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The epiphyllous habit in the hepatic genus *Frullania*

Matthew J. von Konrat & John E. Braggins

Plant Science, School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand

Abstract. We report for the first time 11 species of *Frullania* growing as epiphylls in New Zealand, New Caledonia, and Colombia . Also listed are 29 *Frullania* species that have previously been recorded growing as epiphylls in other regions of the world. The highest diversity of *Frullania* epiphyllous species are in the floristic regions of New Zealand, New Caledonia, Macraonesia, and Madagascar. *Frullania* epiphylls range in altitude from sea-level to 2500m and can be categorised into facultative or accidental epiphylls. The number of *Frullania* species currently recorded growing as epiphylls will no doubt increase as more revisions of the genus in different floristic regions take place. This number may also increase if botanists were to explore leaf surfaces as a potential substrate for *Frullania* species, in addition to bark and rock habitats that have traditionally been described as microhabitats for the genus.

INTRODUCTION

The surfaces of leaves provide a microenvironment which, in suitable conditions, may develop a complete miniature ecosystem, including lichens, mosses, algae, fungi, small animals such as rotifers, and populations of micro-organisms as well as hepatics (Richards, 1984). Some of the most important components of these epiphyllous communities are hepatics, especially members of the Lejeuneaceae (Pócs, 1997). This paper provides evidence that species in the genus *Frullania* Raddi, in the family Jubulaceae, may also be a significant member of such communities in some habitats.

Bryophytes growing on the leaves of trees are usually regarded as characteristic of humid tropical montane forests (Richards, 1984; Pócs, 1997), but outside these regions epiphyllous bryophytes have been frequently reported in favourable areas, such as British Columbia (Vitt et al., 1973), China (Chen & Wu, 1964), Japan (Kamimura, 1939), the Macaronesian islands (Sjögren, 1975), northern India (Pandre & Misra, 1943), southeastern North America (Davison, 1997 & Schuster, 1959), Southern Africa (Arnell, 1963), and even England (Porley, 1996).

For New Zealand there are few formal reports on epiphyllous bryophytes, in spite of their being conspicuous in forests throughout the

region. Herzog (1949) records *Colura saccophylla* Herzog on *Lycopodium scariosum* Forst. f. and Glenny (1996) records *Nephelolejeunea* spp., *Colura saccophylla* and *C. pulcherrima* var. *bartlettii* Ast. on the moss *Dendroligotrichum dendriodes* (Hedw.) Broth.. On seed plants, Schuster (1968) noted *Cololejeunea ellipsoidea* growing on leaves of a southern beech, *Nothofagus menziesii* (Hook. f.) Oersted.

During the course of field work for a revision of the genus *Frullania* in New Zealand, we have observed that the species usually grow on bark, twigs and frequently as epiphylls, occasionally on rock and rarely on soil. This concurs with views expressed by previous authors, e.g., Hodgson (1949); Kamimura (1962); Allison & Child (1975); Scott (1985); and Schuster (1992). There are no previous reports of species of *Frullania* growing as epiphylls from New Zealand, and in revisional and monographic studies of *Frullania* from regions elsewhere, species of this genus are rarely noted growing as epiphylls. In Schuster's (1992) revision of North American *Frullania* he comments that a few species are sporadically and rarely epiphyllous.

This paper documents for the first time the occurrence of several *Frullania* species growing as epiphylls in New Zealand (based on our own observations); one species in New Caledonia (Dr. Hans Hürlimann, pers. com.) and one species in Colombia (Jaime Uribe M., pers. comm.) In addition, we present an extensive list of *Frullania* species growing as epiphylls in other regions of the world, compiled from the literature, and comment on the biodiversity, biogeography and ecology of epiphyllous *Frullania* species.

MATERIAL & METHODS

A list of *Frullania* species epiphyllous on seed plants, and their associated collection data, was prepared based upon literature and our own herbarium records. Previously unpublished data from other collectors from New Zealand, New Caledonia and Colombia was also used. These are classified according to floristic region (Fig. 1), modified from Polunin (1967).

We also apply one of three categories (typically; facultatively; or accidentally epiphyllous) to the *Frullania* species collected as epiphylls. These were based on the criteria outlined in Fig. 2 and were derived from a composite of definitions provided by Pócs (1997), Richards (1984), and Vanden Berghen (1982).

The age of host leaves was estimated by counting the number of bud bract scar zones on the branchlets, each group representing one growth season.

The subgeneric classification of Schuster (1992) is followed.

Representative specimens

Representative specimens of *Frullania* species from New Zealand and New Caledonia that have not previously been recorded as epiphylls are listed. *F. aterrima*: New Zealand, North Island, Gisborne District, *MJ von Konrat 97/104* (AKU); *F. chevalieri*: New Zealand, North Island, Northland District, *JE Braggins 97/511a* (AKU); *F. deplanata*: New Zealand, North Island, Gisborne District, *MJ von Konrat 98/211* (AKU); *Frullania fugax*: New Zealand, North Island, Auckland District, *JE Braggins 86/105* (AKU); *F. rostrata*: New Zealand, North Island, Northland District, *JE Braggins 97/511b* (AKU) & North Island, Gisborne District, *MJ von Konrat 97/102* (AKU); *F. patula*: New Zealand, North Island, Gisborne District, *MJ von Konrat & RK Barraclough 97/126* (AKU) and South Island, Otago District, *JE Braggins 98/389c* (AKU); *F. ptychantha*: New Zealand, North Island, Northland District, *JE Braggins 97/511d* (AKU); *F. pycnantha*, New Zealand, North Island, Gisborne District, *MJ von Konrat & RK Barraclough 97/125* (AKU); *F. scandens*: New Zealand, North Island, Gisborne District, *MJ von Konrat 98/214* (AKU).

Percentage cover calculations

For some New Zealand collections total leaf areas and areas occupied by epiphylls were obtained from scanned photographs using the computer application NIH Image. Cover of epiphylls was calculated by dividing the area of the epiphyll by the total area of the leaf expressed as a percentage.

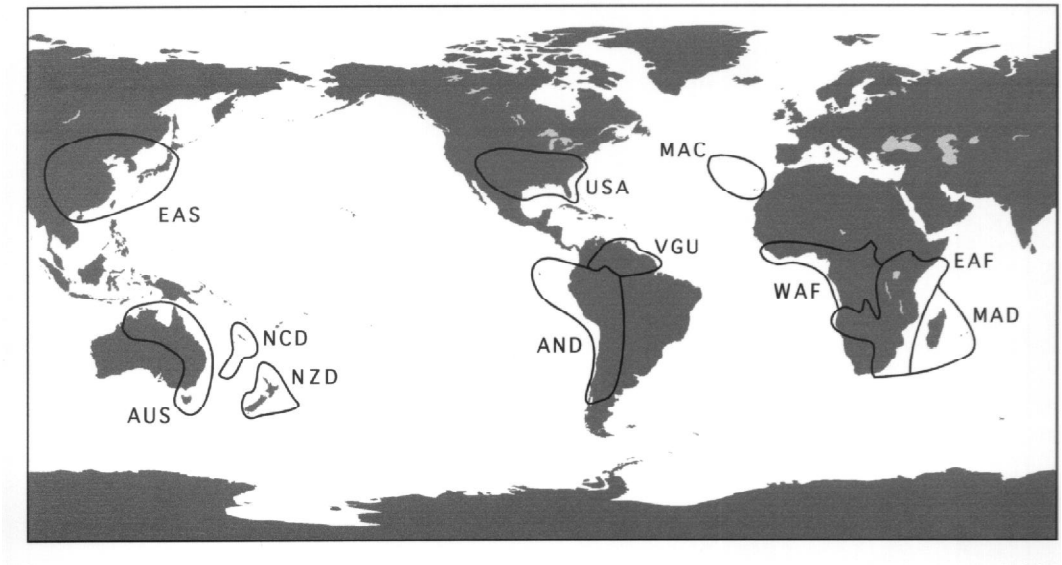

Figure 1. Floristic regions where *Frullania* species have been recorded growing as epiphylls. **AND:** Andine including the Galapagos Islands and Colombia; **AUS:** North and East Australia; **EAF:** East African Steppe, including Malawi; **EAS:** Continental East Asia including Kowloon Peninsula (Hong Kong) and mainland China; **MAC:** Macaronesia, including the Azore Islands and Madiera Island; **MAD:** Madagascar and neighbouring islands; **NCD:** New Caledonia; **NZD:** New Zealand; **USA:** The SE of the United States of America; **VGU:** Venezuela-Guiana including Guyana; **WAF:** West African Forest including Zaire and Rwanda.

RESULTS

29 *Frullania* species that have previously been noted growing as epiphylls and 11 which are recorded for the first time are listed in Table 1, together with subgenus, locality, and original reference. Epiphyllous *Frullania* were recorded from 11 floristic regions (Fig. 1) including Africa, Australia, mainland China, North America and South America.

Figure 3 shows the number of *Frullania* species growing as epiphylls, in each subgenus, for each of the 11 floristic regions for which records were obtained. New Zealand has the highest number of epiphyllous taxa with nine species from four subgenera, while Venezuela-Guiana, North America, East Africa, Australia and the Andine floristic regions each has only two species.

The subgenus *Frullania* was represented by the greatest number of species (15) that grow as epiphylls and the subgenera *Australes* and *Saccophyla* were least represented, each with only one species growing as epiphylls (Fig. 4).

In most regions there are species that have rarely been collected as epiphylls, for instance, *F. fugax, F. ptychantha* and *F. scandens* from New Zealand have each been collected as epiphylls only once despite extensive collections of epiphyllous hepatics in the region. In contrast, there are several *Frullania* species that are commonly found growing as epiphylls and are subsequently represented by many collections. These include: *F. rostrata* and *F. aterrima* from New Zealand; *F. chevalieri* from New Caledonia and New Zealand; *F. microfrullania, F. teneriffae,* and *F. tamarisci* from Macaronesia; *F. vandenberghenii* from Madagascar; and *F. apiculata* from Rwanda and Zaire.

Frullania epiphylls have a wide altitudinal range with *F. purpura* from Madagascar the lowest (at sea-level) to *F. variegata* reported from Rwanda at 2500m. The majority of *Frullania* epiphylls appear to be from sites ranging in elevation from approximately

Table 1. A list of *Frullania* species previously reported growing as epiphylls or reported for the first time. * = reproductive states present ◆ = new report as epiphyll

subgenus	species	locality	collector/reference
Australes	*F. fugax* (Hook. f. & Tayl.) Tayl.	New Zealand	JEB 86/105 (AKU) ◆
Chonanthelia	*F. arecae* (Spreng.) Gott.	Zaire; Madagascar; Malawi	Tixier, 1995; Vanden Berghen, 1982; Nick Hodgetts pers. comm.
Chonanthelia	*F. riojaneirensis* (Raddi) Spr.	Colombia	Jaime Uribe M. pers. comm.
Diastaloba	*F. baumanii* Hatt.	New Caledonia	Hattori, 1986
Diastaloba	*F. huerlimannii* Hatt.	New Caledonia	Hans Hürlimann pers. comm. (HH 3624c)◆
Diastaloba	*F. tixieri* Hatt.*	New Caledonia	Hattori, 1976, 1977, 1984
Diastaloba	*F. obcordata* (Lehm. & Lindenb.) Lehm. & Lindenb.	Guyana; North America	Cornelissen & Gradstein, 1990; Schuster, 1992 & Davison, 1997.
Diastaloba Spruce.	*F. purpurea* Steph.	Madagascar	Vanden Berghen, 1976, 1982; Pócs, 1997
Diastaloba	*F. ptychantha* Mont.	New Zealand	JEB 97/511d (AKU) ◆
Frullania	*F. apiculata* (Reinw. Bl. & Nees) Dum.	Rwanda; Zaire; Australia	Tixier, 1995; Pócs & Streimann, 1999
Frullania	*F. apicalis*	Madagascar	Pócs, 1997
Frullania	*F. asagrayana* Mont.	North America	Davison, 1997
Frullania	*F. brasiliensis* Raddi	Galapagus Islands	Gradstein & Weber, 1982
Frullania	*F. capensis* Lindenb. & Nees	Mt Mulanje, Malawi	Nick Hodgetts pers. comm.
Frullania	*F. densiloba* Evans	China	Luo, 1990
Frullania	*F. kunzei* (Lehm. & Lindenb.) Lehm. & Lindenb.	Mabura Hill, Guyana	Cornelissen & Gradstein, 1990
Frullania	*F. microphylla* (Gott.) Pears.	Canary Islands; Azore Islands	Boecker et al., 1993; Sjögren, 1997
Frullania	*F. moniliata* (Rein. , Bl. & Nees) Mont.	China	Luo,1990 ; Zhu et al., 1994
Frullania	*F. multilacera* Steph.	New Caledonia	Hattori, 1984
Frullania	*F. polysticta* Lindenb.	Madeira Island	Sjögren, 1975
Frullania	*F. repandistipula* Sande Lac.	La Reunion	Vanden Berghen, 1976; Pócs, 1997
Frullania	*F. tamarisci* (L.) Dumort.	Madeira Island	Sjögren, 1975
Frullania	*F. teneriffae* (F. Web.) Dumort.	Azore Islands	Sjögren, 1997
Frullania	*F. vandenberghenii* Pocs	Madagascar	Vanden Berghen, 1982; Pócs, 1997
Microfrullania	*F. aterrima* (Hook. f. & Tayl.) Hook. f. & Tayl.	New Zealand	MVK 97/104 (AKU)◆
Microfrullania	*F. chevalieri* (Schust.) Schust.	New Caledonia; New Zealand	Hattori, 1984; JEB 97/ 511b (AKU)
Microfrullania	*F. rostrata* (Hook. f. & Tayl.) Hook. f.	New Zealand	JEB 97/ 511b (AKU)◆
Saccophora	*F. pancheri* Steph.	New Caledonia	HH 2367, Hattori, 1986
Trachycolea	*F. deplanata* Mitt.	New Zealand	MVK 98/211 (AKU)◆
Trachycolea	*F. dilatata* (L.) Dumort.	Madeira Island	Sjögren, 1975
Trachycolea	*F. ericoides* (Nees) Mont.	Rwanda	Tixier, 1995
Trachycolea	*F. muscicola* Steph.	China	But & Gao, 1991; Luo, 1990, Zhu et al., 1994
Trachycolea	F. *nishiyamensis* Steph.	China	Luo, 1990
Trachycolea	*F. pycnantha**	New Zealand	MVK & RKB 97/125

			(AKU) ◆
Trachycolea	*F. patula* Mitt.	New Zealand	JEB 98/389c (AKU)◆
Trachycolea	*F. scandens* Mont.	New Zealand	MVK 98/ 214 (AKU)◆
Trachycolea	*F. variegata* Steph.	Rwanda	Tixier, 1995
unknown	*F. angulata*	Madagascar	Pócs, 1997
unknown	*F. scottiana*	Australia	Hattori 1987

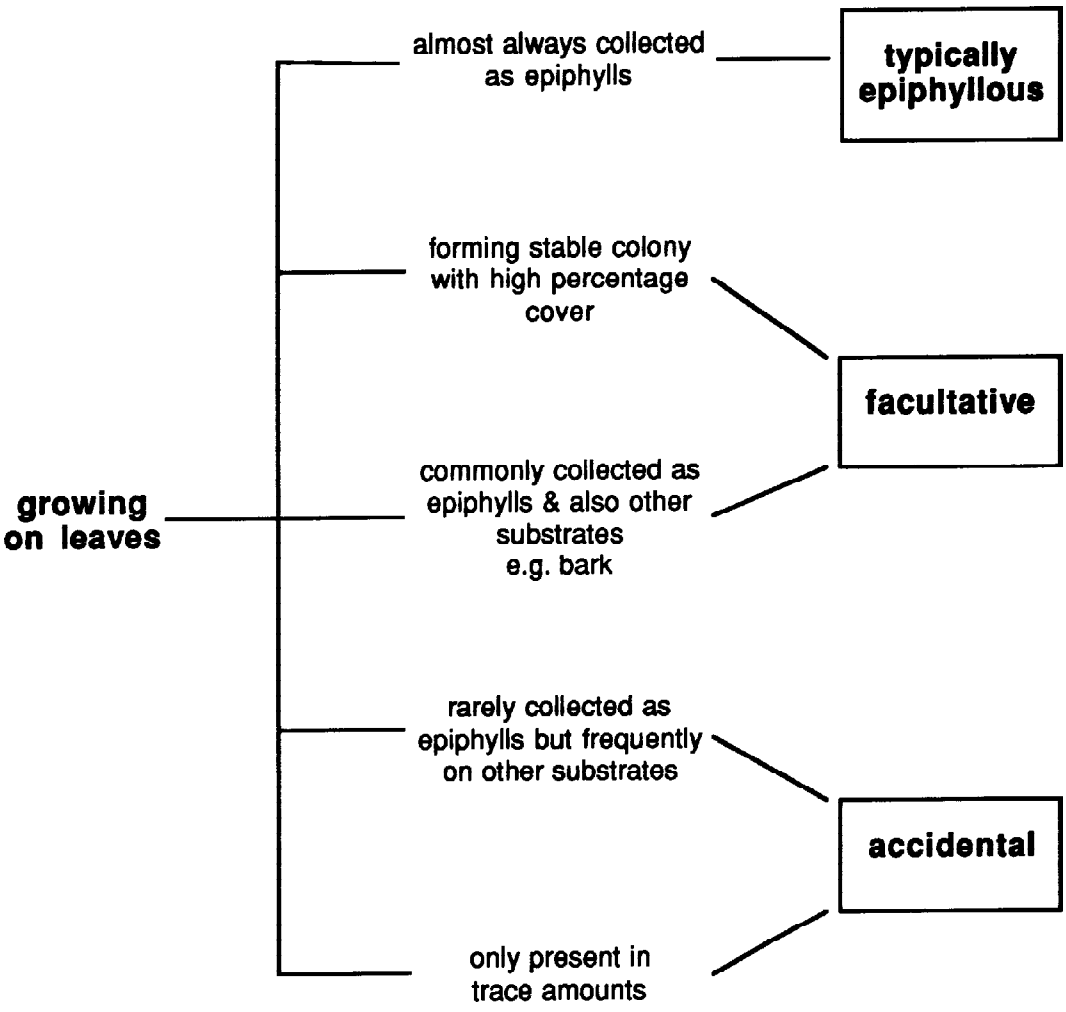

Figure 2. Key to the criteria defining the three different categories used to describe bryophytes growing as epiphylls.

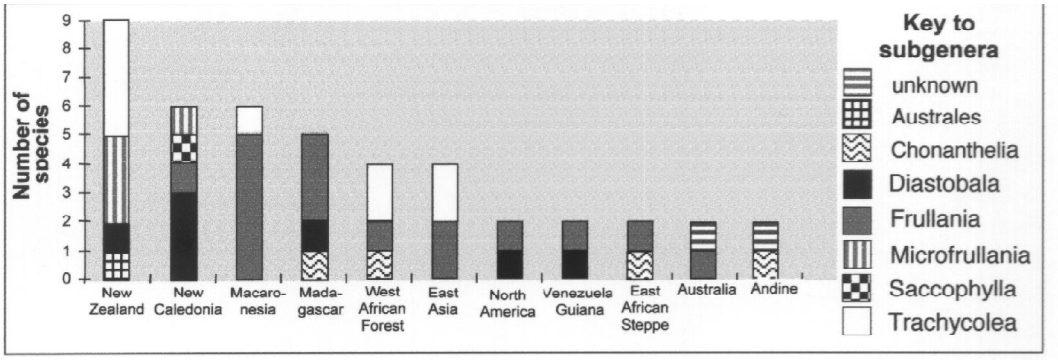

Figure 3. A comparison of the number of *Frullania* species recorded as epiphylls in different floristic regions.

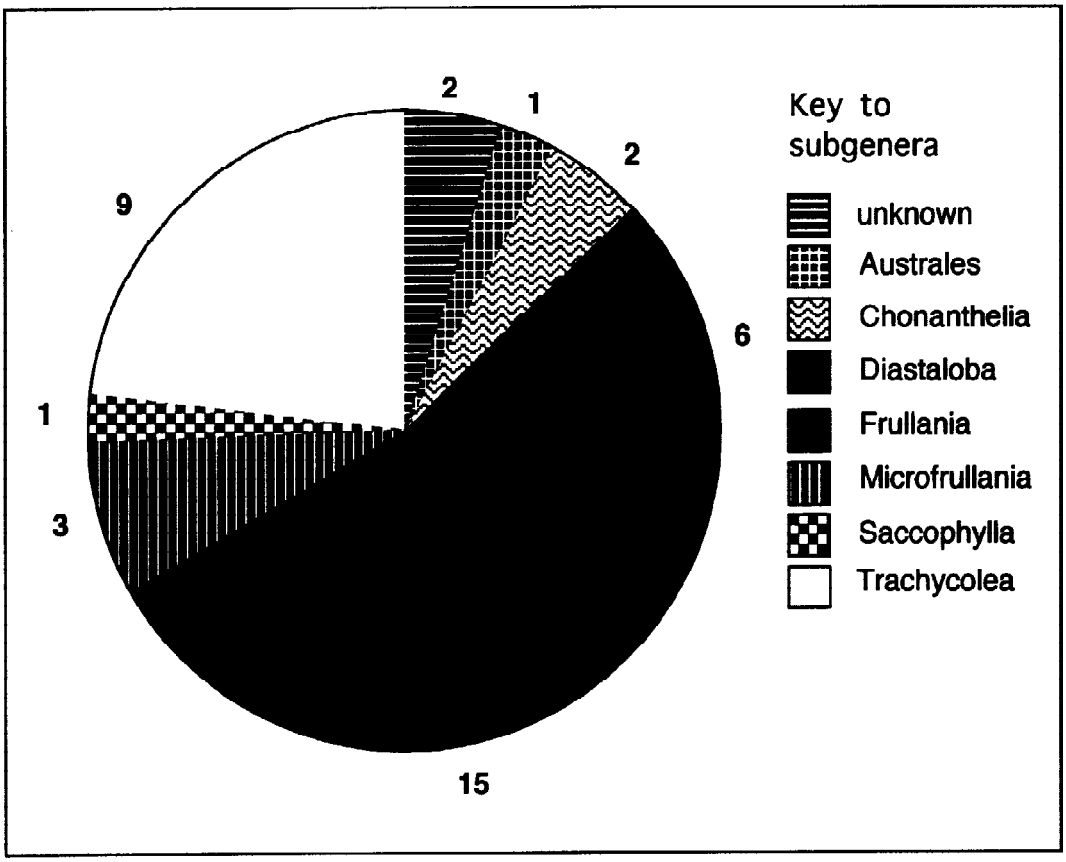

Figure 4. Pie-chart illustrating the number of epiphyllous *Frullania* species represented in different subgenera.

500-1200 m.

In New Zealand, *Frullania* epiphylls are very common in sites with a gorge topography, frequently growing on leaves of the gymnosperm *Podocarpus hallii*. In this habitat *F. rostrata*, *F. aterrima* and *F. pycnantha* are particularly common. Rarely does more than one *Frullania* species occupy the same leaf. Generally, the New Zealand *Frullania* epiphylls are found growing either in trace amounts amongst other epiphyllous bryophytes or as the sole or dominant hepatic (Fig. 5a, c & e).

Table 2 compares percentage cover between some New Zealand and North American species. In New Zealand, a few species, e.g., *F. aterrima*, *F. rostrata* and *F. pycnantha*, occasionally occupy greater than 70% of the leaf. The mean percentage cover for these species ranges from 25% to 60%. In contrast, most of the New Zealand species occupy less than 5% of the leaf area. Similarly, both North American taxa occupy less than 5% of the leaf surface.

The vast majority of *Frullania* epiphylls observed by us were on the upper surface of leaves. Only one collection was recorded growing on the lower surface (Fig. 5f). The underside of the host leaf in this instance was densely hairy.

In New Zealand, *Frullania* species have been collected as epiphylls on *Podocarpus hallii* (Podocarpaceae), *Phyllocladus trichomanoides* (Podocarpaceae), *Beilschmiedia tawa* (Lauraceae), and *Pseudowintera colorata* (Winteraceae). Host plants from other floristic regions include species of *Garcinia* (Clusiaceae), *Freycinetia* (Pandanaceae) and *Zygogynum* (Winteraceae) in New Caledonia; *Serenoa repens* (Arecaceae) and *Rhododendron maximum* (Ericaceae) in North America; *Pothos chinensis* (Araceae) and *Pandanus forceps* (Pandanaceae) from the Kowloon Peninsula and China; and *Laurus azorica* (Lauraceae), *Prunus lusitanica* (Rosaceae), *Ilex perada*, *I. canariensis* (Aquifoliaceae) and *Clethra arborea* (Clethraceae) from Macaronesia.

Epiphyllous *Frullania* are rarely found fertile and the reproductive state has only been reported for 8 epiphyllous species, including the New Zealand taxa *F. aterrima* (Fig. 5a & b), *F. pycnantha* (Fig. 5c & d) and *F. rostrata* and the New Caledonian *F. tixieri*. These four taxa were frequently found fertile with perianths and androecia. The remaining New Zealand species were all sterile when collected and with no evidence of any asexual reproduction.

DISCUSSION

In a recent worldwide review of epiphyllous liverwort diversity, Pócs (1997) focused on taxa that predominantly grow on leaves. These were mainly genera in the family Lejeuneaceae. Pócs suggested that genera such as *Frullania*, in which a given species may be found on leaves as well as on other substrates, are best considered to be facultative or accidental epiphylls.

Frullania vandenberghenii and *F. microphylla* have previously been reported to frequently grow on leaves, and were subsequently classified as facultative epiphylls by Pócs (1997). Other taxa that may also be considered facultative in this sense include: *F. apiculata*, *F. aterrima*, *F. chevalierii*, *F. microphylla*, *F. rostrata*, *F. pycnantha*, *F. tamarisci*, and *F. teneriffae*. All these taxa have frequently been reported growing as epiphylls and, at least for the New Zealand species, can be found in some sites growing equally both on leaves and other substrates such as bark. Furthermore, the New Zealand species often occupy a large percentage cover of the host leaf which further attests to their ability to establish themselves as facultative epiphylls.

Davison (1997) suggested that both of the North American *Frullania* species reported as epiphylls, *F. obcordata* and *F. asagrayana*, probably represent fleeting colonization attempts by spores, gemmae, or shoot fragments from nearby sources. Schuster (1992) also noted that North American *Frullania* species occur sporadically and only rarely as epiphylls. Likewise, the New Zealand taxa *F. fugax*, *F. patula*, *F. ptychantha* and *F. scandens* are rarely found as epiphylls, occurring on leaves only in trace amounts and in these situations appearing to be always sterile. Species such as these, with a poor ability to establish as epiphylls (indicated by the infrequent collections and low percentage cover) can be considered to be accidental epiphylls.

Pócs (1997) stated that bryophyte communities inhabit living leaves only when superoceanic conditions prevail, and illustrated

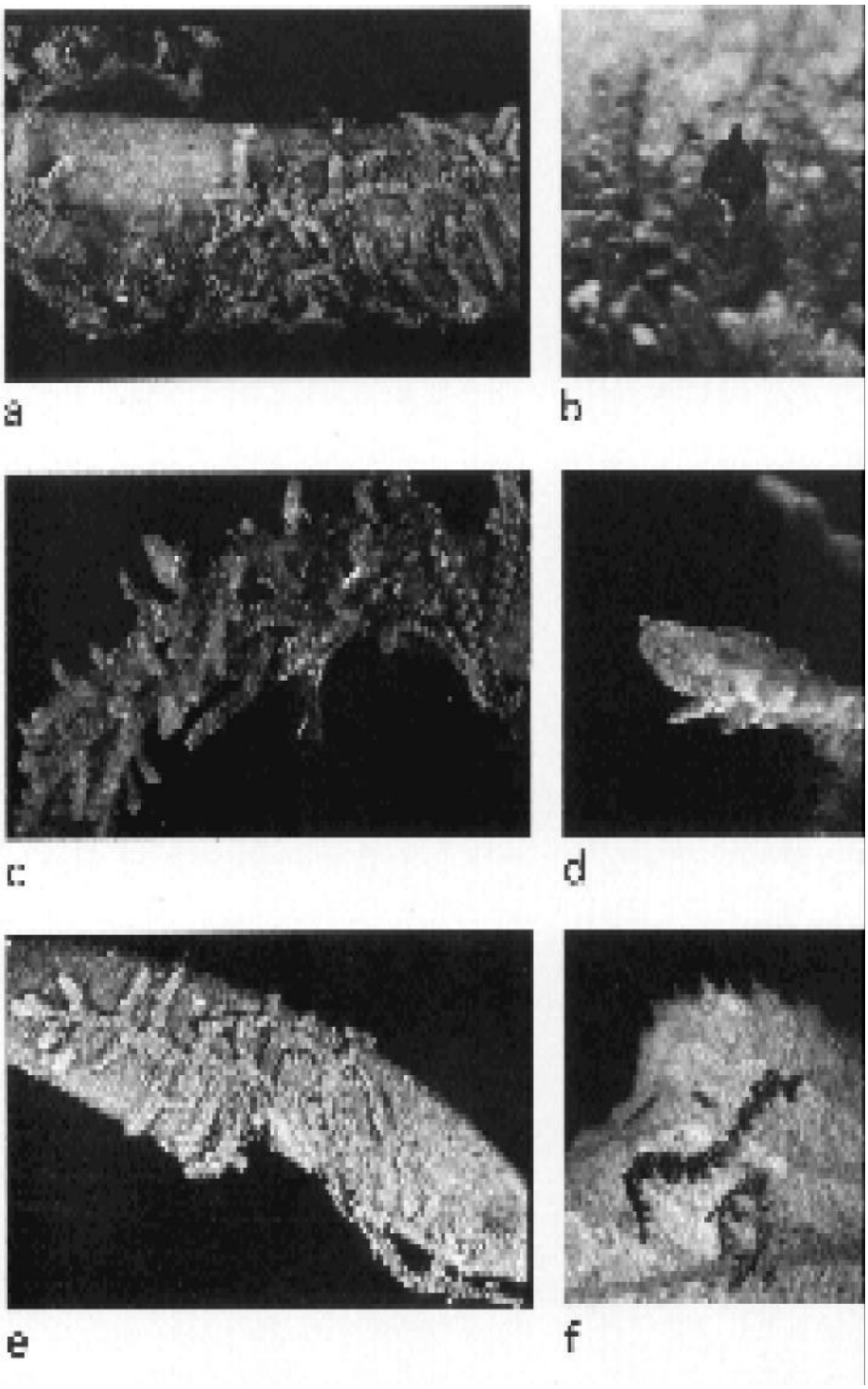

Figure 5. Photographs of *Frullania* species growing as epiphylls on the leaves of *Podocarpous hallii* **(a-e)** and on *Olearia colensoi* **(f)** in New Zealand: **a**, *F. aterrima*; **b**, close up of perianth of *F. aterrima*; **c**, *F. pycnantha*, **d**, close up of perianth of *F. pycnantha*; **e**, *F. rostrata*; **f**, *F. aterrima* on the abaxial surface.

that the centres with highest epiphyllous hepatic diversity were in areas such as Madagascar and its neighbouring Indian Ocean islands and oceanic islands such as Micronesia. A similar trend is apparent in the present study in which New Zealand, New Caledonia, Madagascar and Macaronesia all have a greater number of epiphyllous *Frullania* species than the larger land masses of Asia, Africa and the Americas (Fig.3).

Biotic and abiotic factors affecting epiphyllous liverworts have been investigated by Coley et al. (1993) and Monge-Nagera & Blanco (1995). In our study, although no quantitative data are available, there appear to be two key environmental factors affecting the distribution of epiphyllous *Frullania* species. Moisture appears to be a critical factor that may determine the existence of epiphyllous *Frullania.* Habitat records attest to this, as they are frequently reported from humid cloud forest habitats and habitats which are in close proximity to running water, typical of gorge topography. This agrees with the views of Davison (1997); Richards (1984) and Pócs (1997).

Leaf longevity must also play a significant role in an epiphyll's survival. In the literature surveyed, quantitative data for leaf longevity of the host plants is scarce. However, Davison (1997) recorded *Rhododendron* leaves living up to five years, and likewise we estimate leaves of *Podocarpus hallii* also living up to five years.

Richards (1984) noted that many hepatics, which usually grow on bark, spread on to leaves, e.g., in Guyana *Stictolejeunea squamata* (Willd.) Spruce, *Symbiezidium granulatum* (Nees) Trevis and *Plagiochila* sp. (Richards, 1984). Schuster (1992) also reports that *Frullania* species from the tropics also commonly grow on small twigs and spread on to leaves. However, in addition to merely spreading on to the leaves from twigs, it appears that a number of New Zealand's epiphyllous species have the ability to establish colonies *de novo* on the leaves. Interestingly, it is likely that for some host species, e.g., *Podocarpus hallii*, the branchlets and leaves offer a more stable substrate than the bark of the trunk, which is shed regularly.

The potential effect on the leaves by epiphylls with a high percentage cover, as exhibited by New Zealand *Frullania* species, has been discussed by various authors (e.g., Winkler, 1967; Richards, 1984). Recently, Coley et al. (1993) suggested shading by epiphylls could be a major disadvantage for host leaves and estimated photosynthesis could be reduced by 20%. However, there is also a possibility that they have beneficial effects on the rainforest ecosystem as a whole. For instance, Jordon *et al.* (1980) suggested that epiphylls may play a similar role to other epiphytic bryophytes in absorbing and recycling nutrients, which may be important in ecosystems such as South American rain forests on podzols where nutrient levels are low. This may also be important in New Zealand forests where soil fertility is poor in some regions (Wardle, 1984).

Finally, in most of the floristic regions throughout the world, angiosperms are the favoured hosts for *Frullania* species that colonise leaves. In contrast, the majority of epiphyllous *Frullania* species from New Zealand appear to show a preference for the leaves of gymnosperms. One feature that many of the host plants have in common is the coriaceous nature of the leaves, and indeed, species of *Podocarpus, Pseudowintera, Ilex, Garcinia, Laurus* and *Beilschmiedia* all share this feature. However, the reasons for the preference of some leaves over others are unknown but may be influenced by factors such as leaf longevity, microclimate and fine structure of the host cuticle.

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