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# An Overview of the Lejeuneaceae in Australia

Barbara M. Thiers
New York Botanical Garden, Bronx, New York 10458-5126

**Abstract**. As currently understood, the Lejeuneaceae flora of Australia consists of 122 species in 27 genera. The family occurs almost exclusively in rainforested areas along the eastern coast of the continent. Based on species composition, three floristic regions are recognized: tropical, subtropical and temperate. The tropical region contains 80 percent of the total number of Lejeuneaceae found in Australia, the subtropical region contains 45 percent, and the temperate region only 15 percent of the total flora. The affinities of the Lejeuneaceae in the tropical and subtropical regions are strongest with the Asian flora, and those of the temperate region are strongest with the New Zealand flora. The diversity of the Lejeuneaceae flora in Australia is higher than might be expected for a non-equatorial region. This diversity may result from the wide variety of rainforest habitats that are available along both latitudinal and altitudinal gradients. The temperate flora is probably derived from that which existed in Australia, New Zealand, Antarctica and probably southern South America prior to the breakup of Gondwanaland. The modern tropical flora is probably a mixture of species that were part of the original northern Gondwanan flora and those that have invaded more recently.

## Introduction

Approximately 65 species of Lejeuneaceae were reported from Australia during the early descriptive phase of work on the Australian bryoflora, prior to about 1925. These reports, from both temperate and tropical regions of the country, were made primarily in the publications of Bailey (1913), Bastow (1888), Carrington & Pearson (1888a, b, c), Gottsche (1880), Lehmann (1847-48), Pearson (1922, 1924), Rodway (1916a, b), Stephani (1889, 1912-1917), Stephani and Watts (1914), Taylor (1846), Watts (1902, 1902-03, 1904-05), and Weymouth (1903). Revisionary work on the Lejeuneaceae of Australia followed more slowly. Verdoorn (1934) reviewed some tropical Australian members of subfamily Ptychanthoideae, and Schuster (1963), Grolle (1982) and Scott (1985) have treated some elements of the temperate flora found in the southern states of Tasmania and Victoria.

During the past five years I have been studying the Lejeuneaceae of Australia (Thiers 1985, 1987a, b, 1988, Thiers & Gradstein 1989). As a result, approximately half of the original 65 species reported from the continent have been excluded or reduced to synonymy, but recent collecting efforts by me and others (see acknowledgements) have raised the number of species currently known on the continent to 122. Almost all of the newly reported species were found in the poorly collected tropical and subtropical areas. The purpose of this paper is to summarize the content and distribution of the Australian Lejeuneaceae flora, with emphasis on the tropical and subtropical


**Fig. 1.** Map of Australia, showing approximate distribution of rainforest in Australia (after Webb & Tracey 1981). NSW = New South Wales; NT = Northern Territory; QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; WA = Western Australia.

a general characterization of the flora.

The Lejeuneaceae is the largest family of Hepaticae, with probably 1000-1500 species in approximately 70 genera. Although some species penetrate temperate and even sub-arctic and sub-antarctic zones, the family is largely tropical in distribution. The plants are highly conspicuous in rainforest areas, covering bark and living leaves of trees and vines, sometimes forming extensive mats or festoons in regions of particularly high humidity. Lejeuneaceae may be found in tropical and subtropical rainforests anywhere in the world, with the richest areas (in terms of diversity and biomass) being the equatorial regions of South America and Asia.

Rainforest covers about 2 million ha. in Australia, forming an archipelago of habitats stretching over 6000 km along the eastern coast of the continent, with small outposts along the north coast (Fig. 1). Rainforests occur usually in fire-proof niches, in subcoastal areas with a rainfall of at least 600 mm per year (Webb & Tracey 1981). The area of Australia covered by rainforest is approximately 0.3 percent of the total continent. The rainforests of Australia have been classified qualitatively and quantitatively into a series of structural types (Webb 1968). The main categories are based primarily

**TABLE I.** Diversity of Lejeuneaceae in the rainforests of Australia.

| Region | # Genera | % of Total (27) | # Species | % of Total (122) |
|---|---|---|---|---|
| Tropical | 23 | 82% | 96 | 80% |
| Subtropical | 18 | 64% | 55 | 45% |
| Temperate | 11 | 39% | 17 | 15% |

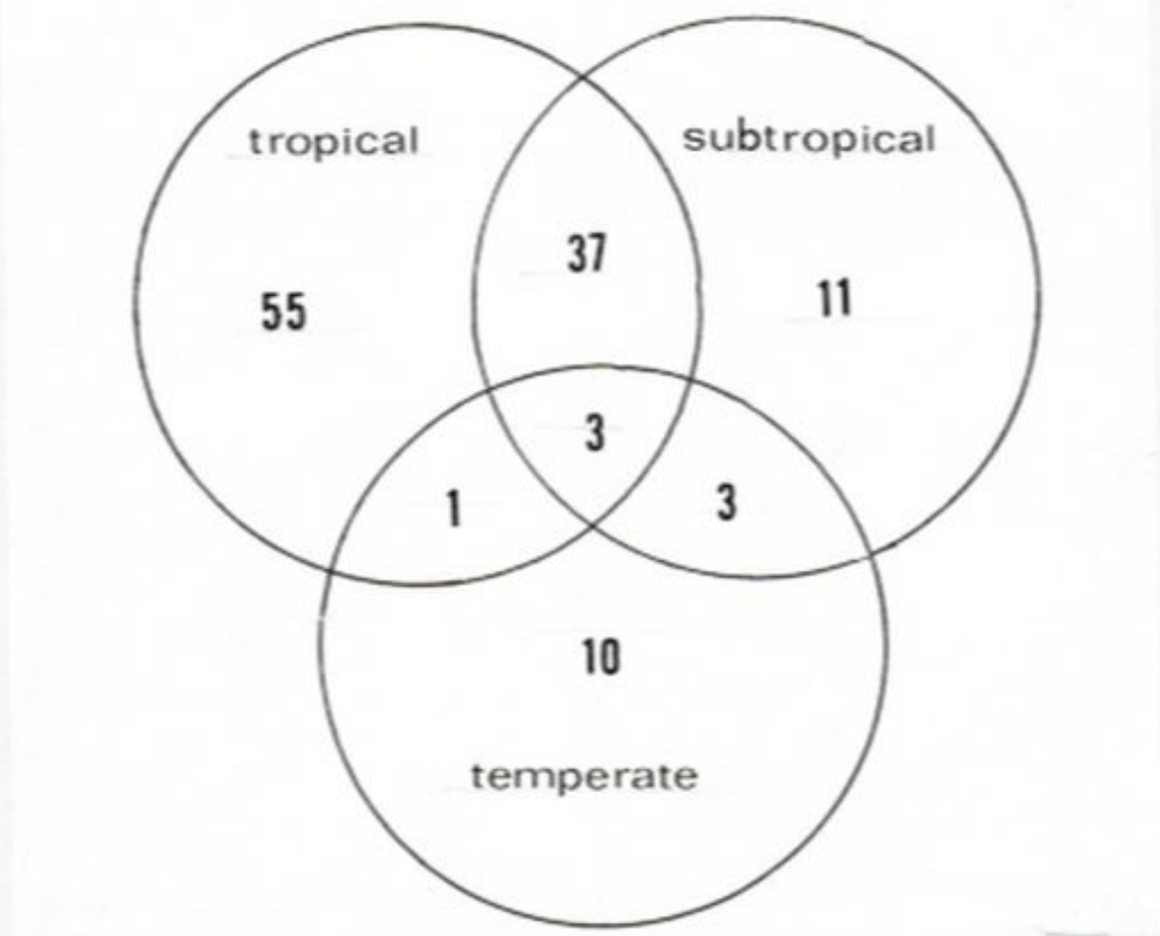


**Fig. 2.** Interrelationships of Lejeuneaceae floras in tropical, subtropical and temperate regions of Australia. Numbers in single circles refer to the number species unique to a given region. Numbers in areas of overlap between circles indicate the number of species shared by those regions

outposts along the north coast (Fig. 1). Rainforests occur usually in fire-proof niches, in subcoastal areas with a rainfall of at least 600 mm per year (Webb & Tracey 1981). The area of Australia covered by rainforest is approximately 0.3 percent of the total continent. The rainforests of Australia have been classified qualitatively and quantitatively into a series of structural types (Webb 1968). The main categories are based primarily on the non-tree elements of the forest, i.e., whether vines (lianas), ferns or mosses (bryophytes) predominate in the understory. Finer divisions are based on periodicity of leaf loss (evergreen versus rain-green) and leaf size class of the dominant forest elements (e.g., mesophyll, notophyll, microphyll, etc.). These physiognomic types correlate well with thermal regions, and thus the tropical, subtropical and temperate regions of the country each have distinctive rainforest characteristics. Not surprisingly, a similar pattern emerges for the Lejeuneaceae, that are found in the rainforest areas of the continent. The tropical region has the richest flora, the temperate region the poorest (Table I). The tropical and subtropical floras are most similar to one another (Fig. 2), and are most closely related to the tropical and subtropical floras of Asia, whereas the temperate flora is most similar to that of New Zealand.

## The Floristic Components of the Australian Lejeuneaceae Flora

### The Tropical Region

Tropical rainforest covers approximately 759,000 ha. in northern Queensland (Webb & Tracey 1981). Rainforested areas form patches of varying sizes at altitudes ranging from sea level to the summits of coastal mountains (1600 m). Rainfall ranges from 1300-4000 mm per year, in most areas with two-thirds of this amount falling between January and April (Tracey 1982). The Australian tropics are considered marginal 'outer tropics' in a world perspective, because the annual temperature range exceeds 5°C. According to the classification of Webb (1968), the rainforests of the tropical zone are all vine forests, ranging from wet evergreen forests in the vicinity of Cairns to dry, rain-green monsoon forests on Cape York. Floristically the tropical rainforests show a high degree of affinity to those of Malesia, but have a high rate of endemism, particularly among primitive angiosperms. Of the 14 families considered primitive by Takhtajan (1969), eight are found in the tropical rainforests of Australia (Webb & Tracey 1981).

Three of the four subfamilies of Lejeuneaceae found in Australia occur in the tropical region (Cololejeuneoideae, Lejeuneoideae and Ptychanthoideae; Tuyamaelloideae is lacking). For all three subfamilies this region is the richest in Australia, with 96 species in 23 genera, accounting for 80 percent of the total number of species found in Australia. Eight genera (*Caudalejeunea, Ceratolejeunea, Lepidolejeunea, Leucolejeunea, Otolejeunea, Ptychanthus, Pycnolejeunea, Stictolejeunea)* and 55 species occur only in tropical Australia.

Within this region, the Lejeuneaceae flora correlates to a certain extent with altitude, allowing the recognition of three floristic subregions, which I have termed lowland, upland and submontane.

The lowland habitat comprises the coastal rainforest from Cape Tribulation south to the Russell River and Tully areas, all averaging above 2500 mm of rain per year (Tracey, 1982). The rainforest here is less seasonal than elsewhere, and this subregion supports the largest number of Lejeuneaceae (65 species). All genera of Lejeuneaceae that occur in the tropical region can be found in lowland areas. The epiphyllous flora is particularly well-

developed, with good representation of species of *Caudalejeunea* (3 species), *Cololejeunea* (10 species), and *Leptolejeunea* (5 species). Four endemic species appear to be restricted to the lowland forest: *Cheilolejeunea sp. nov.* 1 (in press), *Colura crispiloba* Jovet-Ast, *C. australiense*, Jovet-Ast, and *Lepidolejeunea queenslandica* B. Thiers.

In the upland habitat I include rainforests of the Atherton and Windsor Tablelands, the slopes of Mt. Lewis, and the Cardwell range. Elevation ranges from 800-1200 m, and 1200-1500 mm of rain falls per year, in a more seasonal pattern than is found in the lowland forest. The patches of rainforest in the upland subregion are more dissected than in lowland areas, but this area has almost as many Lejeuneaceae (59 species), and is similar in floristic composition to the lowland subregion. In addition to appressed corticoles and epiphylls, the uplands are characterized by the presence of large, festooning species, e.g., *Ptychanthus striatus* (Lehm. & Lindenb.) Nees, *Thysananthus spathulistipus* (Reinw. et al. & Nees) Lindenb., and *T. fruticosus* (Lindenb. & Gott.) Schiffn., especially near waterfalls and steep escarpments, where clouds and mist provide extra humidity. Thirteen species have been found in tropical Australia only in the upland region. Among these, three are found also in the subtropics (*Spruceanthus thozetianus* (Gott. & F. v. Muell.) B. Thiers, *Cololejeunea mamillata* (Aongst.) Hodgs., and *Harpalejeunea filicuspis* (Steph.) Mizut.); two have a worldwide distribution (*Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans and *Cololejeunea appressa* (Evans) Bened.); and five are primarily Asian (*Cheilolejeunea clavata* Mizut., *Cololejeunea ocelloides* (Horik.) Mizut., *Colura conica* (Sande Lac.) Goeb., *Drepanolejeunea intermedia* Zwick., and *Lejeunea punctiformis* Tayl. Apparent upland endemics are *Cheilolejeunea incisa* var. *nov.* (in press), *Colura simplicior* Jovet-Ast, and *Lopholejeunea streimannii* B. Thiers & Gradst.

The summits and upper slopes of Mt. Bellenden Ker, Mt. Bartle Frere and Thornton Peak provide habitats for the submontane floristic subregion, at elevations usually above 1200 m. The summit of the central peak of Mt. Bellenden Ker is the best studied because of easy access via cable car. The vegetation here is predominantly a microphyll vine thicket, with a dense canopy 10-12 m high (Tracey, 1982). Rainfall is very high, and cloud cover contributes significantly to maintaining a high moisture level. Lejeuneaceae grow here intermixed with other hepatics in dense, sometimes pendant mats on bark of trees and shrubs. The biomass is large, but the number of species is less than at lower elevations (20 species). However, the flora is distinctive. Seven species are known in Australia only from submontane areas (*Colura acroloba* (Mont.) Steph., *C. bisvoluta* Herz. & Jovet-Ast, *Drepanolejeunea dactylophora* (Gott. Lindenb. & Nees) Schiffn., *D. hampeana* Steph., *D. pentadactyla* (Mont.) Steph., *D. levicornua* Steph., and *Lopholejeunea loheri* Steph.). Two species growing in the submontane subregion are not known elsewhere in the tropical region, namely *Cheilolejeunea falsinervis* (Sande Lac.) Kachroo & Schust., which also occurs in the subtropical region, and *Drepanolejeunea aucklandica* Steph., known also from the temperate region. However, no Australian endemics are restricted to the submontane flora.

Of the species shared by lowland, upland and submontane subregions, five have a worldwide distribution (*Lejeunea cucullata* (Reinw. et al.) Nees, L. flava (Sw.) Nees, *Drepanolejeunea ternatensis* (Gott.) Steph., and *Leptolejeunea maculata* (Mitt.) Schiffn. and the others are widespread in the Asia.

Very little is known about the

Lejeuneaceae of the monsoon forests of Cape York. Because of the long dry period each year, the Lejeuneaceae flora may be fairly depauperate in this area. Two species occurring here (*Mastigolejeunea indica* Steph. and *Cololejeunea wightii* Steph.) have not been found commonly elsewhere in Australia, suggesting that although limited, the monsoon forest flora may represent a distinctive floristic region for the Lejeuneaceae.

**The Subtropical Region**

In terms of Lejeuneaceae, the subtropical region extends from central Queensland (near Mackay) to the vicinity of Sydney in New South Wales. The boundaries of the region are particularly ill-defined, because throughout its range, the subtropical region contains elements from both the tropical and temperate regions. As delimited here, the subtropical area includes also the warm temperate region, from which it cannot be distinguished based on differences in the Lejeuneaceae flora. The rainforests in general also show a mixture of elements from tropical and temperate regions. Lowland areas may be evergreen or rain-green notophyll vine forests similar to those of the tropical region, but at higher elevations these may be replaced by evergreen noto- or microphyll fern or vine-fern forests more similar to those of the temperate zone (Webb 1968).

Many of the species originally described from Australia by W. W. Watts and Stephani (Stephani & Watts 1914, Watts 1902, 1902-03, 1904-05) came from the subtropical forests near Ballina and the Richmond River area in northern New South Wales. The subtropical flora contains 18, or 64% of the total number of Lejeuneaceae genera found in Australia, and 55 (45%) of the total number of species. Most species are corticolous. All four subfamilies of Lejeuneaceae found in Australia occur in the subtropical region. *Cololejeunea* (Cololejeuneoideae), *Mastigolejeunea*, *Lopholejeunea* (Ptychanthoideae), *Cheilolejeunea* and *Lejeunea* (Lejeuneoideae) are particularly well represented. The epiphyllous flora is reduced to one species of *Leptolejeunea* (*L. elliptica* Lehm. & Lindenb.) Steph. and several of *Cololejeunea* (e.g., *C. appressa* (Evans) Bened., *C. cardiocarpa* (Nees & Mont.) Steph., *C. mamillata* (Aongst.) Hodgs., and *C. minutissima* (Sm.) Schiffn. Well-defined examples of the subtropical Lejeuneaceae flora can be found in Queensland in the vicinity of the Sunshine Coast north of Brisbane (e.g., the area from Coolum Beach to Cooloola National Park), and on the Lamington Plateau on the Queensland- New South Wales border. Although there seem to be some differences in species composition at different altitudes, these are not great enough, based on current knowledge, to warrant segregation into separate subregions.

The subtropical Lejeuneaceae flora, although not as rich, shares many species with the tropical flora. Afro-Asian or pantropical species, such as *Cheilolejeunea intertexta* (Lindenb.) Steph, *C. trifaria* (Reinw. et al.) Mizut., *Lejeunea flava* (Sw.) Nees, and *Lopholejeunea subfusca* (Nees) Steph. are typical elements, as are some species with more restricted Asian distributions, such as *Archilejeunea planiuscula* (Mitt.) Steph., *Cheilolejeunea ceylanica* (Gott.) Schust. & Kachroo, and *Lejeunea discreta* Lindenb. Likewise, temperate species such as *Cheilolejeunea mimosa* (Hook. & Tayl.) Schust., *C. campbelliensis* (Hook. & Tayl.) Schust. and *Lejeunea drummondii* are not uncommon in the subtropical region. Eight species found in the subtropical region (15% of the flora) appear to be endemic to Australia. Four of these are commonly encountered in both tropical and subtropical areas (*Cheilolejeunea longidens* (Steph.) Kachroo & Schust., *Cheilolejeunea sp. nov.* 2 (in press), *Lejeunea cuspidistipula* (Steph.) Steph., and

Sapindaceae and Sterculiaceae, with *Nothofagus* and Proteaceae present as well. The Cinnamomum assemblage may be a segment of the original Gondwandlanic flora, judging from the world-wide distribution of its principal angiospermous elements (Beadle 1981). Throughout the Cenozoic there was substantial climatic fluctuation, but generally as Australia moved northward the continent became more arid, and the rainforest areas were largely replaced by more dry-adapted vegetation (Kemp 1981, Galloway & Kemp 1981). The size of the rainforest-covered areas in the northeast began to increase again about 10,000 years ago, due to an increase in temperature and precipitation (Galloway & Kemp 1981). However, rainforested areas were still restricted to coastal and subcoastal areas along the eastern coast. Because the shallow Torres Straits separating present day Australia and New Guinea is a very recent phenomenon (developing since the Pleistocene), a dry land connection between Australia and New Guinea has existed more often than not in the past few million years (Galloway & Kemp 1981).

Current phytogeographic theory based upon the above tectonic and palynological data holds that both the temperate and tropical rainforests are derived from the original flora that was present in Gondwanaland before the breakup (Webb et al. 1986). This theory supercedes the hypothesis that Australian rainforests, at least in the north, were completely eliminated during the period of very dry conditions, and have been re-established from the Indo-malayan region in the past few million years (Barlow 1981). If the current theory is correct, modern day rainforests can be considered refugia, and are probably for the most part older than the dry-adapted vegetation that surrounds them. The relictual nature of the rainforest flora might help explain the high rate of endemism of Angiosperms, especially primitive ones.

The affinities of the temperate Lejeuneaceae flora of Australia with New Zealand suggest that this flora or its precursor may be a relict of that which existed in southern Australia, Antarctica, New Zealand and probably southern South America prior to the breakup of Gondwanaland. The northern limit of the southern Gondwanan Lejeuneaceae flora in the late Cretaceous-early Tertiary rainforests in Australia is impossible to determine, but it seems reasonable to suggest that it covered the same basic area as the *Nothofagus*-dominated forest, and that it was replaced in the north by a different flora that was associated with the Cinnamomum flora.

Probably some elements of the original northern Gondwanan Lejeuneaceae flora persisted in the rainforest refugia that withstood the aridification of the Australian continent, and have remained there until today. However, some Lejeuneaceae appear to be capable of long distance dispersal, and the fairly close contact that has existed during the past 15-20 m.y (and especially in the past 10,000 years) between Australia and Asia via New Guinea makes it impossible to rule out the possibility that some members of the modern tropical and subtropical floras are relatively recent arrivals. There is, of course, no way to know which elements are autochthonous and which are invasive, but based on reproductive and ecological differences, some speculation can be ventured. A genus such as *Cheilolejeunea* may be a good candidate for a member of the original northern Gondwanan flora. It is represented in Australia by 17 species, including three species and one variety that seem to be endemic. The genus is not likely to be a rapid colonizer of a new area, because most species are unisexual, and none have any specialized means of asexual reproduction. Also, the species found in Australia seem fairly tolerant of rather dry rainforest habitats, and thus

*Spruceanthus thozetianus*), but the remaining four are known only from the subtropical region (*Austrolejeunea bidentata* B. Thiers, *Colura queenslandica* B. Thiers, *Siphonolejeunea elegantissima* (Steph.) Grolle, and *Thysananthus australis* (Steph.) B. Thiers & Gradst.).

Four of the species currently known in Australia only from the subtropical region are also known from other countries, these are *Lopholejeunea colensoi* Steph. and *L. plicatiscypha* (Hook. f. & Tayl.) Steph. from New Zealand, *L. hispidissima* Steph., known previously only from New Caledonia and *Rectolejeunea ocellata* Herz., also from New Zealand.

**The Temperate Region**

According to the classification by Webb (1968) the cool temperate forests found in Victoria and Tasmania are classified as fern forests, or in montane areas, mossy forests. These are evergreen, and are usually mixed with wet sclerophyll forest. Nothofagus is usually the dominant tree genus, and the forests in this zone are uniformly wet. Lejeuneaceae occur mainly in montane areas, as epiphytes and also over rock. Most species are minute to small, and there are few if any pendant or epiphyllous forms.

The main subfamilies represented in this region are Cololejeuneoideae, Lejeuneoideae and Tuyamaelloideae, with Ptychanthoideae represented by two species (*Acrolejeunea aulacophora* (Mont.) Steph. and *Lopholejeunea sp.*, Grolle, 1982). The temperate flora, with only 17 species, is the smallest of the floristic units of Australian Lejeuneaceae. Among the more common species are *Cheilolejeunea campbelliensis*, *C. mimosa, Drepanolejeunea aucklandica, Harpalejeunea latitans,* (Hook. f. & Tayl.) Grolle, *Lejeunea drummondii,* and *Siphonolejeunea nudipes* (Hook. & Tayl.) Herz. Sixteen of the 17 species in the temperate flora are also found in New Zealand, and one species, *Lejeunea norrisii* Grolle, is apparently endemic to Tasmania. The three species shared with the subtropical and tropical zones, namely *Lejeunea flava, L. cucullata,* and *Cololejeunea minutissima,* have worldwide distributions. *Drepanolejeunea aucklandica,* occurs in the temperate region and in the submontane tropical region (on Mt. Bellenden Ker), but has not yet been found in the subtropical region.

**Origin of the Australian Lejeuneaceae Flora**

Recent advances in the study of plate tectonics and paleopalynology have helped to reconstruct the history of the Australian continent. Australia was originally part of the super-continent of Gondwanaland, which began breaking up about 135 m.y. before present (Crook 1981). In the late Cretaceous- early Paleocene period (60-80 m.y. before present) New Zealand became separated from Australia-Antarctica, with the formation of the Tasman Sea. Australia separated from Antarctica in the late Paleocene (60-53 m.y. before present) as Australia began rafting northward. The northward movement of Australia has continued ever since, the northern edge of the continent (represented by at least part of the current New Guinea land mass) colliding with the Sunda Arc about 15-20 m.y. before present (Powell et al. 1981).

Pollen data indicate that at the time of its separation from the rest of Gondwanaland, the Antarctic-Australian land mass was covered in the south to a large extent by a broad-leaved forest dominated by Angiosperms, especially *Nothofagus*. The northern portion of the continent was vegetated by the 'Cinnamomum' flora, dominated by such families as Elaeocarpaceae, Lauraceae, Meliaceae, Moraceae, Myrtaceae, Palmae,

**TABLE II.** Comparison of Australian Lejeuneaceae flora to other regions. (*Complete citation in literature cited).

| Region | Source* | Number of species reported |
|---|---|---|
| Colombia | Gradstein & Hekking, 1979 | 204 |
| Western Melanesia | Grolle & Piippo, 1984 | 183 |
| Philippines | Tan & Engel, 1986 | 165 |
| Costa Rica | Herzog, 1951 | 118 |
| Australia | | 122 |
| Tropical East Africa | Bizot & Pócs, 1974, 1979 | 66 |
| Japan | Mizutani, 1961 | 64 |
| North America | Schuster, 1980 | 63 |
| New Zealand | Hamlin, 1972 | 45 |

The seasonality of even the wettest Australian rainforests probably discourages the growth of some species, but the periods of drier, cooler conditions are apparently not as limiting as might be assumed. Even during seasons of low rainfall in the Australian rainforest, the moisture level in the very narrow zone above the substrate where these plants grow may remain high enough for most Lejeuneaceae. In areas such as the Atherton Tableland where waterfalls and fogs are common, the humidity may be higher than indicated by rainfall. The seasonal drop in temperature during the drier months may limit the growth of some equatorial species, but may actually encourage the growth of others. It has been suggested by Richards (1984) that very high temperatures, such as are found in equatorial lowland forests, may be limiting to many tropical bryophytes. In my experience, the Lejeuneaceae flora is richer in a well-developed lowland Australian rainforest (such as that found at Mossman Gorge National Park, or at 'The Boulders' in Bellenden Ker National Park) than that of an aseasonal, Amazonian rainforest, such as that found in the Culebra valley of Territorio Federal Amazonas, Venezuela). Many factors could be responsible for the differences in floristic richness of these two sites, but possibly the cooler temperatures in the Australian lowland tropics may actually allow more species to grow there than might be expected in an equatorial lowland region.

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maintenance of three fairly distinct floras. Also, most rainforested areas in Australia have a fairly high topographic relief, and the variation in altitude of rainforested sites clearly influences which Lejeuneaceae grow there, as described above for the tropical region. Therefore, although the area they cover is small, the rainforests of Australia offer a variety of habitats, and are thus able to accommodate a wide range of species with different growth preferences or requirements.

The restriction of rainforest to patches that are often separated from one another by large areas inhospitable to Lejeuneaceae may have been a factor in the evolution of at least some of Australia's endemic species, which make up 18% of the flora. The isolation of rainforested sites reduces the possibility for interbreeding among populations, and thus allows mutations to become fixed.

The seasonality of even the wettest Australian rainforests probably discourages the growth of some species, but the periods of drier, cooler conditions are apparently not as limiting as might be assumed. Even during seasons of low rainfall in the Australian rainforest, the moisture level in the very narrow zone above the substrate where these plants grow may remain high enough for most Lejeuneaceae. In areas such as the Atherton Tableland where waterfalls and fogs are common, the humidity may be higher than indicated by rainfall. The seasonal drop in temperature during the drier months may limit the growth of some equatorial species, but may actually encourage the growth of others. It has been suggested by Richards (1984) that very high temperatures, such as are found in equatorial lowland forests, may be limiting to many tropical bryophytes. In my experience, the Lejeuneaceae flora is richer in a well-developed lowland Australian rainforest (such as that found at Mossman Gorge National Park, or at 'The Boulders' in Bellenden Ker National Park) than that of an aseasonal, Amazonian rainforest, such as that found in the Culebra valley of Territorio Federal Amazonas, Venezuela). Many factors could be responsible for the differences in floristic richness of these two sites, but possibly the cooler temperatures in the Australian lowland tropics may actually allow more species to grow there than might be expected in an equatorial lowland region.

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