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Diversity and distribution of Asian Lejeuneaceae subfamily Ptychanthoideae

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(Studies on Lejeuneaceae subfam. Ptychanthoideae XX)

Abstract. A synopsis is provided of 88 species in 17 genera currently recognized in Lejeuneaceae subfamily Ptychanthoideae *sensu lato* (including *Nipponolejeunea*) of Asia. Taxonomic novelties include ***Thysananthus flavescens*** (Hatt.) **comb. nov**. (for *Mastigolejeunea flavescens* (Hatt.) Mizut.), ***Spruceanthus macrostipulus*** (Steph.) **comb. nov**. (for *Archilejeunea macrostipula* (Steph.) Verd.) and the reduction of *Platylejeunea* Mizut. to synonymy under *Lopholejeunea*.

The ptychanthoid flora of Asia has more species but fewer genera than the neotropical flora. Moreovere, the taxonomic make-up of the two floras is very different, Asia being the centre of diversity for the tribe Ptychantheae whereas the New World is particularly rich in Brachiolejeuneae. The larger number of neotropical genera reflects the unusually high generic diversity in the New World (Schuster 1990). The high species richness in Asia is probably due to a greater latitudinal extension of the rain forest in the Far East as compared with the New World. 22% of the ptychanthoid species of the Far East are "non-tropical", whereas in the New World it is less than 2%.

Contrasting biogeographic trends are seen among the endemic genera of the two subfamilies of Lejeuneaceae in Asia, Ptychanthoideae and Lejeuneoideae. In Ptychanthoideae the endemic genera are largely restricted to the subtropical and temperate areas of Asia and the majority are also known as fossils in Eocenic amber of Europe (Ginkgo-type distribution). They are considered to be palaeoendemic, relictual groups. Endemic genera of Lejeuneoideae, however, occur mainly in the tropical rain forests of the Malesian archipelago, are often highly specialized and are lacking in the fossil record. They should have co-evolved in the Tertiary with the rain forest and are considered neoendemics. Ptychanthoideae seem to be older than Lejeuneoideae and presumably already existed in the Mesozoic before the break-up of Laurasia and Gondwanaland.

Lejeuneaceae is the most important bryophyte family of the humid tropics in terms of species richness. An estimated 30% of the liverwort species of the tropics are Lejeuneaceae and up to 50% of the bryophytes of a lowland rain forest may be members of this family (Cornelissen & Gradstein 1990).

Based on seta anatomy two subfamilies of Lejeuneaceae are recognized (Mizutani 1985): Ptychanthoideae and Lejeuneoideae. In Ptychanthoideae the seta consists of 4 rows of inner cells surrounded by 16 or more rows of outer cells, whereas in Lejeuneoideae the 4 inner rows are surrounded by only 12 rows of outer cells. Other characters have also been attributed to these groups, but none of them are as constant as the differences between the "ptychanthoid" and the "lejeuneoid" seta, which were first noted more than a hundred years ago by Spruce

(1884). Several other subfamilies in Lejeuneaceae have been described, based mainly on characters of the gametophyte: Bryopteridoideae (Stotl.) Gradst. Nipponolejeunoideae Schust., Myriocoleoideae Schust., Tuyamaelloideae Schust., Cololejeuneoideae Herz. and Metzgeriopsidoideae Schust. Since sporophyte characters seem to be more stable in Lejeuneaceae (e.g. Mizutani 1961, Van Slageren 1985), I have chosen not to attribute subfamily rank to these groups. We certainly need more information on their sporophytes, in particular of the groups with a lejeuneoid seta.

The Ptychanthoideae include fewer genera and species than Lejeuneoideae and are much better known. In Asia 68 species in 14 genera were recognized by Verdoorn (1934) in his "Studien über Asiatische Jubuleae", which is the most recent comprehensive treatment available for the region. Since the appearance of Verdoorn's monograph, the Asiatic Ptychanthoideae have been studied in detail by Mizutani (e.g. 1961, 1968, 1969, 1979a, 1985a, 1986, 1987, 1988) as well as by others (e.g. Gradstein 1975, 1985, Gradstein & Terken 1981, Udar & Awashti 1982, Thiers & Gradstein 1989). As a result, more than half of the species names recognized by Verdoorn have changed or fallen into synonymy and 37 species and 5 genera have been added to the flora (Gradstein in prep). The new genera include 1) *Tuzibeanthus* Hatt. and *Nipponolejeunea* Hatt., endemic to eastern Asia (Hattori 1947), 2) *Stictolejeunea* (Spruce) Schiffn., a mainly neotropical genus collected in Sarawak by P.W. Richards (Herzog 1950) and found elsewhere in Asia since, 3) *Phaeolejeunea* Mizut., a small genus mainly occurring in the Pacific region (Mizutani 1968), and 4) *Cephalolejeunea* Mizut., discovered in Borneo by W. Meijer (Mizutani 1979). New species were described in most of the genera, especially in *Lopholejeunea* which has become the largest genus of Ptychanthoideae with 26 species recognized in Asia and about 40 world wide. The species concept in *Lopholejeunea* is not very solid, however, and is mainly based on characters of the gynoecium. I would suspect that the number of species accepted in this genus will become considerably lower when a thorough revision is undertaken.

At present, 88 species in 17 genera of Ptychanthoideae are recognized in Asia (see List). The majority of the species occur in Malesia, especially in New Guinea which has the highest species diversity with 55 species recorded, including 8 endemic species. According to Piippo et al. (1987) endemism in New Guinean hepatics, based on data for 22 families, is 48%. In Ptychanthoideae, however, it is only 15%. This difference may be explained by assuming that the Ptychanthoideae are a rather "conservative" group (e.g. Schuster 1980). Indeed, many genera of Ptychanthoideae seem to be of old age and are supposed to have arisen in the Mesozoic or early Tertiary (see below). Another explanation would relate to the species concept employed in the different groups of New Guinean hepatics. Many groups have only been studied on a regional basis and it may therefore be expected that some endemics will turn out to be taxonomic synonyms of species of other areas. For New Guinean Musci this was demonstrated by Koponen & Norris (e.g. 1985). Ptychanthoideae have received considerable attention from monographers and this may well be responsable for the rather low level of endemism in this group.

Japan also has a relatively rich ptychanthoid flora, with about 20 species including 4 endemic. The vast majority of the species (76) are restricted to Southeast Asia, sometimes extending into Pacific or Australasian regions. About twelve species also occur in Africa and six species are pantropical, occurring also in the New World: *Acrolejeunea emergens* and *Frul-*

lanoides liebmanniana (both mainly Afro-American in distribution), *Lopholejeunea eulopha, L. subfusca, Mastigolejeunea auriculata* (= *M. humilis*), and *Stictolejeunea balfourii*.

At the generic level, ptychanthoid endemism in Asia is rather low and the majority of the genera also occur in Africa and the New World. The endemic Asiatic genera include:

1. *Trocholejeunea* Schiffn., with 2 species, *T. infuscata* and *T. sandvicensis*, occurring mainly in subtropical and temperate eastern Asia and one species, *T. crassicaulis* in inner Malesia. The range of *T. sandvicensis* extends to the northern Pacific. A fourth species, *T. contorta* (Göppert & Berendt) Grolle & Gradst. is known as a fossil in amber from the Eocene of the European Baltic area (Grolle 1982).
2. *Nipponolejeunea* Hatt., with 2 species, *N. pilifera* and *N. subalpina*, in Japan and neighbouring temperate areas of East Asia. A third species, *N. europea* Grolle, is known as a fossil in amber from the Eocene of the European Baltic area (Grolle 1981).
3. *Tuzibeanthus* Hatt., monotypic, with only *T. chinensis* from temperate China and Japan.
4. *Cephalolejeunea* Mizut., monotypic, with only *C. parvilobula* from Borneo.
5. The genus *Spruceanthus* Verd. might be added to this list as it is largely restricted to the Far East. Five species are currently recognized in Southeast Asia, a sixth species occurs in subtropical Australasia (*S. thozetianus* (Gott. & F. Müll.) Thiers & Gradst. and one species occurs in the New World (*S. theobromae* (Spruce) Gradst.). The New World species is very rare and only known from the coastal region of Ecuador (Prov. Los Rios), whereas in Asia and Australasia the genus is common and widespread. Interestingly, the genus is also now known as a fossil from Baltic amber of Europe (*S. polonicus* Grolle 1985). In view of its current distribution, I consider *Spruceanthus* an Asiatic element.

The list of genera of Ptychanthoideae ± endemic to Asia reveals that, surprisingly, the majority occur *outside* the tropical zone of Asia and are subtropical or even temperate taxa. Moreover, three out of five are known as fossils from the Eocene of Central Europe (*Nipponolejeunea*, *Spruceanthus*, *Trocholejeunea*). It thus seems plausible that these genera were widespread in Laurasia in the early Tertiary but have become extinct in the glaciated, Euro-Siberian portion of the ancient continent. The extinction of these genera in Euro-Siberia and their survival in eastern Asia is clearly paralleled by various families and genera of seed plants, most notably the genera *Ginkgo* and *Liriodendron* (e.g. Good 1974). The ptychanthoid genera *Nipponolejeunea*, *Trocholejeunea* and *Spruceanthus* seem to be the first examples of bryophytes with such a relict, "*Ginkgo*-type" distribution. Interestingly, each of them is currently representive of a different climatic zone, *Nipponolejeunea* being a temperate East Asiatic genus, *Trocholejeunea* a mainly subtropical genus and *Spruceanthus* a predominantly tropical genus. Their occurrence in the Eocenic flora of Central Europe thus illustrates the mixed make-up of the flora of the early Tertiary of Europe, which was made-up of temperate, subtropical and tropical taxa (e.g. Walter & Straka 1970).

As compared to Ptychanthoideae, generic endemism in Asiatic Lejeuneoideae suggests a very different biogeographic history. Nine genera of Lejeuneoideae are only known from Asia: 1) *Aphanotropis* Herz. (Herzog 1952): 1 sp. in Sarawak. 2) *Calatholejeunea* Goebel (Mizutani 1984): 2 spp. in eastern Malesia. 3) *Campylolejeunea* Hatt. (e.g. Schuster 1963, Mizutani 1966): ca. 5 spp. in tropical and subtropical Southeast Asia. 4) *Cardiolejeunea* Schust & Kachroo (Schuster 1963): 1 sp. in Java. This genus is considered doubtfully distinct (Tixier 1980). 5) *Dactylophorella* Schust. (Schuster 1980a): 1 sp. in western Malesia.

Table 1. Comparison of the Ptychanthoideae floras of Asia (this paper), Australasia (Australia & New Zealand: Thiers & Gradstein 1989) and the New World (Gradstein 1987, 1990).

	Number of species		
	Asia	Australasia	New World
Ptychantheae Bischler			
Bryopteris complex:			
Bryopteris	-	-	3
Ptychanthus complex:			
Ptychanthus	1	2	-
Tuzibeanthus	1	-	-
Thysananthus	9	4	3
Mastigolejeunea	9	5	2
Schiffneriolejeunea	6	2	2
Acrolejeunea complex:			
Trocholejeunea	2	-	-
Frullanoides	1	-	6
Acrolejeunea	11	5	3
Caudalejeunea complex:			
Caudalejeunea	5	3	1
Archilejeunea complex:			
Spruceanthus	5	1	1
Archilejeunea	2	3	5
Verdoornianthus	-	-	2
Phaeolejeunea	2	-	-
Cephalolejeunea	1	-	-
Lopholejeunea complex:			
Lopholejeunea	26	8	4
Marchesinia	-	-	2
Nipponolejeunea complex:			
Nipponolejeunea	2	-	-
Brachiolejeuneae van Slag. & Berendsen			
Brachiolejeunea complex:			
Brachiolejeunea	-	-	5
Blepharolejeunea	-	-	5
Acanthocoleus	3	-	2
Dicranolejeunea	-	-	1
Odontolejeunea	-	-	3
Lindigianthus	-	-	1
Symbiezidium complex			
Symbiezidium	-	-	2
Stictolejeunea complex:			
Stictolejeunea	2	1	2
Neurolejeunea	-	-	4
Total	88	34	59

6) *Hattoriolejeunea* Mizut. (Mizutani 1986a): 1 sp. in the Moluccas. 7) *Metzgeriopsis* Goebel (e.g. Tixier 1974): 1 sp. in Malesia and New Caledonia. 8) *Stenolejeunea* Schust. (e.g. Grolle 1966): 3 spp. in equatorial Malesia. The genus is of doubtful status. 9) *Tuyamaella* Hatt. (Tixier 1973): 5 spp. in tropical and subtropical Southeast Asia. A sixth species is known from Peru, but this New World record is probably based on an erroneous label (Grolle, pers. comm.). 10) To the list might be added *Rhaphidolejeunea* Herz. which has 8 spp. in tropical Asia and 1 in the New World (Bischler 1968, Grolle 1974).

This brief listing of the Asiatic endemic genera of Lejeuneoideae reveals that all of them occur in the tropical belt of East Asia, mostly in Malesia. Only two of them (*Campylolejeunea, Tuyamaella*) extend to the subtropical belt, to Japan. The genera mostly grow in the rain forests of Malesia, often as epiphylls on the surface of living leaves, and some of them show rather specialized morphological features involving paedomorphosis (*Metzgeriopsis, Aphanotropis, Campylolejeunea, Calatholejeunea, Tuyamaella*). Interestingly, none of these genera are known as fossils. Their present-day distribution thus suggests that they co-evolved with the tropical rain forests of East Asia during the Tertiary and Quaternary.

It thus appears that the endemic genera of the Ptychanthoideae of Asia are mostly palaeo-endemic, relictual groups which evolved in the non-tropical part of Asia or elsewhere in Laurasia. They probably arose in the Mesozoic or, at the latest, in the early Tertiary. The endemic genera of Lejeuneoideae, on the other hand, may be considered neo-endemics which probably originated in more recent geological times in the tropical belt, synchronous with the evolution of the tropical rain forest. The contrasting evolutionary trends (Fig. 1) suggest that Ptychanthoideae are a more ancient group than Lejeuneoideae, at least in Asia. An old age for this group is corroborated by the results of recent monographic studies on other genera of Ptychanthoideae, not endemic to Asia, e.g. *Bryopteris* (Stotler & Crandall-Stotler 1974), *Acrolejeunea* (Gradstein 1975), *Frullanoides* (van Slageren 1985), *Dicranolejeunea* and *Acanthocoleus* (Kruijt 1988). All of these studies suggest Mesozoic origins, mostly in western Gondwanaland, before the break-up of the landmass. Their occurrence in Asia is usually postulated as the result of migration northwards with portions of the old landmass, possible through rafting via India (*Acrolejeunea*). Long distance air transport has also been considered. The available data hardly allow for further speculation on the origin of the subfamily, however. Further monographic work on the genera, including careful phylogenetic analysis as done for *Acanthocoleus* and *Dicranolejeunea* (Kruijt 1988) , may help to elucidate the evolutionary history of the Ptychanthoideae and of the family Lejeuneaceae as a whole.

Comparison of Asiatic Ptychanthoideae flora with other areas

In Table 1 the Asiatic Ptychanthoideae flora is compared with other areas for which up-to-date lists are available, viz. Australasia (Thiers & Gradstein 1989, Thiers 1990) and of the New World (Gradstein 1987, 1990).

Thirty-four species are currently known from Australia and New Zealand, of which two third are also known from Asia. Furthermore, all of the genera of Australasia also occur in Asia and the general make-up of the two floras is indeed very similar. The flora of Australasia is of course less diversified as only a small portion of the area is located in the tropical zone. The majority of the species occur in the tropical rain forests of northern Queensland (Thiers 1990), whilst ten

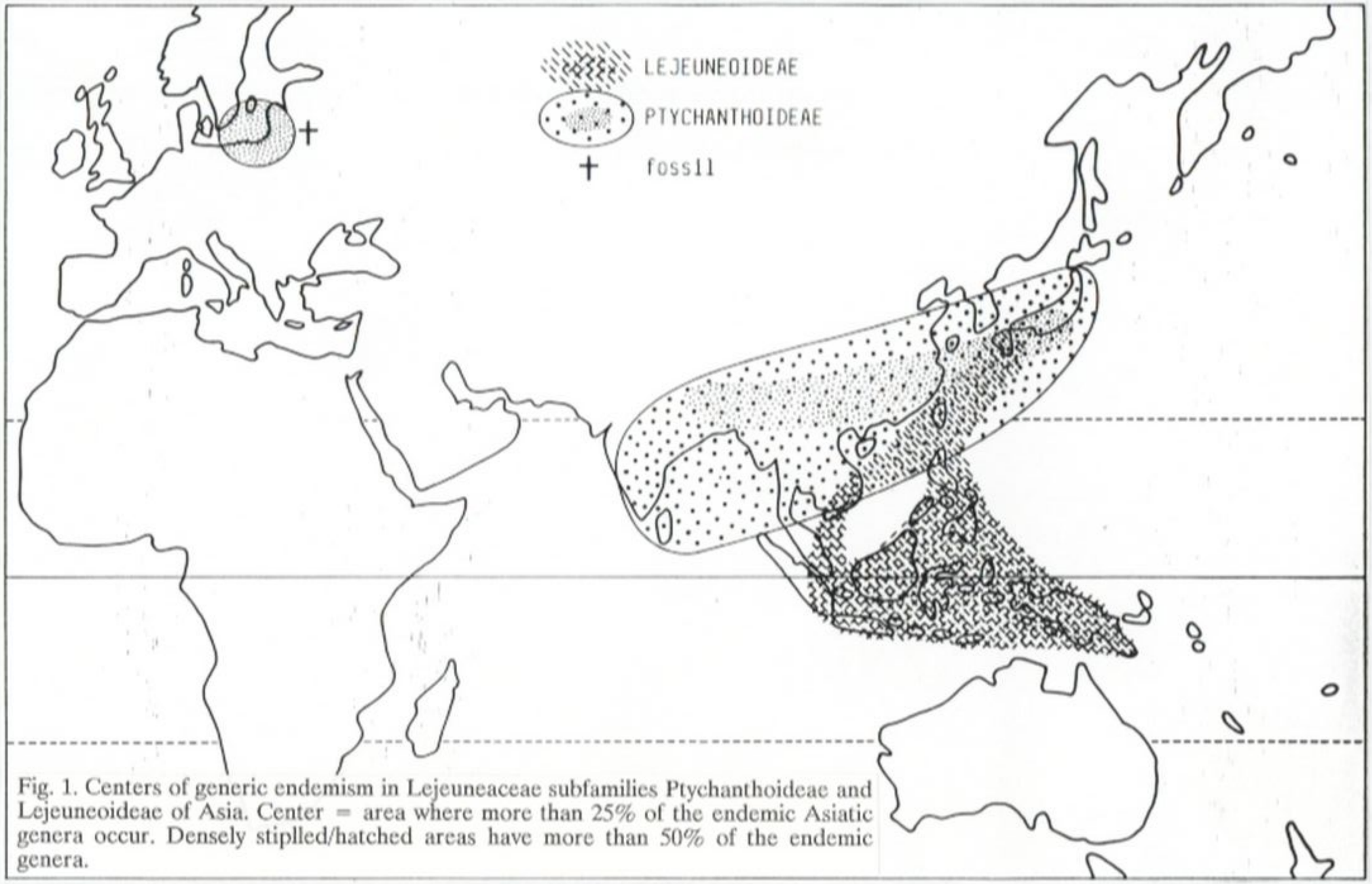

Fig. 1. Centers of generic endemism in Lejeuneaceae subfamilies Ptychanthoideae and Lejeuneoideae of Asia. Center = area where more than 25% of the endemic Asiatic genera occur. Densely stiplled/hatched areas have more than 50% of the endemic genera.

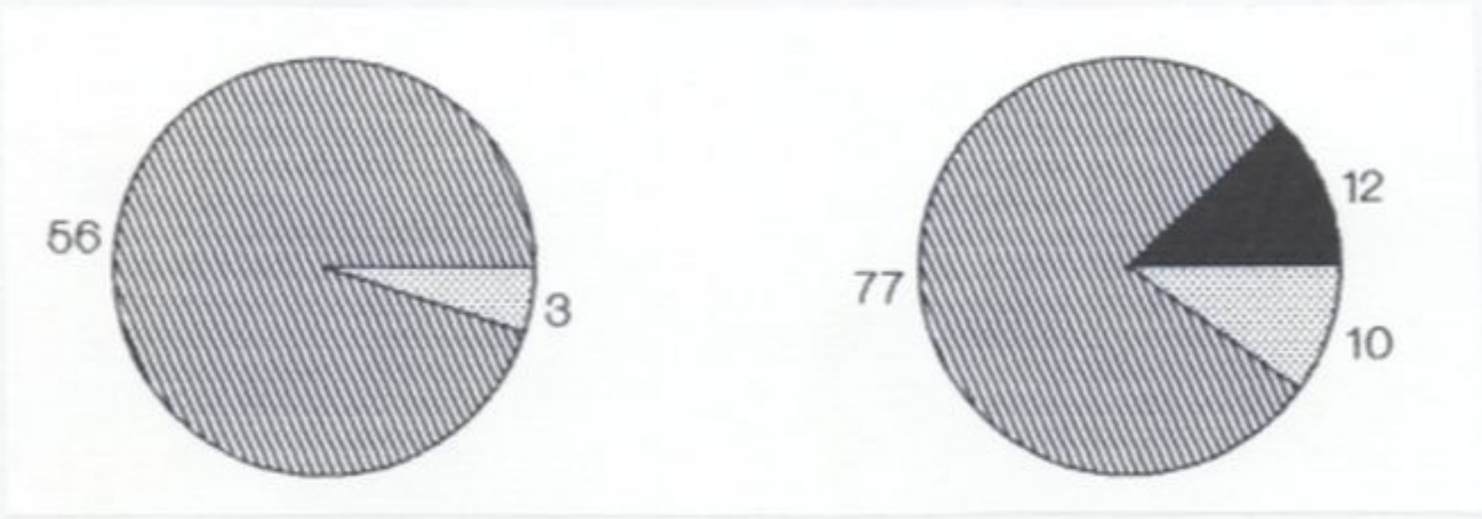

Fig. 2. Number of tropical and non-tropical species in the ptychanthoid floras of Asia/Australasia and the New World. Stippled: northern non-tropical species. Black: southern non-tropical species.

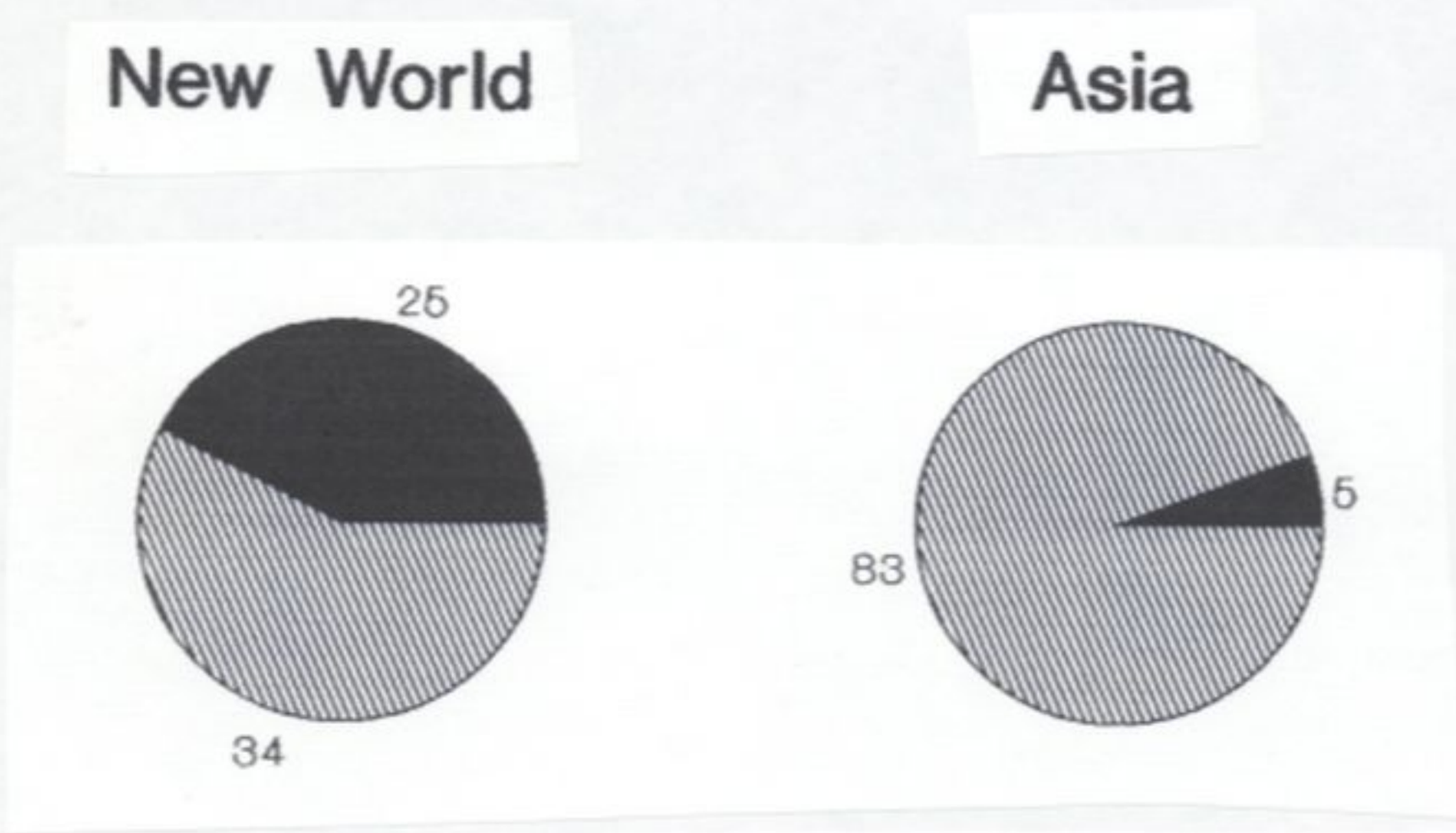

Fig. 3. Comparison of the ptychanthoid floras of Asia and the New World. Hatched: number of species of tribe Ptychantheae. Black: number of species of tribe Brachiolejeuneae.

species are essentially subtropical or temperate in distribution: *Acrolejeunea allisonii, A. mollis, Archilejeunea olivacea, Lopholejeunea colensoi, L. hispidissima, L. plicatiscypha, Mastigolejeunea anguiformis, Ptychanthus stephensonianus, Spruceanthus thozetianus* and *Thysananthus australis*. All of these non-tropical species are endemic to Australasia.

Fifty-nine species in 21 genera of Ptychanthoideae are currently known from the New World (Table 1). Apparently, the New World has more genera but fewer species than Asia. The larger number of genera in the New World reflects the unusually high generic diversity in the neotropics (Schuster 1990) but the lower number of species in the New World is somewhat unexpected. One reason may be that the species concepts applied in the two areas are not the same. Several genera with rather large numbers of species in Asia have not yet been monographed, including *Lopholejeunea, Mastigolejeunea* and *Thysananthus*. Probably, the differences in species richness between the two areas would become smaller after revision of these groups.
Another reason for the higher diversity in Asia may be due to the large number of taxa occuring outside the geographical tropics in Japan, China and the Himalayas. As stated earlier, this area is relatively rich in endemic genera of Ptychanthoideae and represents a center of diversity for the subfamily. There are about thirty species in subtropical and temperate Asia, twelve of which are only known from these regions: *Acanthocoleus yoshinaganus, Acrolejeunea sikkimensis, Lopholejeunea gradsteinii, L. kiushiana, L. nipponica, L. sikkimensis, Nipponolejeunea pilifera, N. subalpina, Spruceanthus mamillilobus, Stictolejeunea iwatsukii, Thysananthus flavescens, Tuzibeanthus chinensis.* In addition, *Trocholejeunea infuscata* and *T. sandivicensis* mostly occur in the subtropical regions of eastern Asia.

In sharp contrast with Asia, there are no species of Ptychanthoideae restricted to North America, north of the geographical tropics. Schuster (1980) in his "Manual of the Hepticae and Anthocerotae of North America East of the 100th Meridian" treats only eight species, all of which occur also in the tropical zone. The richer ptychanthoid flora of subtropical and temperate Asia as compared with North America is probably due to a greater extension northwards of evergreen rain forests in eastern Asia, correlated with the occurrence of mild, monsoon-type climates at high latitudes (Whitmore 1984). Another reason may be the lack of Pleistocenic glaciations in the "Sino-Japanese" region as opposed to corresponding areas of North America where tropical taxa became extinct due to the past climatic changes (Good 1974).

The dissimilarities between Eastern Asia and North America in terms of the species richness and latitudinal extension of its ptychanthoid floras, are also seen in the Southern Hemisphere. As pointed out earlier, there are ten species of Ptychanthoideae endemic to the subtropical or temperate region of Australasia. In contrast, only three New World species of Ptychanthoideae are endemic to southern South America, south of the Tropic of Capricorn: *Archilejeunea fuegiana, Brachiolejeunea fernandeziana* and *B. spruceana* (Gradstein 1987). Surprisingly, all of them occur in the cool temperate, oceanic regions of the continent. No endemic species of Ptychanthoideae is known from subtropical South America, which seems to hold a rather depauperate tropical flora made up largely of common, weedy species (e.g. *Acanthocoleus aberrans, Brachiolejeunea phyllorhiza, Neurolejeunea breutelii*, etc.: see Gradstein 1990). According to Thiers (1990), the high diversity of Australian Lejeuneaceae may be due to discontinuities of rain forest patches distributed from North to South along the coasts of Queensland and New

South Wales, ranging from the tropics to well into the temperate zone. These forests offer a great variety of habitats for inhabitation by Lejeuneaceae. A somewhat similar latitudinal gradient of rain forest is seen to the North in Eastern Asia but in the New World it is lacking. This, then, might be the main reason for relatively higher species diversity in subtropical and temperate Asia as compared with the New World. Indeed, 22% of the ptychanthoid species of the Far East (Asia/Australasia) are "non-tropical", whereas in the New World it is less than 2% (Fig. 2). It appears that some elements of the non-tropical Asiatic flora are relicts of an old, Laurasian Lejeuneaceae flora (see above). Others may be more recent invaders from Malesia. A similar mixed origin for the Lejeuneaceae flora of Australia was postulated by Thiers (1990).

Another significant difference between the Asiatic and New World Ptychanthoideae is the taxonomic composition of the two floras. As shown in Table 1, two tribes may be recognized: Ptychantheae and Brachiolejeuneae. Asiatic Ptychanthoideae almost exclusively belong to the tribe Ptychantheae, which has its largest diversity in that area. The most important genera are*Acrolejeunea,Lopholejeunea, Mastigo-lejeunea, Schiffneriolejeunea, Spruceanthus*, and *Thysananthus*. Also the endemic ptychanthoid genera of Asia are all members of this tribe (*Cephalolejeunea, Nipponolejeunea, Phaeolejeunea, Trocholejeunea, Tuzibeanthus*).
In contrast, the New World flora is characterized by a poorer Ptychantheae flora and a rich flora of Brachiolejeuneae, which appears to be a largely neotropical group. Of 9 genera and 31 species currently recognized in Brachiolejeuneae, all of the genera and 25 species occur in the New World whereas only 2 genera and 5 species occur in Asia. Best represented in Asia is the genus *Acanthocoleus* with 3 species. According to Kruijt (1988), the most primitive species of *Acanthocoleus* are found in the New World whereas the Asiatic species are more advanced types. This genus is therefore not of Asiatic origin. The other genus of Brachiolejeuneae occurring in Asia, *Stictolejeunea*, is probably also not of Asiatic origin as the highest diversity is in the New World (Gradstein 1985a).
It would appear that the different ptychanthoid diversities of Asia and the New World are correlated with very different evolutionary histories of the subfamily in the two regions, Asia being the centre of diversity for the Ptychantheae (but *not* the centre of origin of this group, see above) and the New World being the area where Brachiolejeuneae have mainly evolved. In addition, the New World might be considered a secondary centre of diversity for Ptychantheae (*Frullanoides, Archilejeunea* subg. *Archilejeunea, Verdoornianthus, Acrolejeunea* subg. *Acrolejeunea, Bryopteris*). The floristic differences between Asia and the New World are shown in Fig. 3.

List of the genera and species of Lejeuneaceae subfamily Ptychanthoideae in Asia

Acanthocoleus Schust.
Ref.: Kruijt 1988
A. gilvus (Steph.) Kruijt - Himalayas, India
A. javanicus (Steph.) Kruijt - Malesia
A. yoshinaganus (Hatt.) Kruijt - Japan, Korea

Acrolejeunea (Spruce) Schiffn.
Ref.: Gradstein 1975
A. arcuata (Nees) Grolle & Gradst. - Malesia
A. aulacophora (Mont.) Steph. - palaeotropics
A. emergens (Mitt.) Steph. - tropical America, Africa, Sri Lanka
A. fertilis (Reinw. et al.) Schiffn. -

Indomalesia
A. parvula (Mizut.) Gradst. - Indochina (Thailand, Andaman Is.)
A. pusilla (Steph.) Grolle & Gradst. - southern Japan, China
A. pycnoclada (Tayl.) Schiffn. - palaeotropics
A. pycnoclada ssp. *latistipula* Gradst. - New Guinea
A. recurvata Gradst. - India, Indochina
A. securifolia (Nees) Watts ex Steph. ssp. *hartmannii* (Steph.) Gradst. - eastern Malesia
A. sikkimensis (Mizut.) Gradst. - Himalayas
A. tjibodensis (Verd.) Grolle & Gradst. - Malesia

Archilejeunea (Spruce) Schiffn. **1)**
Ref.: Thiers & Gradstein 1989; Udar & Awashti 1981
A. planiuscula (Mitt.) Steph. (= *A. mariana* auct., non (Gott.) Steph.) - Indopacific
A. polymorpha (Sande Lac.) B. Thiers & Gradst. - Indopacific

Caudalejeunea (Steph.) Schiffn.
Ref.: Thiers & Gradstein 1989; Mizutani 1988
C. cristiloba (Steph.) Gradst. (=*C. circinata* Steph.) - Indopacific
C. lessonii Steph. - Indomalesia
C. pluriplicata Udar et al. - India
C. recurvistipula (Gott.) Schiffn. - Malesia
C. reniloba (Gott.) Steph. - Indopacific, may be palaeotropics

Cephalolejeunea Mizut. **2)**
Ref.: Mizutani 1979
C. parvilobula Mizut. - Borneo

Frullanoides Raddi
Ref.: van Slageren 1985
F. liebmanniana (Lindenb. & Gott.) van Slag. (= *F. poeltii* Grolle = *F. tristis* (Steph.) van Slag. fide Gradstein & Hekking 1989) - India, Nepal

Lopholejeunea (Spruce) Schiffn. **3)**
Ref.: Verdoorn 1934, Mizutani 1961, 1979a, 1985a, Onraedt 1985, Thiers & Gradstein 1989
L. abortiva (Mitt.) Steph. - Africa, Sri Lanka
L. acutifolia Mizut. & Piippo - New Guinea
L. applanata (Reinw. et al.) Schiffn. - Malesia, China
L. borneensis (Steph.) Verd. - Borneo
L. ceylanica Steph. - Sri Lanka, western Malesia
L. dentifolia Mizut. & Piippo - New Guinea
L. eulopha (Tayl.) Schiffn. - palaeotropics
L. evansiana Verd. (= *Plagiolejeunea zantenii* Mizut.) **4)** - New Guinea
L. gradsteinii Udar et al. - India
L. herzogiana Verd. - Malesia
L. horticola Schiffn. - western Malesia
L. javanica (Nees) Steph. - Indopacific
L. kiushiana Horik. (= *Archilejeunea kiushiana* (Horik.) Hatt.) **5)** - southern Japan
L. latialata Mizut. - western Malesia
L. latilobula Verd. - New Guinea
L. loheri Steph. - Indomalesia, Australasia
L. magna Mizut. - Sabah
L. nigricans (Lindenb.) Steph. - Southeast Asia
L. nicobarica Steph. - Southeast Asia
L. nipponica Horik. - Japan, China
L. pullei Verd. - N. Guinea
L. recurvata Mizut. - Java
L. sikkimensis Steph. - Himalayas
L. subfusca (Nees) Steph. - pantropical
L. wiltensii Steph. - Malesia
L. zollingeri Steph. - western Malesia

Mastigolejeunea (Spruce) Schiffn. **6)**
Ref.: Thiers & Gradstein 1989, Mizutani 1987
M. auriculata (Wils.) Schiffn. (= *M. humilis* (Gott.) Steph.) - pantropical
M. indica Steph. - Indomalesia
M. ligulata (Lehm. & Lindenb.) Schiffn. - Indopacific
M. recondita (Steph.) Mizut. - eastern Malesia
M. recurvifolia Mizut. - Malesia
M. repleta (Tayl.) Evans - Indomalesia

M. truncatula Mizut. - Borneo
M. undulata Gradst. & Grolle - eastern Malesia
M. virens (Aongstr.) Steph. - Indopacific

Nipponolejeunea Hatt. **7)**
Ref.: Mizutani 1961, Inoue et al. 1981, Piippo 1990
N. pilifera (Steph.) Hatt. - East Asia
N. subalpina (Horik.) Hatt. - East Asia

Phaeolejeunea Mizut.
Ref.: Mizutani 1968
P. inermis (Steph.) Mizut. - New Guinea
P. latistipula (Schiffn.) Mizut. - China, eastern Malesia, Pacific

(*Plagiolejeunea* Mizut. = *Lopholejeunea*: see note **4**)

Ptychanthus Nees
Ref.: Thiers & Gradstein 1989, Mizutani 1961
P. striatus (Lehm. & Lindenb.) Nees - palaeotropics

Schiffneriolejeunea Verd.
Ref.: Gradstein 1974, Gradstein & Terken 1981, Udar & Awashti 1982, Thiers & Gradstein 1989
S. cumingiana (Mont.) Gradst. - eastern Malesia
S. nymannii (Steph.) Gradst. & Terken - eastern Malesia
S. omphalanthoides Verd. - eastern Malesia
S. polycarpa (Nees) Gradst. - tropical America, Africa, Sri Lanka
S. pulopenangensis (Gott.) Gradst. **8)** - Indomalesia
S. tumida (Nees & Mont.) Gradst. var. *tumida* - Indomalesia
S. tumida var. *haskarliana* (Gott.) Gradst. & Terken - Indopacific

Spruceanthus Verd.
Ref.: Thiers & Gradstein 1989, Gradstein 1981, 1985
S. macrostipulus (Steph.) ***comb. nov.*** **9)** - New Guinea
S. mamillilobulus (Herz.) Verd. - China
S. pluriplicatus (Steph.) Gradst. - N. Guinea
S. semirepandus (Nees) Verd. - Indomalesia
S. sulcatus (Nees) Gradst. - western Malesia

Stictolejeunea (Spruce) Schiffn. (subgenus *Leptostictolejeunea* Schust.)
Ref.: Thiers & Gradstein 1989, Gradstein 1985a
S. balfourii (Mitt.) E.W. Jones var. *balfourii* - pantropical
S. iwatsukii Mizut. - southern Japan

Thysananthus Lindenb.
Ref.: Thiers & Gradstein 1989, Mizutani 1969, 1987, Verdoorn 1934
T. aculeatus Herz. - East Asia
T. comosus Lindenb. - Malesia
T. convolutus Lindenb. (= T. gottschei (Jack & Steph.) Steph.) - Indopacific
T. flavescens (Hatt.) **comb. nov. 10)** - southern Japan
T. fruticosus (Lindenb. & Gott.) Schiffn. - Indopacific
T. minor Verd. - Malesia
T. mollis Steph. - New Guinea
T. retusus (Reinw. et al.) B. Thiers & Gradst. (= *T. planus* Sande Lac.) - Indopacific
T. spathulistipus (Reinw. et al.) Lindenb. - palaeotropics

Trocholejeunea Schiffn.
Ref.: Mizutani 1989
T. crassicaulis (Steph.) Mizut. - eastern Malesia
T. infuscata (Mitt.) Verd. - Himalayas, Sri Lanka, China
T. sandvicensis (Gott.) Mizut. - IndoChina, Japan, northern Pacific

Tuzibeanthus Hatt.
Ref.: Mizutani 1961
T. chinensis (Steph.) Mizut. - East Asia

Notes

1) *A. apiculifolia* Steph. and *A. minutilobula* Udar & Awashti from India are very close to *A. planiuscula* and may be synonyms of the latter. *Archilejeunea kiushiana* (Horik.) Hatt. is considered to belong to *Lopholejeunea* (see note **5**) and *A. macrostipula* Steph. is transferred to *Spruceanthus* (see note **9**).

2) *Cephalolejeunea* Mizut. is a small, monotypic genus known only from a few localities in Borneo, where it grows on wood or rock presumably at low altitudes (Mizutani 1979). The genus is a member of the tribe Ptychantheae because of its fenestrate-type sporophyte, but its generic relationship remains unresolved. Mizutani placed the genus in the *Acrolejeunea* complex (= "*Brachiolejeunea* complex") but from that group it deviates by the leaves which remain flat when dry and do not become convoluted, by its isodiametric leaf cells with simple, non-cordate trigones, and by its saccate, hypostatic male bracts. Because *Cephalolejeunea* lacks any trace of secondary pigmentation I would tentatively place the genus in the *Archilejeunea* complex, although the presence of an epidermis of enlarged cells and the peculiar pluriplicate perianth separate *Cephalolejeunea* from other members of that group except, may be, *Phaeolejeunea* which also has a stem hyaloderm. A more careful study of *Cephalolejeunea* and *Phaeolejeunea*, including examination of living material with oil bodies (which remain unknown in either genus), would be needed to elucidate the generic relationships of these two peculiar Indopacific ptychanthoids.

3) The genus *Lopholejeunea* is in need of revision. Presumably several of the species listed will prove to be synonyms. Some species of doubtful status are excluded from the list, including *L. aberrantia* Horik. and *L. muensis* Steph.

4) *Lopholejeunea evansiana* Verd. 1934 is a conspicuous, subalpine endemic species of New Guinea. I have collected copious fertile material, with sporophytes, from bushes along the shore of lower lake Pindaunde at Mount Wilhelm, 3500 m. alt., very near to the former Australian research station. Mizutani (1984) described a new genus and species from New Guinea, *Plagiolejeunea zantenii* Mizut., which appears to be identical to *Lopholejeunea evansiana*.

A peculiar character of *L. evansiana*, and main reason that led Dr. Mizutani to establish the genus *Plagiolejeunea*, is the common presence of *Frullania*-type branches which occasionally may be produced as true subfloral innovations. *Frullania*-type branches are rare in *Lopholejeunea* but have also been found in *L. hispidissima* and *L. macroloma* (Thiers 1985). Subfloral innovations of the *Frullania*-type, however, had not been reported before from *Lopholejeunea* and were only known from *Trocholejeun*ea. The latter also produces "normal" *Radula*-type innovations, but in *L. evansiana* innovations are always of the *Frullania*-type and *Radula*-type ones have not been observed.

My study of specimens of *L. evansiana* identified by Dr. Mizutani as *Plagiolejeunea zantenii* and of my own materials of this species, revealed a rather complex and unusual situation as regards the development of *Frullania*-type innovations in *L. evansiana*. Contrary to Dr. Mizutani's observation, true subfloral innovations, originating between the inner bract and the perianth, are not very common in *L. evansiana*. Most of the innovations are "pseudo-innovations", originating below the inner bracts or further down the stem. Only occasionally they originate between the inner bract and the perianth, leaving the inner bract without lobule. Such true innovations are as a rule produced on one side only. I have not seen paired innovations although Mizutani recorded

their occurrence.
What is more striking, however, is that the true subfloral innovations are always associated with morphological aberration of the gynoecium or the innovating branch. The subfloral innovation may originate from fertile or sterile gynoecia. When from a sterile gynoecium (lacking outgrowth of a perianth) the innovation grows into an elongated branch which may become fertile at the tip. When from a fertile gynoecium with perianth, however, the innovation remains a short, vegetative branchlet. The lower leaves of this branchlet are suberect and more elongate than the upper leaves and resemble young female bracts. Such short, vegetative subfloral innovations appeared to be not uncommon whereas well-developed ones were only rarely observed. Innovation development is apparently triggered by the abortion of the associated gynoecium and is suppressed in "normal", fertile gynoecia. In this respect, *L. evansiana* does not differ from other species of *Lopholejeunea* which may also produce abnormal innovations (Thiers 1985). However, thus far only abnormal *Lejeunea*-type innovations had been reported and *L. evansiana* thus represents the first species of the genus *Lopholejeunea* with abnormal development of innovations of the *Frullania*-type. Abnormal *Lejeunea*-type (or *Radula*-type) innovations are also known from other ptychanthoid genera which normally lack them (Gradstein 1975, Thiers 1985) but abnormal *Frullania*-type innovations were thus far unknown in Lejeuneaceae. They have been reported for Frullaniaceae, viz. *Amphijubula spruceana* (= *Frullania spruceana*), by Schuster (1970).

The establishment of a new genus based on these abnormal innovations would thus not seem justified. Although Mizutani mentioned a few other characters for *Plagiolejeunea* in addition to the innovations (number of bracts, thickwalled stem cells, inflation of perianth), none of these seem to furnish sufficient basis for separating *L. evansiana* from *Lopholejeunea* and placing it in a genus of its own. *Plagiolejeunea* Mizut. is therefore reduced to synonymy under *Lopholejeunea.*

Specimens examined: Papua New Guinea, Chimbu province: Mt. Wilhelm, on bushes around lower Pindaunde lake, alt. 3500 m., S.R. Gradstein 3981, 3992, 14-17 August 1981 (U); Central District: Mt. Albert Edward, en route from Abios Hut to tent site, ca. 3000 m., H. Inoue 31612, 31862, 25 October 1975, identified by Dr. Mizutani as *Plagiolejeunea zantenii* Mizut. (NICH).

5) Thiers & Gradstein (1989) have argued that *A. kiushiana* should be returned to *Lopholejeunea* because of its homogeneous oil bodies and stem hyaloderm. Moreover, the subfloral innovations are abnormal and usually of the *Lejeunea*-type (see also note **4**).

6) Several further Asiatic species names exist in *Mastigolejeunea* (e.g. *M. borneensis* Steph., *M. minutilobula* Amak., *M. takakii* Horik.). Their status is doubtful. *Mastigolejeunea paradoxa* Verd. is a synonym of *Archilejeunea planiuscula* (Gradstein & Buskes 1985) and *M. flavescens* (Hatt.) Mizut. belongs in *Thysananthus* (see note **10**)

7) Following Mizutani (1985) *Nipponolejeunea* is placed in the Ptychanthoideae based on the presence of a seta with 16 rows of outer cells and *Frullania*-type branching. Because of its fenestrate capsule the genus belongs in the tribe Ptychantheae, in which it stands apart by a number of unusual gametophytic features, including the almost transverse leaf insertion, the short bifid underleaves and the ciliate leaf apex. *N. pilifera*,

moreover, is unique among Lejeuneaceae by the possession of two archegonia instead of one. The very short leaf insertion of *Nipponolejeunea* is reminiscent of Tuyamaelloideae, Cololejeuneoideae and Frullaniaceae, and is also seen in juvenile leaves of all Lejeuneaceae. This character may therefore be considered a juvenile trait retained in the adult plant of *Nipponolejeunea* (and other taxa), a phenomenon commonly known as paedomorphosis. The pendulum "cololejeuneoid" leaf sequence of Cololejeuneoideae and some Tuyamaelloideae, Myriocoleoideae and Lejeuneoideae s.str. (Thiers 1984, Mizutani 1984), and the lack of underleaves in *Cololejeunea* and *Aphanolejeunea*, are further examples of paedomorphosis in Lejeuneaceae, as was pointed out for the first time by Crandall (1969). Paedomorphic traits may be very stable in some groups, but in others they are more variable especially with respect to leaf segmentation (Thiers 1984). For example, the two species of *Calatholejeunea* recognized by Mizutani (1984) have different leaf segmentation: cololejeuneoid in *C. paradoxa* and lejeuneoid in *C. lamii*. The variation of these and other gametophytic traits of Lejeuneaceae is apparently larger than previously assumed. The author would therefore attribute less weight to suprageneric groups in Lejeuneaceae recognized solely on the basis of gametophytic characters. For that reason, a subdivison of Lejeuneaceae in only two subfamilies Ptychanthoideae and Lejeuneoideae, and inclusion of *Nipponolejeunea* in Ptychanthoideae tribus Ptychantheae, is accepted in this paper.

8) The following names are new synonyms of *Schiffneriolejeunea pulopenangensis* (Gott.) Gradst. :

Archilejeunea indica Steph. (*Schiffneriolejeunea indica* (Steph.) Udar & Awashti). Type: Mangalore, J. Pfleiderer s.n. (G holo).
Ptychocoleus grandiflorus Herz. Type: "West Borneo, am Ufer bei Nanga Krocab", H. Winkler 3001, 9 September 1924 (JE holo).
Ptychocoleus mangaloreus Steph. Type: Mangalore, J. Pfleiderer s.n., Aug. 1907, ex hb. Levier 6131 (fertile) & 6133 (sterile) (G syntypes).

9) *Spruceanthus macrostipulus* (Steph.) Gradst. **comb. nov.** (*Mastigolejeunea macrostipula* Steph., Spec. Hep. 4: 767, 1912; *Archilejeunea macrostipula* (Steph.) Verd., Nova Guinea 18: 3, 1934).
Type: New Guinea, "Bergwald an Bäumen", Naumann s.n., 17 June 1875 (G holotype).

Spruceanthus macrostipulus seems closely related to *S. pluriplicatus* (Steph.) Gradst., also from New Guinea, from which it differs by the smaller, often reduced lobules without teeth (2 small teeth are present in *S. pluriplicatus*) and the longer, oblong leaves, ca. 1.6-2 x longer than wide (ovate-suborbicular in *S. pluriplicatus*). The material of *S. macrostipulus* only contains juvenile gynoecia, mature perianths being lacking. If the two species prove to be identical, the name *S. pluriplicatus* would fall into synonymy of *S. macrostipula*, the latter one being the older name.

10) ***Thysananthus flavescens*** (Hatt.) Gradst. **comb. nov.** (*Archilejeunea flavescens* Hatt., Bull. Tokyo Sci. Mus. 11: 95, 1944; *Mastigolejeunea flavescens* (Hatt.) Mizut., Journ. Hattori Bot. Lab. 24: 159, 1961).
Type: Japan, Kagoshima Pref., Osumi Prov., Satamura, S. Hattori 2399, 18 April 1939 (NICH iso). Further material investigated: Japan, Kagoshima Pref., Oshumi Peninsula, near pass between Hanaze and Mekka, Mizutani 41481, 11

May 1959 (NICH).

Thysananthus flavescens belongs in the subgenus *Sandeanthus* B. Thiers & Gradst., a small, mainly Asiatic subgenus containing two further species (see Thiers & Gradstein 1989): the widespread Indopacific *T. retusus* (Reinw. et al.) B. Thiers & Gradst. (= *T. planus* Sande Lac.) and *T. australis* (Steph.) B. Thiers & Gradst. known only from New South Wales, Australia. Characteristic for *T.* subgenus *Sandeanthus* are the vittate leaves with entire margins, the small, isodiametrical, rather evenly thickened leaf cells (except for the vitta cells) and the small size of the plants and stems. By their peculiar leaf areolation the species of *T.* subgenus *Sandeanthus* approach the otherwise very different *T. pterobryoides* from tropical America.
T. flavescens resembles *T. retusus*, but differs from the latter by the more obscure vitta, the subentire margins of the female bracts and bracteoles (heavily toothed in *T. retusus*) and the dioicous (?) inflorescence (autoicous in *T. retusus*). By its obscure vitta and ± entire involucre *T. flavescens* is similar to *T. australis* from which it otherwise differs by its longer lobule, longer lobule tooth and the presumably dioicous inflorescence. The three species currently recognized in *T.* subg. *Sandeanthus* are certainly very close and their relationships and status are in need of further study.

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