

STUDIES ON LEJEUNEACEAE SUBFAM.
PTYCHANTHOIDEAE. I.
NOMENCLATURE AND TAXONOMY OF
PTYCHOCOLEUS, *ACROLEJEUNEA*
AND *SCHIFFNERIOLEJEUNEA*

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The present paper is preliminary to a monographic treatment of the genera *Acrolejeunea* (Spruce) Schiffn. and *Schiffneriolejeunea* Verd. The main purpose of this paper is to reestablish *Acrolejeunea* as the nomenclaturally correct name of a genus of Lejeuneaceae to which in this century commonly the name *Ptychocoleus* Trev. was applied.

NOMENCLATURE

The genus *Ptychocoleus* was established by Trevisan (1877) to include the species previously assigned to *Phragmicoma* Dum. β *Ptychanthoides* Gott. et al., Synopsis Hepaticarum (1845). More than 30 years the genus *Ptychocoleus* was neglected until Evans (1908) restored it by selecting *Phragmicoma aulacophora* Mont.—the first species listed in *Ptychocoleus* by Trevisan—as the lectotype. Since *Phragmicoma aulacophora* Mont. had been placed in *Acrolejeunea* (Spruce) Schiffn. by Spruce (1884) and Schiffner (1893), Evans (l.c.) reduced *Acrolejeunea* (Spruce) Schiffn. 1893 to synonymy under *Ptychocoleus* Trev. 1877. Evans' interpretation of *Ptychocoleus* Trev. has been followed in all 20th century works treating *Ptychocoleus* (cf. Stephani 1912, Verdoorn 1934, Vanden Berghen 1948, Jones 1954, Schuster 1961, Mizutani 1962, Bischler 1965). A few years ago Dr. R. Grolle, Jena (in lit.) draw my attention to the fact that Evans' lectotypification of *Ptychocoleus* Trev. is not in agreement with the protologue of the genus. It appears that *Ptychocoleus* Trev. is in fact a substitute for the much older and neglected genus *Frullanoides* Raddi 1822. A short historical survey may serve to clarify the nomenclature of the genera involved.

I. *Frullanoides* Raddi 1822 = *Ptychocoleus* Trev. 1877

Raddi (1822) established the genus *Frullanoides* for two new species from Brazil: *F. riojaneirensis* Raddi and *F. densifolia* Raddi. Gottsche et al. (1845) realized their very different affinities and placed them in the two older genera *Frullania* Raddi 1818 and *Phragmicoma* Dum. 1822, respectively.

When Trevisan (1877) presented a reclassification of the system of Hepaticae he treated *Frullanoides* in the following way:

(1) He lectotypified the genus *Frullanoides* Raddi in rather a modern way by calling

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F. densifolia Raddi "specie tipica" of *Frullanoides* and excluding *F. riojaneirensis* Raddi from that genus.

(2) He proposed *Ptychocoleus* Trev. as a substitute for *Frullanoides* Raddi, a name whose form Trevisan considered to be objectionable.

Essential in the protologue are the statements:

p. 404: "Gen. 25. *Ptychocoleus* Trevis. (*Frullanoides* Raddi in Mem. della Soc. Ital. di Modena, XIX. pag. 35, esclusa *Fr. Riojaneirensis*)."

p. 405: "*Frullanoides* di Raddi, denominazione generica inammissibile, vi corrisponde, quanto alla specie tipica." (*Frullanoides* Raddi, which is an inadmissible name for a genus, corresponds with it [*Ptychocoleus*] in respect to the typical species).

p. 447: "*Frullanoides* Raddi 1823 . . . = *Ptychocoleus* Trevis. . . N. 25"

According to art. 7 of the I.C.B.N. (Stafleu et al. 1972): "A name . . . which was nomenclaturally superfluous when published is automatically typified by the type of the name . . . which ought to have been adopted under the rules, unless the author of the superfluous name or epithet has indicated a definite type." *Ptychocoleus* Trev. is a synonym of *Frullanoides* Raddi, as was correctly realized by Schiffner (1893, p. 128).

Schuster (1966, p. 89) designated *F. riojaneirensis* as the type of *Frullanoides* Raddi. According to Art. 8 of the I.C.B.N. this lectotypification cannot be accepted.

For the correct interpretation of the neglected *Frullanoides* Raddi I had to refer to the original material of *F. densifolia* Raddi. Fortunately I could receive on loan the well preserved holotype from the Raddi Herbarium (PI). I found that the holotype material corresponds with the traditional circumscription of *Brachiolejeunea densifolia* (Raddi) Evans (= *Frullanoides densifolia* Raddi) as given by Stephani (1912).

The lectotype (Evans 1908) of *Brachiolejeunea* (Spruce) Schiffn. is *B. laxifolia* (Tayl.) Schiffn. If *B. laxifolia* and *B. densifolia* are indeed congeneric, I think it becomes necessary to conserve *Brachiolejeunea* (Spruce) Schiffn. 1893 against *Frullanoides* Raddi 1822. This question will be discussed in a following paper. It should be noted here that the two species differ in a considerable number of morphological and anatomical characters and were placed in different subgenera by Schuster (1963). Undoubtful is the following synonymy:

Frullanoides Raddi, Atti Soc. Ital. Sci. Modena 19: 37:(13) 1822. Lectotypus (Trevisan 1877 p. 404-405): *F. densifolia* Raddi. — *Ptychocoleus* Trev., Mem. Reale Ist. Lombard. Sci. Mat. Nat., ser. 3, 4: 404 (1877), *nom. superfl. illegit.*; non Evans 1908 = *Phragmicoma* β *Ptychanthoides* Gott. et al., Syn. Hep.: 294 (1845). Lectotypus (*nov*): *Jungermannia bicolor* Nees (= *Frullanoides densifolia* Raddi *vide* Syn. Hep.: 294). = *Brachiolejeunea* subg. *Plicolejeunea* Schust., Nova Hedwigia Beih. 9: 104 (1963). Typus: *B. bahamensis* Evans.

II. *Acrolejeunea* (Spruce) Schiffn. 1893 = *Ptychocoleus* Evans 1908; non Trev. 1877

Spruce (1884) in his epoche-making treatment of the liverworts of tropical South America established *Acro-Lejeunea* as one of his 37 subgenera of *Lejeunea* to include species lacking subfloral innovations and having entire leaf-lobes and underleaves, female bracts with relatively large lobules and a perianth with 4-5 keels or 7-10 plicae, the keels and plicae being essentially smooth.

Acro-Lejeunea was subsequently raised to generic rank by Schiffner (1893).

Schiffner's treatment of the Lejeuneae, which for nomenclatural reasons is one of the most important publications on this group, is often dated "1895". This refers to the dates of publication printed on the last "Inhalt" page of Engl. & Prantl. Die natürliche Pflanzenfamilien 1(3), giving "10 Oktober 1893" for the first part of the Hepaticae and "15 January 1895" for the second part in which the Lejeuneae appeared. However, Margadant (1956) and Stafleu (1972) have shown that "September 1893" should be considered the publication date of both parts, apparently because of the existence of previously published reprints marked on the frontispiece "Erschienen September 1893". I have been able to trace three copies of this reprint (Geneva, Prague, Utrecht). Consequently, I consider September 1893 the "starting point" for valid combinations in the "Schiffnerian" genera of Lejeuneaceae. Bonner et al. (1961) consider *Acro-Lejeunea* and some other subgenera to be validly published as genera by Stephani before 1893. Having studied the publications on *Lejeunea*, mostly by Stephani, that appeared between 1884 and 1893, I find no justification for this viewpoint.

Spruce (l.c.) included nine species in *Acro-Lejeunea*, two of which occurred in South America and therefore were given full descriptions: *Lejeunea torulosa* (Lehm. & Lindenb.) Spruce and *Lejeunea marsupifolia* Spruce. Since *Acrolejeunea* (Spruce) Schiffn. has not yet been typified I propose *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. as the lectotype because this species matches best the original concept of *Acrolejeunea*. The position of the peculiar *Lejeunea marsupifolia*, collected by Spruce near S. Carlos along the Rio Negro in Brazil and only known from type material, is still doubtful and it possibly should be transferred to some other genus.

When Evans (1908) reduced *Acrolejeunea* to synonymy under *Ptychocoleus* by choosing *Acrolejeunea aulacophora* (Mont.) Schiffn. as the lectotype of *Ptychocoleus* Trev., a great number of new species had in the meantime been added to *Acrolejeunea* by Stephani. In his Species Hepaticarum (1912), Stephani listed 85 species (sub *Ptychocoleus*), thus making it the largest genus of the subf. Ptychanthoideae. Through subsequent revisions of the Asian species by Verdoorn (1934) and the African species by VandenBerghen (1948) and Jones (1954), the number of species was reduced to ± 45 . From the foregoing it becomes clear that a considerable number of nomenclatural changes on the species level are involved when *Ptychocoleus* sensu Evans is replaced by *Acrolejeunea* (Spruce) Schiffn. In order to avoid unnecessary new combinations it was decided to reexamine the taxonomy of this group.

TAXONOMY

The circumscription of *Ptychocoleus* as given by Evans (l.c.) remained unchallenged until Schuster and Hattori (1954) discovered the presence of two different types of oilbodies in this group. In *Ptychocoleus heterophyllus* and *P. nipponicus* they found numerous, small and homogeneous oilbodies in the cells whereas in the African *P. pappeanus* there were few and larger oilbodies, each oilbody being com-

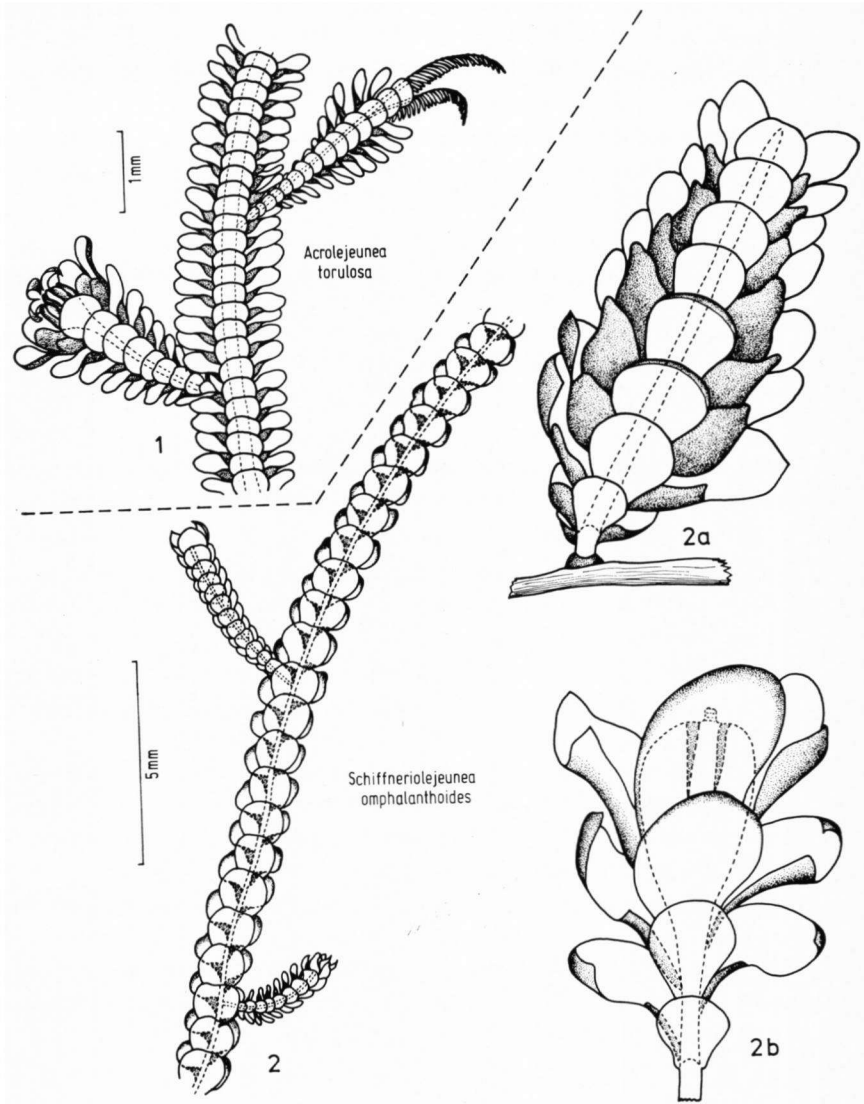
posed of a number of small droplets ("segmented"). For the latter species Schuster established the new genus *Phragmilejeunea* Schust. 1954 which besides the different oilbody type was characterized by the lobule having only 1 tooth and the perianth being virtually without keels.

In 1961 Schuster transferred the African *Ptychocoleus molleri* to *Phragmilejeunea*, a species which indeed is closely related to *P. pappeanus*. At the same time he stressed the close relationship between *Phragmilejeunea* and the poorly known monotypic *Schiffneriolejeunea* Verd. 1933. The latter genus was based on rather scanty material of a robust species from the mountains of southern Celebes which Verdoorn described as *Schiffneriolejeunea omphalanthoides*. In 1934 Verdoorn placed his monotypic genus close to *Ptychocoleus*. Mizutani (1969) quite recently advocated the presence of two natural groups within the southeastern Asiatic members of *Ptychocoleus*. The groups are said to be different in the number of perianth keels, the form and outline of the female bracts and bracteoles and in the form of the lobule and its number of teeth.

My study of the whole genus so far has revealed the existence of *two* well-defined groups which combine the concepts of Schuster and Mizutani. I regard these groups as distinct genera, differing essentially in the anatomy of the stem, the oilbody type and the morphology of the gametoezia. No diagnostic differences could be found in the sporophytes of both groups. Oilbodies could be studied in a number of species, either from fresh material which I received by air mail from colleagues in the field, or from recently collected and well-preserved herbarium material. I have seen homogeneous oil-bodies in *Ptychocoleus torulosus*, *P. emergens*, *P. aulacophorus* and *P. pycnocladus*. This group of species belongs to *Acrolejeunea* (Spruce) Schiffn. s. str. Segmented oilbodies were seen in *P. polycarpus* (= *P. molleri*), *P. pappeanus*, *P. cumingianus* (= *P. hasskarlianus*?) and *P. pulopenangensis*. This group belongs to Schuster's genus *Phragmilejeunea* which I consider a synonym of the older *Schiffneriolejeunea* Verdoorn. In addition to the type material of *S. omphalanthoides* (F, Holo+ Iso) I have been able to study some excellent recent collections from New Guinea (leg. Schuster (JE), van Zanten (GRO), S. Bergman (S)) and although its oilbodies remain unknown I could not find essential differences between this species and the genus *Phragmilejeunea*. Consequently, this part of the genus *Ptychocoleus* sensu Evans should be transferred to *Schiffneriolejeunea*.

The genera *Acrolejeunea* and *Schiffneriolejeunea* are separated by (Pls. I & II):

	<i>Acrolejeunea</i>	<i>Schiffneriolejeunea</i>
Stem	fragile, with thin-walled, pale cortical cells; medullar cells with wide ends	rigid, with thick-walled cortical cells which become brownish (especially ventral); medullar cells tapering to narrow ends
Oilbodies	homogeneous	segmented
Androecium	bracts weakly saccate with "epistatic" lobule; 1 antheridium per bract	bracts strongly saccate with "hypostatic" lobule; 2(-3) antheridia per bract
Gynoecium	perianth with 5-12 keels and plicae	perianth with 0-5 keels



PL. I. Generitypes of *Acrolejeunea* (Spruce) Schiffn. and *Schiffneriolejeunea* Verd.
 Fig. 1. *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn., with female branch, sporophyte and two specialized shoots producing caducous leaves. Fig. 2. *Schiffneriolejeunea omphalanthoides* Verd., with two female branches. Fig. 2a. Male spike, showing hypostatic lobules (80×). Fig. 2b. Gynoecium (20×). Fig. 1 from Vital 2109, Sao Paulo State, Brazil (U). Fig. 2 from Van Zanten 68-3523, Papua, Mnt. Gilowe (JE). Figs. 2a-b from the type (F).

It appears that *Acrolejeunea* is most closely related to *Brachiolejeunea* and *Trocholejeunea*. *Schiffneriolejeunea* is related to *Caudalejeunea* and *Mastigolejeunea*.

Acrolejeunea (Spruce) Schiffn. in Engl. & Prantl, Nat. Pfl.-fam. I, 3(1): 128 (1893).

BAIONYM: *Lejeunea* Lib. subg. *Acrolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 115 (1884).

LECTOTYPUS (*novus*): *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. 1893.

SYNONYM: *Ptychocoleus* Evans 1908 *non* Trev. 1877; Lectotypus: *Ptychocoleus aulacophorus* (Mont.) Trev. 1877.

The following species should be placed in *Acrolejeunea* at the present time:

Acrolejeunea arcuata (Nees) Grolle & Gradst. *comb. nov.*

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

Ptychocoleus arcuatus (Nees) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).
Distr.: Malesia.

Acrolejeunea aulacophora (Mont.) Steph., Bot. Jahrb. 20: 317 (1895).

Phragmicoma aulacophora Mont., Ann. Sci. Nat. Bot. 2(19): 259 (1843).

Ptychocoleus aulacophorus (Mont.) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

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

Acrolejeunea renauldii (Steph.) Steph., Spec. Hep. 5: 26 (1912) *comb. inval. pro syn.*

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

Distr.: Malesia, Australasia, the Pacific, and East African Islands.

Acrolejeunea emergens (Mitt.) Steph. in Engl., Die Pflanzenwelt Ostafrikas, C: 65 (1895).

Phragmicoma emergens Mitt., Philos. Trans. 168: 397 (1879).

Ptychocoleus emergens (Mitt.) Steph., Spec. Hep. 5: 24 (1912).

Ptychocoleus torulosus auct. *non* Lehm. & Lindenb.; *pro parte, quoad plantas americanas.*

Distr.: Tropical Africa and Tropical America (!)

Acrolejeunea fertilis (Reinw., Blume & Nees) Schiffn. in Engl. & Prantl, Nat. Pfl.-fam. I, 3(1): 128 (1893).

Jungermannia fertilis Reinw., Blume & Nees, Hep. Jav., Nova Acta Phys. Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12(1): 211 (1824).

Ptychocoleus fertilis (Reinw., Blume & Nees) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Distr.: Indo-Malesia and the Pacific.

Acrolejeunea heterophylla (Evans) Grolle & Gradst. *comb. nov.*

Ptychocoleus heterophyllus Evans, Amer. J. Bot. 5: 144 (1918).

Distr.: Florida and Central America (Mexico, Honduras, Nicaragua).

Acrolejeunea pusilla (Steph.) Grolle & Gradst. *comb. nov.*

Archilejeunea pusilla Steph., Spec. Hep. 4: 731 (1911).

Ptychocoleus nipponicus Hatt., Bot. Mag. Tokyo 57: 358 (1943). (*non Acrolejeunea pusilla* Steph. in Paris, Rev. Bryol. 35: 6 (1908) *nom. nud.* = *Ptychocoleus pusillus* Steph., Spec. Hep. 5: 26 (1912) = *Acrolejeunea emergens* (Mitt.) Steph.).

Distr.: Japan.

Acrolejeunea pycnolada (Tayl.) Schiffn. in Engl. & Prantl, Nat. Pfl.-fam. I, 1(3): 128 (1893).

Ptychanthus pycnocladus Taylor, London J. Bot. 5: 385 (1846).

Ptychocoleus pycnocladus (Tayl.) Steph., Spec. Hep. 5: 52 (1912).

Distr.: Tropical Africa (!), Indo-Malesia and the Pacific.

Acrolejeunea securifolia (Endl.) Watts, Proc. Linn. Soc. New South Wales 26: 215 (1901).

Jungermannia securifolia Endl., Prodr. Fl. Norfolk.: 5 (1833).

Acrolejeunea securifolia (Endl.) Steph., Hedwigia 34: 59 (1895) *nom. nud.*

Ptychocoleus securifolius (Endl.) Steph., Spec. Hep. 5: 59 (1912).

Distr.: Australasia.

Acrolejeunea tjibodensis (Verd.) Grolle & Gradst. *comb. nov.*

Ptychocoleus tjibodensis Verd., Recueil Trav. Bot. Neerl. 30: 227 (1933).

Distr.: Java.

Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn. in Engl. & Prantl, Nat. Pfl.-fam. I, 3(1): 128 (1893).

Jungermannia torulosa Lehm. & Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pug. 6: 41 (1834).

Ptychocoleus torulosus (Lehm. & Lindenb.) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Distr.: Tropical America.

Schiffneriolejeunea Verdoorn, Ann. Bryol. 6: 89 (1933).

TYPUS: *Schiffneriolejeunea omphalanthoides* Verd. 1933.

SYNONYM: *Phragmilejeunea* Schust., J. Hattori Bot. Lab. 11: 27 (1954), *syn. nov.*; Typus: *Phragmilejeunea pappeana* (Nees) Schust.

The following species should be placed in *Schiffneriolejeunea* at the present time:

Schiffneriolejeunea cumingiana (Mont.) Gradst. *comb. nov.*

Phragmicoma cumingiana Mont., London J. Bot. 4: 7 (1845).

Ptychocoleus cumingianus (Mont.) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Distr.: Indo-Malesia and the Pacific.

Schiffneriolejeunea ferruginea (Steph.) Gradst. *comb. nov.*

Acrolejeunea ferruginea Steph., Hedwigia 34: 57 (1895).

Ptychocoleus ferrugineus (Steph.) Steph., Spec. Hep. 5: 30 (1912).

Distr.: Tropical West Africa (Nigeria, Camerouns).

Schiffneriolejeunea madagascariensis (Steph.) Gradst. *comb. nov.*

Ptychocoleus madagascariensis Steph., Spec. Hep. 5: 27 (1912).

Distr.: Madagascar.

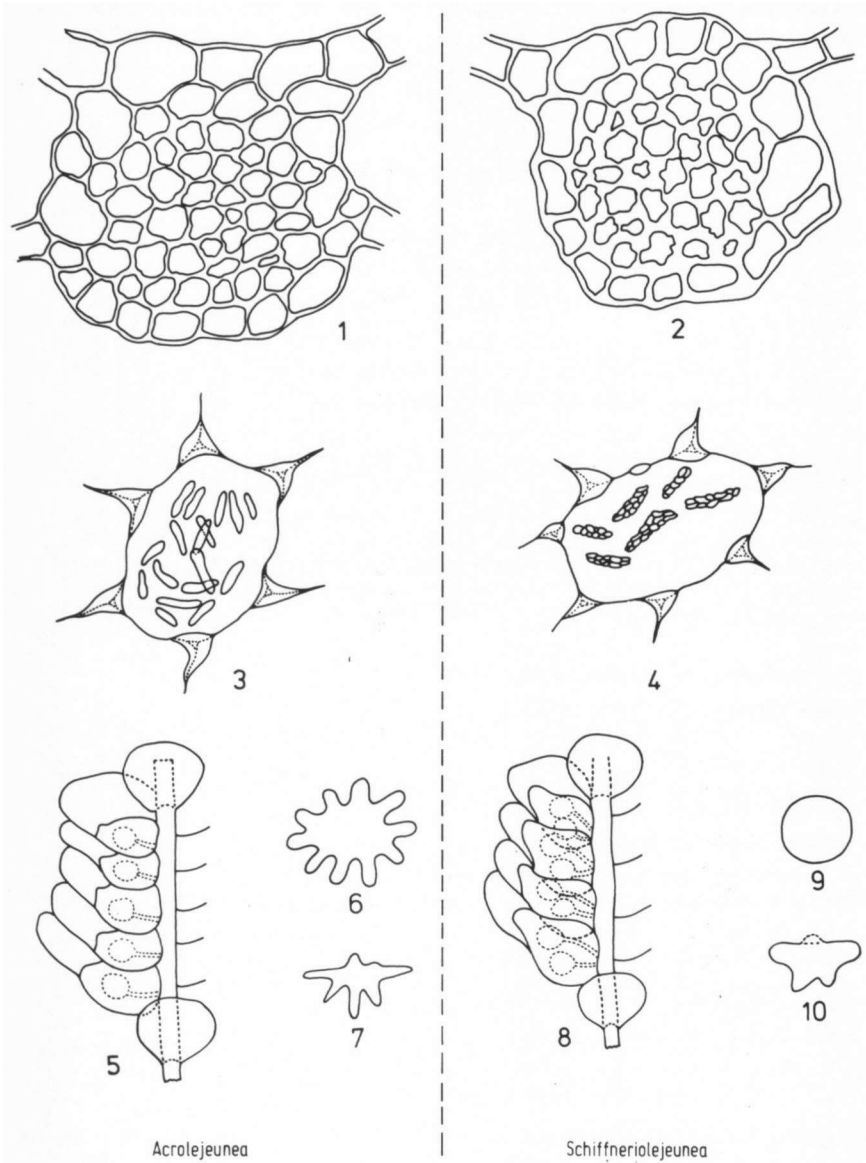
Schiffneriolejeunea occulta (Steph.) Gradst. *comb. nov.*

Lejeunea (subg. *Acrolejeunea*) *occulta* Steph., Hedwigia 27: 112 (1888).

Ptychocoleus occultus (Steph.) Steph., Spec. Hep. 5: 25 (1912).

Phragmilejeunea occulta (Steph.) Bischl. ["Schust."], Rev. Bryol. Lichénol. 33: 428 (1965) *nom. nud.*

Distr.: Tropical West Africa.



PL. II. Diagnostic differences between *Acrolejeunea* and *Schiffneriolejeunea*. Figs. 1-2. Stems, cross section ($270\times$). Figs. 3-4. Leaf cells with oilbodies ($1000\times$). Figs. 5, 8. Male spikes, somewhat diagrammatic (underleaves removed). Figs. 6, 7, 9, 10. Perianths, cross sections in the upper half, diagrammatic. Fig. 1 from *Acrolejeunea emergens*, type (NY). Fig. 2 from *Schiffneriolejeunea polycarpa*, A. W. Evans, Jamaica (NY). Fig. 3 from *Acrolejeunea torulosa*, G. L. Smith et al. P 11728, Brazil, Manaus (U). Fig. 4 from *Schiffneriolejeunea pulopenangensis*, W. Schultze-Motel 4249, Samoa (B).

Schiffneriolejeunea omphalanthoides Verd., Ann. Bryol. 6: 89 (1933).

Distr.: Malesia (Celebes, New Guinea).

Schiffneriolejeunea pappeana (Nees) Gradst. *comb. nov.*

Phragmicoma pappeana Nees in Gottsche et al., Syn. Hep.: 296 (1845).

Ptychocoleus pappeanus (Nees) Steph., Spec. Hep. 5: 28 (1912).

Phragmilejeunea pappeana (Nees) Schust., J. Hattori Bot. Lab. 11: 27 (1954).

Distr.: Tropical Africa, South Africa, East African Islands (Madagascar, Réunion).

Schiffneriolejeunea parviloba (Steph.) Gradst. *comb. nov.*

Ptychocoleus parvilobus Steph., Spec. Hep. 5: 31 (1912).

Lejeunea (subg. *Acrolejeunea*) *parviloba* Steph., Bot. Gaz. 15: 286 (1890) *nom. illeg.*; non. Ångstr. 1876.

Distr.: The Mascarene Islands.

Schiffneriolejeunea polycarpa (Nees) Gradst. *comb. nov.*

Jungermannia polycarpa Nees in Martius, Fl. Bras. 1(1): 350 (1833).

Ptychocoleus polycarpus (Nees) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Phragmilejeunea molleri (Steph.) Schust., Bryologist 64: 164 (1961) *syn. nov.*

Distr.: Tropical America, Tropical Africa, South Africa and East African Islands.

Schiffneriolejeunea pulopenangensis (Gott.) Gradst. *comb. nov.*

Phragmicoma pulopenangensis Gott., Syn. Hep.: 299 (1845).

Ptychocoleus pulopenangensis (Gott.) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Distr.: Indo-Malesia and the Pacific.

Schiffneriolejeunea tumida (Nees) Gradst. *comb. nov.*

Ptychanthus tumidus Nees, Naturgesch. Eur. Leberm. 3: 213 (1838).

Ptychocoleus tumidus (Nees) Trev., Mem. Reale Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 405 (1877).

Distr.: Indo-Malesia.

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