), and Tuzibanthus, Archilejeunea, Spruceanthus, Phaeolejeunea, Marchesinia and Lopholejeunea (all with isodiametric lobe cells, simple-triangular or radiate trigones and widely spreading dry leaves). This tribe contains the genera of the Ptychantheae and Archilejeuneae sensu GRADSTEIN 1975, except for those now placed in the Brachiolejeuneae. GRADSTEIN's tribal subdivision has been based on characters of the gametophyte, and within the emended Ptychantheae his two groups are still visible.

Recently MIZUTANI (1985) proposed a subdivision of the Lejeuneaceae into two (instead of 7-8) subfamilies: the Ptychanthoideae and the Lejeuneoideae. The subdivision is primarily based on sporophyte characters with characters of the gametophyte more additionally. A fenestrate-type sporophyte with a (usually) non articulate seta of at least 16 outer cell rows characterises the subfam. Ptychanthoideae; a nodular-type sporophyte with an articulate seta of 12 outer cell rows characterises the subfam. Lejeuneoideae.

In view of MIZUTANI's subdivision, the tribe Ptychantheae contains the "true" members of the Ptychanthoideae. The tribe Brachiolejeuneae, on the con trary, may be more difficult to classify: capsule type and articulate seta are similar to the Lejeuneoideae, but the number of outer cell rows of the seta, as well as characteristics of the gametophyte (for example the undivided underleaves, robust plants, and cortical cells of the stem in 10-50 longitudinal rows) are as in the Ptychanthoideae.

The Brachiolejeuneae thus emerge as a clearly distinguished group. Applying MIZUTANI's concepts the group might deserve subfamilial status but, in our opinion, it is at present best placed as a rather independent lineage within the Ptychanthoideae. Our decision is based on the consideration that the morphology and anatomy of this tribe is in general accordance with the circumscription of this subfamily, especially with the above mentioned characters of the gametophyte and the seta.

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Plate I. Fenestrate-type sporophyte.

Fig. 1. Fenestrate-type sporophyte, showing four outwardly curved valves and non-articulate seta. Note fenestrate inner valve layer (arrow) (bar = 200 μ m). Fig. 2. Non-articulate seta (bar = 100 μ m). Fig. 3. Two valves outer sur face. Note areas with equally thickened cell walls (arrows) (bar = 200 μ m). Fig. 4. Apical part of valve outer surface (bar = 100 μ m). Fig. 5. Inner surface of a valve and the capsule base. Note radiate cell areolation in apical part, longitudinal cell areolation in central part, seven ridges in valve central part (arrow 1) and "footprint" of elaters on capsule base (arrow 2) (bar = 100 μ m). Fig. 6. Apical part of valve inner surface, showing attachment of 1+3+5+7 elaters (type "1") (bar = 40 μ m).

Figs. 1-2 from Child 2202, New Zealand. Fig. 3 from E. & P. Hegewald 7885, Peru. Fig. 4 from Vital 2846, Brazil. Fig. 5 from Gradstein 3811, Papua New Guinea. Fig. 6 from Vital 6688, Brazil.

Figs. 1-2 = Archilejeunea olivacea; Fig. 3 = Frullanoides tristis; Fig. 4 = Acrolejeunea torulosa; Fig. 5 = Spruceanthus polymorphus; Fig. 6 = Archilejeu nea parviflora.

I



Plate II. Fenestrate-type sporophyte.

Fig. 1. One valve inner surface. Note six longitudinal ridges in the central part (bar = 100 μ m). Fig. 2. Apical part of valve inner surface, showing attachment of 1+3+5 elaters (type "2") (bar = 40 μ m). Fig. 3. Apical part of valve inner surface, showing elater attachment, plurifenestrate thickening and radial cell areolation (bar = 40 μ m). Fig. 4. Narrow acute apical ends of longitudinal ridges (bar = 40 μ m). Fig. 5. Basal end of longitudinal ridges. Note vague "footprints" of elaters on smooth capsule base (bar = 40 μ m). Fig. 6. Valve lateral margin, showing wrinkled surface of valve outer layer and attachment of elaters (bar = 10 μ m).

Figs. 1, 4 from Rapp s.n., U.S.A. Fig. 2 from Reyes 732, Cuba. Figs. 3, 5 from Pócs & Crosby 6856/1, Tanzania. Fig. 6 from Vital 6688, Brazil.

Figs. 1, 4 = Lopholejeunea muelleriana; Fig. 2 = Frullanoides corticalis; Figs. 3, 5 = Caudalejeunea hanningtonii; Fig. 6 = Archilejeunea parviflora.

II



Plate III. Fenestrate-type sporophyte.

Fig. 1. Capsule longitudinal section, showing vertical elaters and piles of spores, arranged in tetrads (Tilt = 50° ; bar = $200 \ \mu$ m). Fig. 2. Central part of capsule longitudinal section (bar = $40 \ \mu$ m). Fig. 3. Basal part of capsule longitudinal section, showing dilated bases of the elaters (bar = $20 \ \mu$ m). Fig. 4. Detail of elater, showing well developed spiral with punctae and small, pitlike depressions (bar = $10 \ \mu$ m). Fig. 5. Capsule transverse section, showing regular arrangement of elaters, isodiametric spores and spore attachment point (arrows) (bar = $40 \ \mu$ m). Fig. 6. Capsule transverse section, showing oblique orientation of a spore tetrad (arrow) (bar = $40 \ \mu$ m).

Figs. 1-2, 5-6 from Child 2202, New Zealand. Fig. 3 from Mosén Hh, Brazil. Fig. 4 from Pearce s.n., Bolivia.

Figs. 1-2, 5-6 = Archilejeunea olivacea; Fig. 3 = Mastigolejeunea auriculata; Fig. 4 = Frullanoides densifolia.

III



Plate IV. Nodular-type sporophyte.

Fig. 1. Nodular-type sporophyte, showing four convex valves and articulate seta (bar = 200 μ m). Fig. 2. Articulate seta (bar = 100 μ m). Fig. 3. Valve outer surface, showing strongly developed thickenings in the centro-basal part (bar = 100 μ m). Fig. 4. Apical part of valve outer surface, showing marginal thickenings as a string of triangular segments (bar = 40 μ m). Fig. 5. Inner surface of three valves, showing marginal (m.e.) and additional (a.e.) elaters (bar = 100 μ m). Fig. 6. One valve of Fig. 5, showing marginal and additional elaters (bar = 100 μ m).

Figs. 1-2, 4 from Dusén s.n., Chili. Fig. 3 from Cleef 2291, Colombia. Figs. 5-6 from Pringle 10690, Mexico.

Figs. 1-2, 4 = Brachiolejeunea spruceana; Fig. 3 = Blepharolejeunea securifolia; Figs. 5-6 = Dicranolejeunea phyllorhiza.





Plate V. Nodular-type sporophyte.

Fig. 1. Capsule longitudinal section (bar = 100 μ m). Fig. 2. Capsule longitudinal section, showing rectangular outline of spores and dilated bases of elaters (bar = 100 μ m). Fig. 3. Lateral part of capsule longitudinal section, showing irregular outline of spores and elaters with a weakly developed spiral (wall thickenings only) (bar = 40 μ m). Fig. 4. Lateral margin of the valve (at apex), showing wrinkled surface of outer valve layer (bar = 10 μ m). Fig. 5. Capsule transverse section (bar = 200 μ m). Fig. 6. Capsule transverse section, showing marginal (m.e.) elaters in two axes, additional (a.e.) elaters, intersecting the spore mass, and attachment location (a.l.) of spores in a tetrad (bar = 100 μ m).

Figs. 1, 3 from Cleef 1990, Colombia. Fig. 2 from Schwab s.n., Mexico. Fig. 4 from Pócs & Reyes 9055/BD, Cuba. Figs. 5-6 from Frahm et al. 1248, Peru.

Figs. 1-3 = Blepharolejeunea securifolia; Fig. 4 = Symblezidium barbiflorum; Figs. 5-6 = Brachiolejeunea laxifolia.



Plate VI. Sporophyte of Frullania, Omphalanthus and Cyclolejeunea.

Fig. 1. Apical part of valve inner surface, showing nodular thickenings on the radial cell walls (500 x). Fig. 2. Apical part of valve outer surface, showing nodular thickenings in the angles and on intermediate cell walls (500 x). Fig. 3. Apical part of valve inner surface, showing marginal (m.e.) and additional (a.e.) elaters (500 x). Fig. 4. Apical part of valve outer surface, showing nodular thickenings in the angles and on intermediate cell walls (500 x). Fig. 5. Apical part of valve inner surface, showing arrangement of 2+4+6+8+10+4 elaters (partially) (bar = 100 μ m). Fig. 6. Apical part of valve outer surface (bar = 40 μ m).

Figs. 1-2 from Duss 612, Martinique. Figs. 3-4 from Bekker 1696a, Surinam. Figs. 5-6 from van Reenen 2513, Colombia.

Figs. 1-2 = Omphalanthus filiformis; Figs. 3-4 = Cyclolejeunea convexistipa; Figs. 5-6 = Frullania ericoides.



Plate VII. Sporoderm ornamentation.

Fig. 1. Acrolejeunea mollis (bar = 4 μ m). Fig. 2. Trocholejeunea sandvicensis, showing a well developed rosette (bar = 4 μ m). Fig. 3. Frullanoides densifolia, showing a weakly developed rosette (bar = 4 μ m). Fig. 4. Acrolejeunea fertilis, showing a weakly developed rosette (bar = 4 μ m). Fig. 5. Frullanoides corticalis, showing one rosette per facet (bar = 4 μ m). Fig. 6. Archilejeunea parviflora (bar = 4 μ m).

Fig. 1 from Hodgson s.n., New Zealand. Fig. 2 from Inoue 15, Japan. Fig. 3 from Lorentz s.n., Argentina. Fig. 4 from Dahlan 35, Riau. Fig. 5 from Reyes 732. Cuba. Fig. 6 from Vital 6688, Brazil. VII



Plate VIII. Sporoderm ornamentation.

Fig. 1. Caudalejeunea hanningtonii (bar = 10 μ m). Fig. 2. Mastigolejeunea humilis (bar = 4 μ m). Fig. 3. Blepharolejeunea securifolia (bar = 20 μ m). Fig. 4. Detail of Fig. 3, showing verrucae and attachment location (bar = 4 μ m). Fig. 5. Spore of Omphalanthus filiformis, showing numerous rosettes (bar = 20 μ m). Fig. 6. Blepharolejeunea incongrua, showing verrucae and rosette (bar = 4 μ m).

Fig. 1 from Pócs & Crosby 6856/1, Tanzania. Fig. 2 from Gradstein 3833, Papua New Guinea. Figs. 3-4 from Schwab s.n., Mexico. Fig. 5 from Duss 612, Martinique. Fig. 6 from Aguirre & Gradstein 1326, Colombia. VIII



Plate IX. Sporoderm ornamentation.

Fig. 1. Brachiolejeunea laxifolia, showing compound, vermiform verrucae (bar = 2 μ m). Fig. 2. Brachiolejeunea spruceana, showing tendency of verrucae towards rosette formation (bar = 4 μ m). Fig. 3. Odontolejeunea sieberiana, showing numerous rosettes and sporoderm verrucae (bar = 10 μ m). Fig. 4. Dicranolejeunea johnsoniana, showing vermiform verrucae and well developed rosettes (bar = 4 μ m). Fig. 5. Symbiezidium transversale, showing roset tes (r), vermiform verrucae (v) and long strings of baculae (b) (bar = 10 μ m). Fig. 6. Symbiezidium barbiflorum, showing similar ornamentation as Fig. 5 (bar = 10 μ m).

Fig. 1 from Gradstein 3570a, Colombia. Fig. 2 from Dusén 466, Chili. Fig. 3 from Vital 2791c, Brazil. Fig. 4 from Bornmüller 158, Madeira. Fig. 5 from Frahm et al. 1396, Peru. Fig. 6 from Pócs & Reyes 9055/BD, Cuba.

IX



Plate X. Valve morphology of Stictolejeunea and Omphalanthus.

Fig. 1. Apical part of inner valve layer, showing elaborate and coalescent nodular thickenings, which superficially resemble a plurifenestrate thickening layer. Fig. 2. Inner valve layer, showing locations of marginal elaters, nodular thickenings (only drawn in the apical part of the valve) and hexagonal area of longitudinal ridges.

Fig. 1 from Sellow s.n., Brazil. Fig. 2 from Duss 612, Martinique.

Fig. 1 = Stictolejeunea squamata; Fig. 2 = Omphalanthus filiformis.


Plate XI. Schematic diagrams of elater attachment.

Fig. 1. Fenestrate-type sporophyte of the subfam. Ptychanthoideae (Type "1"). Fig. 2. Fenestrate-type sporophyte of the subfam. Ptychanthoideae (Type "2"). Fig. 3. *Frullania ericoides*. Arrangement adapted from Plate VI, fig. 5. Fig. 4. Nodular-type sporophyte of the subfam. Ptychanthoideae. Fig. 5. *Cyclolejeunea* (subfam. Lejeuneoideae). Fig. 6. *Omphalanthus* (subfam. Lejeuneoideae).







1+3+5+7+7+4+2







SUMMARY

A revision has been made of the hepatic genus *Brachiolejeunea* (Spruce) Schiffn. (family Lejeuneaceae, subfamily Ptychanthoideae). Within this genus two subgenera were recognised: subg. *Brachiolejeunea* and subg. *Plicolejeunea* Schust. In order to distinguish taxonomic entities within these subgenera and to evaluate their affinities, the morphology and anatomy of the gametophyte and the sporophyte have been studied. Data on cytology and sporeling development, obtained from living and cultured specimens, were added. Sporophyte characters have been studied with light microscopy (LM) and scanning electron microscopy (SEM).

Besides a considerable reduction in the number of accepted species, the main result of this study is that the traditional delimitation of *Brachiolejeunea* cannot be maintained. The two subgenera appear to be different in many characters, several of them new, and are accordingly elevated to generic level. The genus *Brachiolejeunea* (4 species) now comprises only the former subgenus of that name; the generic name *Frullanoides* Raddi is reinstated for the subg. *Plicolejeunea* (7 species and 1 subspecies). For both genera the morphology and anatomy are described, the previously neglected sporophyte generation being treated in particular detail. In each of the genera a different type of sporophyte is present: a "fenestrate-type" in *Frullanoides*, a "nodular-type" in *Brachiolejeunea*.

From a of the distribution patterns it appears that both genera probably originated in the western part of Gondwanaland. *Brachiolejeunea* is confined to that area and may presently be characterized as a Neotropical-montane element. One species of *Frullanoides* is pantropical, the others are neotropical. The species of *Brachiolejeunea* are predominantly epiphytes of mountain forests and have a rather narrow drought tolerance; the species of Frullanoides generally occur in a greater variety of habitats and have a wider drought tolerance. A consideration of generic relationships shows that the affinities of genera are very different.

For both genera identification keys are provided, each species and subspecies is illustrated and for each taxon the following information is provided: synonymy with relevant literature and typification, a description, geographical distribution with distribution map, and notes on ecology, differentiation and variation.

The second part of this study contains a short review of the genus *Blepharolejeunea* S. Arnell, which has been emended to accommodate several diverging species of *Brachiolejeunea* and *Dicranolejeunea*. *Blepharolejeunea* is related to both genera and is characterized as a Neotropical-montane element.

In the third part of this study the sporophyte generation in the subfam. Ptychanthoideae is analysed with Scanning Electron Microscopy. Fenestratetype and nodular-type sporophytes are described and the different affinities of these types are discussed. The new tribe Brachiolejeuneae van Slageren & Berendsen is created to accommodate the genera of Ptychanthoideae with nodular-type sporophytes.

SAMENVATTING

Dit proefschrift bevat een revisie van het levensmosgeslacht Brachiolejeunea (Spruce) Schiffn. (familie Lejeuneaceae, subfamilie Ptychanthoideae) (Hoofdstuk 1). Binnen dit genus worden twee subgenera onderscheiden: subg. Brachiolejeunea en subg. Plicolejeunea Schust. Teneinde de taxonomische eenheden binnen deze subgenera te omgrenzen en om hun systematische verwantschappen nader aan te kunnen duiden, zijn morfologie en anatomie van de gametofyt en de sporofyt bestudeerd. Waar mogelijk zijn cytologische gegevens met betrekking tot de ontwikkeling van de gekiemde spore, verkregen respectievelijk uit levend en uit gecultiveerd materiaal, hieraan toegevoegd. De morfologie van de sporofyt generatie is bestudeerd met behulp van de lichtmicroscoop en de scanning electronenmicroscoop.

Naast een aanzienlijke reductie van het aantal soorten is het voornaamste resultaat van deze studie dat de tot nu toe gehanteerde omgrenzing van het genus *Brachiolejeunea* niet meer gehandhaafd kan worden. De beide subgenera worden op basis van vele, waaronder enkele nieuwe, kenmerken van elkaar onderscheiden. Dit heeft aanleiding gegeven tot het besluit de twee subgenera tot genus te verheffen. Het genus *Brachiolejeunea* (4 soorten) vervangt het vroegere subgenus van die naam; voor het vroegere subgenus *Plicolejeunea* (7 soorten en 1 ondersoort) is de oude genusnaam *Frullanoides* Raddi weer in gebruik genomen. Voor beide genera wordt de morfologie en de anatomie beschreven, waarbij in het bijzonder aan de tot nu toe onderbelichte sporofyt generatie aandacht wordt geschonken. Elk genus heeft een eigen type sporofyt: het "fenestrate-type" is aanwezig in *Frullanoides*, het "nodular-type" in *Brachiolejeunea*.

Een analyse van de verbreidingspatronen maakt aannemelijk dat beide genera zijn ontstaan in het westelijk deel van Gondwanaland. De verbreiding van Brachiolejeunea heeft zich beperkt tot dit gebied en het genus kan momenteel worden aangeduid als een neotropisch-montaan element. Van Frullanoides heeft één soort een pantropische verbreiding; alle andere soorten zijn beperkt tot de neotropen. De soorten binnen Brachiolejeunea zijn overwegend epifyten uit bergbossen en hebben een tamelijk beperkte droogtetolerantie; de soorten binnen Frullanoides komen in het algemeen op een grotere verscheidenheid aan standplaatsen voor en hebben een grotere droogtetolerantie. Een beschouwing van de verwantschappen op genus niveau illustreert de zeer verschillende taxonomische relaties van beide genera.

Voor beide genera zijn determinatie sleutels opgenomen, elke soort en ondersoort is geillustreerd en elk taxon is van de volgende gegevens voorzien: synonymie met relevante literatuur en typificatie, een beschrijving, de geografische verbreiding met verbreidingskaart, en een karakteristiek van de ecologie, differentiatie en variatie.

Het tweede deel van deze studie wordt gevormd door een kort overzicht van het genus *Blepharolejeunea* S. Arnell (Hoofdstuk 2). Dit genus is geëmendeerd en de nieuwe omgrenzing omvat nu een aantal soorten die niet meer binnen de nieuwe omgrenzing van *Brachiolejeunea* en *Dicranolejeunea* vallen. *Blepharolejeunea* is verwant aan deze beide genera en kan verder worden aangeduid als een neotropisch-montaan element.

Het derde deel van deze studie omvat een raster electronen microscopische analyse van de sporofyt generatie in de subfamilie Ptychanthoideae (Hoofdstuk 3). Een "fenestrate-type" en een "nodular-type" sporofyt worden beschreven en de verschillende verwantschappen van deze typen worden geëvalueerd. Een nieuw tribus Brachiolejeuneae van Slageren & Berendsen is gecreëerd, waarin de genera van de Ptychanthoideae met nodular-type sporofyten zijn verenigd; tevens is het tribus Ptychantheae Gradstein geëmendeerd. Bij het voltooien van dit proefschrift wil ik op de eerste plaats graag diegenen bedanken die direct hebben bijgedragen aan de tot stand koming ervan.

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CURRICULUM VITAE

De auteur van dit proefschrift werd geboren op 30 maart 1955 te Eindhoven. Na het behalen van het einddiploma HBS-B in 1972 aan het St. Jorislyceum aldaar begon hij in hetzelfde jaar met de studie biologie aan de Rijksuniversiteit te Utrecht. In september 1975 werd het kandidaatsexamen afgelegd en in november 1979 volgde het doctoraalexamen, met als hoofdvak tropische vegetatiekunde en bryologie (bij Prof. dr. A.L. Stoffers en Dr. S.R. Gradstein), als bijvak plantenfysiologie (bij Dr. H. Konings), en als nevenrichting biohistorie (bij Prof. dr. P. Smit en Drs. R. ter Laage). Tevens leidde een bijvak didaktiek van de biologie tot het behalen van de onderwijsbevoegdheid.

Na zijn afstuderen kreeg hij in 1980 de gelegenheid op basis van een studiebeurs van het Ministerie van Onderwijs en Wetenschappen aan te vangen met een promotieonderzoek in de systematische plantkunde. Aansluitend, van februari 1981 tot april 1984, was hij in dienst van de Nederlandse Organisatie voor Zuiver Wetenschappelijk Onderzoek (ZWO). Gedurende deze vier jaren was hij als gastmedewerker verbonden aan de Vakgroep Bijzondere Plantkunde van de Rijksuniversiteit te Utrecht.

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