

## Ascomycetes on *Dendrologotrichum* (Musci)

by

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With 67 figures and 3 tables

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**Abstract:** Representative herbarium specimens of both species of *Dendrologotrichum* (Polytrichaceae, Musci) from all parts of the distribution area were analysed for the presence of fungi. Forty collections of the gigantic *D. dendroides* from southern South America, Juan Fernández Islands, New Zealand and Auckland Islands and 19 of *D. squamosum* from Fuegia, Falkland Islands and South Georgia were found to be infected by 16 species of ascomycetes. Eleven species occur on *D. dendroides*, nine on *D. squamosum*. The species recorded were: *Bryochiton heliotropicus*, *B. perpusillus*, *Bryomyces* sp., *Bryonectria disciformis* sp. nov., *Epibryon elegantissimum*, *E. eremita*, *E. interlamellare*, *E. pulchellum* sp. nov., *Epibryon* spp., *Lizonia baldinii* subsp. *dendrologotrichi* subsp. nov., *Malvinia endoderma* gen. et sp. nov., *Potridiscus polymorphus*, *Potriphila epiphylla* sp. nov., and *P. navicularis*. All species are keyed out, described and most of them are illustrated.

*Potridiscus polymorphus* and *Potriphila epiphylla* were most frequent. These species occur over the whole geographic range of the host genus. Dispersal of infected host fragments serving as combined diaspore seems to play an important role in parasite distribution. The highly disjunct populations of *D. dendroides* in South America and New Zealand harbour a more homogeneous set of fungal parasites than *D. dendroides* and *D. squamosum* in southern South America. The ascomycetes on *D. dendroides* presumably reflect the Gondwana origin of their host. A close relationship between *D. dendroides* and *D. squamosum* is counterindicated by bryomycological evidence. *Dendrologotrichum squamosum* and *Polytrichadelphus magellanicus* which occur sympatrically in Fuegia, have several fungi in common, whereas *D. dendroides* and *P. magellanicus* in southern South America and *D. dendroides*, *Dawsonia superba*, and *P. innovans* in New Zealand harbour only specific fungal parasites.

With the exception of *Lizonia baldinii*, the fungal species do not normally cause any visible symptoms on the moss. Individual species show strong preferences for specific sites on the host plants for fruit-body formation. The extremely reduced ascomata of *Malvinia endoderma* develop within the epidermal leaf cells of *D. squamosum*. This is a new type of microniche for bryophilous ascomycetes. The present study suggests that populations of *Dendrologotrichum* are universally colonized by some ascomycetes, though their sporadic occurrence, inconspicuous or concealed form, and the small size of many ascomata and pycnidia render their study rather difficult.

**Key words:** Polytrichaceous hosts, bryophilous ascomycetes, *Bryochiton*, *Bryomyces*, *Bryonectria*, *Epibryon*, *Lizonia*, *Malvinia*, *Potridiscus*, *Potriphila*, microniches, Gondwanaland distribution.

## Introduction

*Polytrichum* and its relatives (Polytrichaceae, Musci) with perennial and large or even gigantic gametophytes are excellent substrates for ascomycetes (Döbbeler 1986, 1999b). Approximately 65 species assigned to almost 30 genera and at least seven orders are known to be obligately associated with these gametophytes. The extraordinary and unique structural complexity of these mosses (Limpricht 1893: 586, Smith 1971: 76), is reflected by an array of microhabitats – e.g., subterranean rhizoids, antheridial cups, spaces between the leaf lamellae – for differently adapted fungi (Döbbeler 2002). Another factor influencing the high number of parasites is the longevity of the gametophyte (Döbbeler 1986). The phylogenetic antiquity of the host group may also be important, because colonization and occupation of niches combined with speciation is a time-consuming process. The antiquity of polytrichaceous mosses was recently demonstrated by the discovery of fossils indicating that diverse Polytrichaceae with modern characters existed in the Cretaceous 80 million years ago (Konopka et al. 1997). Only a few polytrichaceous taxa have been studied so far as potential hosts of specifically adapted fungi. The australasian genus *Dawsonia* harbours 21 species of ascomycetes (Döbbeler 1981). On the southern South American *Polytrichadelphus magellanicus* (Hedw.) Mitt., nine different ascomycetes were found (Döbbeler 2001). The tree-like genus *Dendroligotrichum*, with only two species, *D. dendroides* (Hedw.) Broth. in southern South America and New Zealand, a ‘gigantic Polytrichaceae’ (Hampe 1847: 78), and *D. squamosum* (Hook. f. & Wilson) Cardot, endemic in the Fuegian region, has for the most part not been investigated for fungi (e.g., Racovitza 1959, Felix 1988, Index of Fungi), although *Potridiscus polymorphus* Döbbeler & Triebel (Helotiales) was recorded once on each species in South America (Döbbeler & Triebel 2001). The present study aims to investigate the biodiversity and ecological relations of the ascomycetes associated with *Dendroligotrichum*. Of special interest is whether or not the parasites infect both *D. dendroides* and *D. squamosum*, and whether their distributions mirror the Gondwanaland distribution of *D. dendroides*.

## Material and methods

Specimens of *Dendroligotrichum dendroides* and *D. squamosum* from the bryological herbaria AAS, B, GZU, HBG, M, and MSC and from several private herbaria were screened for the presence of fungi. In addition, potential host plants were collected in Chile. All parasites present on each collection were recorded. As the detection of species with scattered and inconspicuous fruit-bodies is time-consuming, the collections had to be selected. Those consisting of several plants and originating from widely separated geographical areas were given preference. Before studying individual plants with a stereomicroscope, it was essential to wet them thoroughly. Polytrichaceae are effective detritus collectors, especially in their basal leaf parts. Plants were cleansed of soil particles and detritus using flowing tap water. Mature or older plants or the basal parts of the branches were given special attention, since the apical young leaves are normally free of visible fungal infections. Microscopic screening (100 ×) of single leaves was done where necessary to locate small or sparsely distributed ascomata. Such small ascomata can otherwise be confounded with detritus and algae. *Potridiscus polymorphus* cannot always be distinguished from colonies of blue-green algae under the stereomicroscope. When searching for fruit-bodies, the whole spectrum of microniches was taken into consideration (antheridial cups, both leaf sides, leaf shoulders, margins and tips). Infected

plants, 59 specimens listed below (p. 37), or parts thereof (normally leaves), were separated and deposited by the fungal name in the corresponding host herbarium. In order to allow reproducible determinations, such specimens normally consisted of at least ten fruit-bodies. In many cases additional ascomata may be found within the original host collection.

All measurements and illustrations of material observed under the compound microscope were done in heated lactophenol-cottonblue. Lugol's solution (Merck 9261) was used to test iodine reactions.

*Epibryon interlamellare* and other species of *Epibryon* with two-celled ascospores are very frequent on *Dendrologotrichum*. Ascomata are often extremely scarce and difficult to analyse. The degree of host specificity is unknown. Due to their unclear relationships with other polytrichicolous taxa, they are not treated in depth here (see remarks under *Epibryon* spp.).

### Key to the species on *Dendrologotrichum*

- 1a Pycnidia; on the adaxial leaf side, between or on the leaf lamellae..... 2
- 1b Ascomata; on the adaxial or abaxial leaf side or within the antheridial cups of male plants..... 4
- 2a Pycnidia uncoloured; New Zealand..... 4. *Bryonectria disciformis*
- 2b Pycnidia black; New Zealand and/or South America..... 3
- 3a Pycnidia completely immersed between the leaf lamellae, strongly laterally compressed, 10-35 µm wide; ostiole visible as a pale spot; conidia 8.5-11 × 2-3 µm; on *D. squamosum*..... 14. *Potriphila navicularis*
- 3b Pycnidia emerging from the interlamellar spaces, in surface view more than 40 µm wide; ostiole not always visible as a pale spot; conidia 4-5 × 1-1.5 µm; on *D. squamosum* and *D. dendroides*..... 13. *Potriphila epiphylla*
- 4a Ascomata uncoloured; setae absent..... 5
- 4b Ascomata light to dark brown or black; setae absent or present..... 6
- 5a Ascomata perithecioid, verruculose, apically applanate; on the leaf lamellae; ascospores two-celled, 8-11 × 2.5-4 µm; New Zealand..... 4. *Bryonectria disciformis*
- 5b Ascomata apothecioid, immersed within the abaxial leaf epidermis; ascospores one-celled, 6.5-8 × 2.5 µm; Falkland Islands..... 11. *Malvinia endoderma*
- 6a Ascomata perithecioid; within the antheridial cups of male plants; ascospores two-celled, brown, 26-34 × 7-8.5 µm..... 10. *Lizonia baldinii* subsp. *dendrologotrichi*
- 6b Ascomata perithecioid or apothecioid; on other parts of the plants; ascospores not as above..... 7
- 7a Ascomata apothecioid, brown; paraphyses and excipular cells often with segmented dark inclusions; ascospores one-celled and brown..... 12. *Potridiscus polymorphus*
- 7b Ascomata apothecioid or perithecioid, brown or black, paraphyses and excipular cells not as above; ascospores septate and hyaline or pale brown..... 8
- 8a Setae present; ascomata perithecioid, pale to dark brown..... 9
- 8b Setae absent; ascomata perithecioid or apothecioid, brown or black..... 13
- 9a Ascomata superficial on the leaf lamellae or immersed between them; apical leaf regions preferred; ascospores two-celled..... 10
- 9b Ascomata superficial on the leaf lamellae; lowermost leaf parts (transition zone to sheath) preferred; ascospores four-celled or muriform..... 11
- 10a Ascomata up to 50 µm diam; ascospores 7-8.5 × 2.5 µm..... 7. *Epibryon interlamellare*
- 10b Ascomata more than 50 µm diam; ascospores larger..... 9. *Epibryon* spp.
- 11a Setae curved and directed towards the substrate; ascospores with only three transverse septa; on *D. dendroides*..... 12
- 11b Setae straight and directed upwards; ascospores with three transverse and one or two longitudinal septa; on *D. squamosum*..... 6. *Epibryon eremita*

12a	Ascospores 11.5-15 µm long, without mucilaginous droplets; South America.....	5. <i>Epibryon elegantissimum</i>
12b	Ascospores 15-19 µm long, with a fine mucilaginous droplet at each end; New Zealand.....	8. <i>Epibryon pulchellum</i>
13a	Ascospores more than 5 µm wide, pale brown.....	3. <i>Bryomyces</i> sp.
13b	Ascospores up to 4 µm wide, hyaline.....	14
14a	Ascomata perithecioid, up to 70 µm diam, formed underneath the cuticula on the abaxial leaf side.....	15
14b	Ascomata apothecioid, more than 100 µm diam; formed on the adaxial leaf side between or upon the leaf lamellae.....	16
15a	Ascospores two-celled.....	2. <i>Bryochiton perpusillus</i>
15b	Ascospores three-celled; only once recorded on <i>D. squamosum</i> .....	1. <i>Bryochiton heliotropicus</i>
16a	Ascomata more or less completely immersed between the leaf lamellae, laterally compressed; ascospores 9-11 × 2.5 µm; on <i>D. squamosum</i> .....	14. <i>Potriphila navicularis</i>
16b	Ascomata superficial on the leaf lamellae, not laterally compressed; ascospores 6-8.5 × 1.5-2.5 µm; on <i>D. squamosum</i> and <i>D. dendroides</i> .....	13. <i>Potriphila epiphylla</i>

### The ascomycetes recorded

#### 1. *Bryochiton heliotropicus* Döbbeler (Döbbeler 1978)

Figs 1-3

Ascomata (38-)45-70(-75) µm diam, depressed globose, black, glabrous. Excipulum of small thick-walled cells. Interascal filaments absent. Asci 19-28 × 10-15 µm, ovoid or broadly ellipsoidal, eight-spored. Iodine-negative. Ascospores 9-11 × 3-3.5(-4) µm, ellipsoidal, apical cell almost hemispherical, with 2 transverse septa, uncoloured. Hyphae uncoloured, inconspicuous.

Hosts: *Dendroligotrichum squamosum* (and *Polytrichastrum sexangulare* (Brid.) G.L. Sm., Döbbeler 1978, 1987).

Known distribution on *D. squamosum*: Falkland Islands (on *P. sexangulare* recorded from Austria, Scotland, Scandinavia, Altai mountains in Russia).

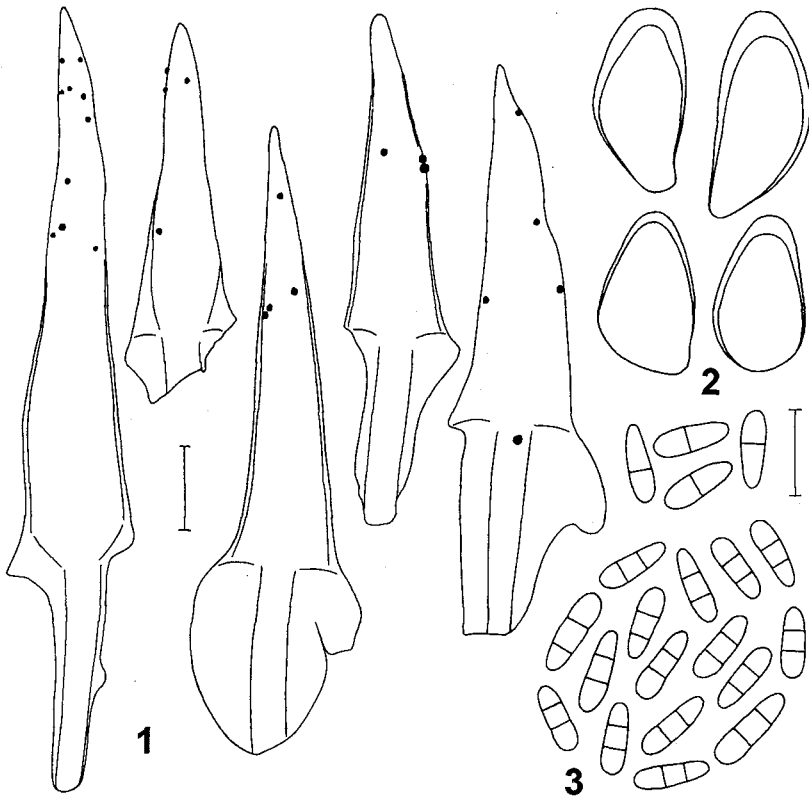
Specimen examined: 55 (see p. 37).

Ascomata are formed underneath the cuticula on the abaxial leaf side, predominantly in the distal region. Ascomata, asci and spores of specimens on *P. sexangulare* are slightly larger than those on *D. squamosum* (Döbbeler 1978, 1987). *Polytrichastrum sexangulare* grows in areas with late snow cover in the farthest north, and in the alpine zone of the mountains (Nyholm 1969, Long 1985). The host rarely occurs below the treeline. The infected *D. squamosum* was collected at the highest elevation of the Falkland Islands where climatic conditions may be similar.

#### 2. *Bryochiton perpusillus* Döbbeler (Döbbeler 1978, 1981, 2001)

Ascomata as in *B. heliotropicus*, but ascospores 8.5-11(-12) × 3-4 µm, two-celled, hyphae brownish.

Hosts: *Dendroligotrichum squamosum* (and other bryophytes including Polytrichaceae, Döbbeler 2001).

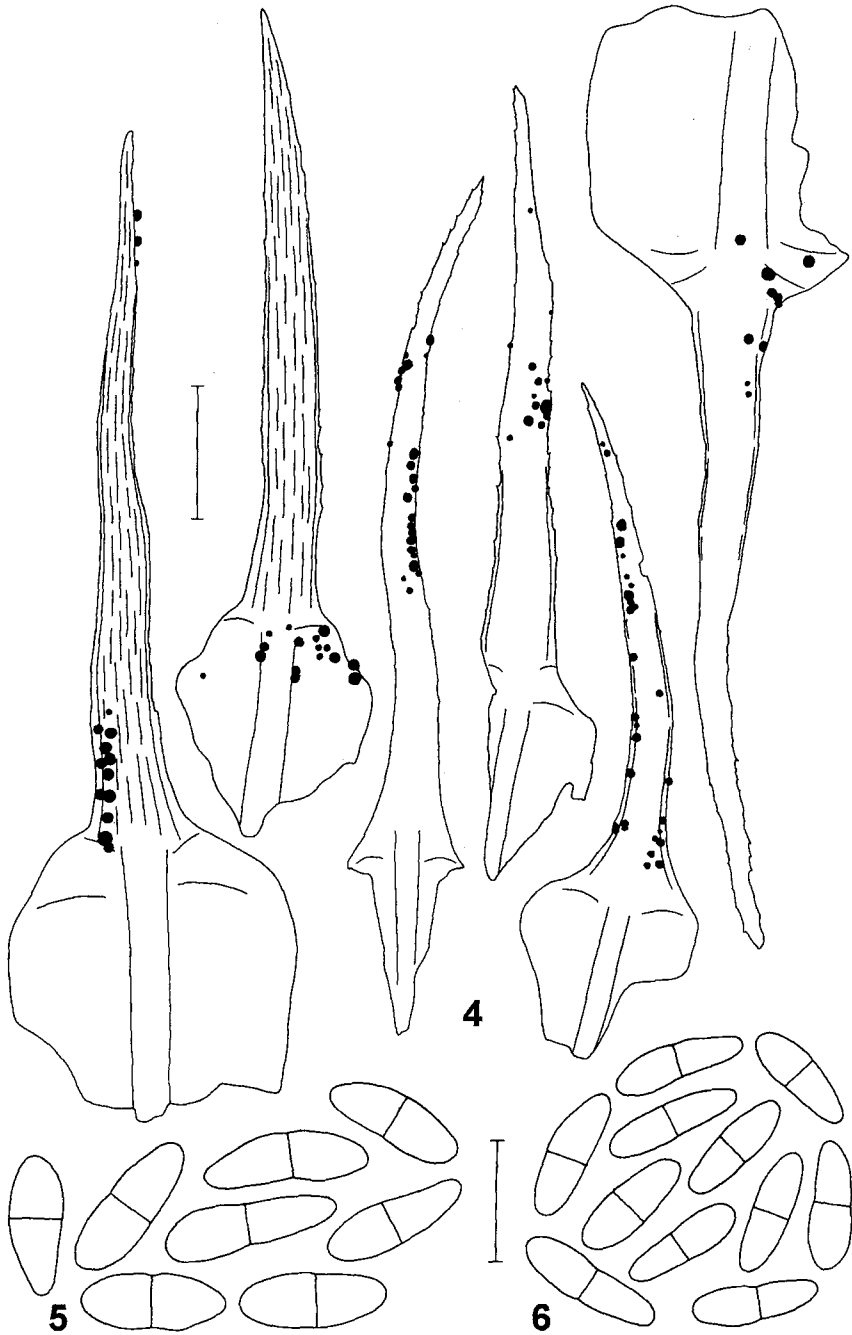


Figs 1-3: *Brychiton heliotropicus* on *Dendroligotrichum squamosum* (collection 55). 1. Subcuticular ascomata on the abaxial leaf side. Scale = 0.5 mm. 2. Asci. 3. Ascospores, the upper four immature. Scale in 2, 3 = 10  $\mu$ m.

Known distribution on *D. squamosum*: Argentina (on other bryophytes probably cosmopolitan).

Specimen examined: 46.

Ascomata develop, as in *B. heliotropicus*, subcuticularly in the apical region of the abaxial side of older leaves. In order to avoid confusion with *B. heliotropicus*, mature ascospores must be considered. A few additional fruit-bodies have been observed widely scattered on other collections of *D. squamosum*. Presumably, based on its recorded growth on a wide variety of mosses, *B. perpusillus* also infects *D. dendroides*. One or two species related to *B. perpusillus* may occur on *Dendroligotrichum*, but species delimitation is as yet uncertain. However, *D. squamosum* and *D. dendroides* can be excluded from the list of preferred hosts of *B. perpusillus*. This species is present on nearly all collections of *Polytrichum piliferum* Hedw. It was observed few times on *Polytrichadelphus magellanicus* from southern South America and on *P. innovans* from New Zealand (Döbbeler 2001).



Figs 4-6: *Bryomyces* sp. on *Dendrologotrichum dendroides*. 4. Leaves with ascomata, the left two seen adaxially, the four right ones abaxially (collection 32). Scale = 1 mm. 5. Ascospores (collection 32). 6. Ascospores (collection 20). Scale in 5, 6 = 15  $\mu$ m.

### 3. *Bryomyces* sp.

Figs 4-6, 26

Ascomata (50-)60-90(-100)  $\mu\text{m}$  diam, globose, black, glabrous but surface often verruculose due to wall thickenings of the outermost layer of excipular cells. Excipulum composed of rectangular cells, carbonized. Interascal filaments absent. Asci 25-40  $\times$  (11-)12-16(-18)  $\mu\text{m}$ , ovoid to broadly ellipsoidal, apically thick-walled, the two layers splitting at discharge (fissitunicate), eight-spored. Iodine-negative. Ascospores (13-)14-17(-18)  $\times$  5-6.5(-7)  $\mu\text{m}$ , ellipsoidal, two-celled, initially uncoloured, later often slightly brownish. Hyphae brown, short-celled, forming more or less closed pellicles on the host cells surrounding the ascomata.

Specimens from Juan Fernández Islands (collection 24) and New Zealand (collection 32) deviate by having ascomata up to 130  $\mu\text{m}$  diam, asci 35-52  $\times$  18-24  $\mu\text{m}$ , and ascospores 16-22  $\times$  6-7.5  $\mu\text{m}$ .

Host: *Dendroligotrichum dendroides*.

Known distribution: Chile, Juan Fernández Islands, New Zealand.

Specimens examined: 2, 6, 8, 10, 11, 20, 24, 32.

Ascomata normally develop on the lower older leaves of a plant. The leaves often show incipient decomposition. Usually several fruit-bodies are connected by a common hyphal pellicle. The dark and gregarious fruit-bodies and the brown mycelium cause a black discolouration of infected leaf regions. Another typical feature is that ascomata are not restricted to a specific microsite of the leaf but colonize the upper or lower leaf region of the adaxial and abaxial side including the sheath. It is often difficult to find fruit-bodies that contain asci and ascospores.

The genus *Bryomyces* was established by Döbbeler (1978) with nine species on a variety of hepatics and mosses including Polytrichaceae. Some of these fungi are frequent and widespread, but species not always easy to distinguish. The species on *Dendroligotrichum* is more common than the eight records indicate. It may represent a taxon of its own, but should be carefully compared with related species. Suitable type material does not exist amongst the available specimens.

### 4. *Bryonectria disciformis* Döbbeler, sp. nov.

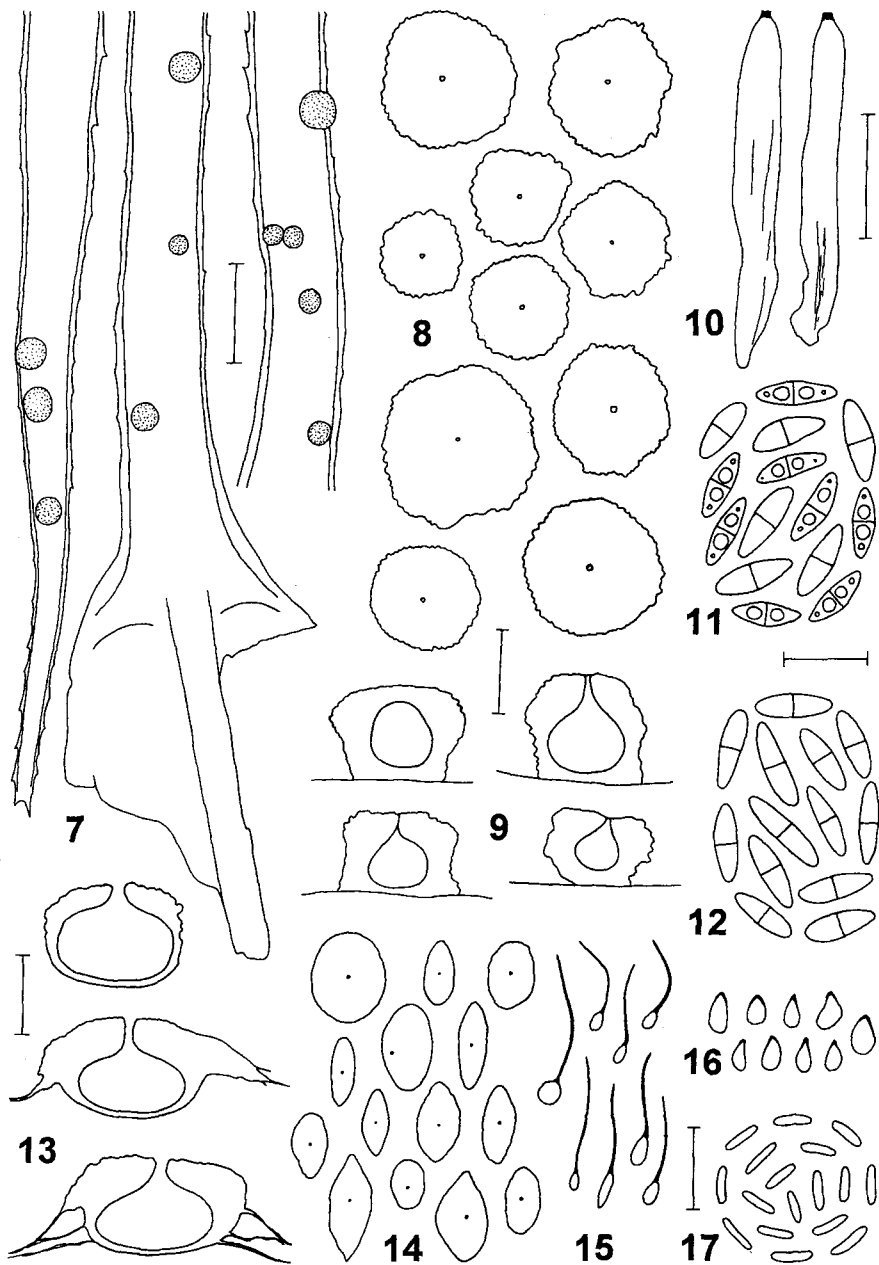
Figs 7-17

Species *Bryonectriae cuneiferae* similis sed ab ea peritheciis separatis, majoribus (90-200  $\mu\text{m}$ ), apicaliter applanatis valde differt. Pariet perithecorum extus verrucis praeditus. Habitat parasitice in parte adaxiali foliorum inferiorum musci *Dendroligotrichum dendroides*.

Type (collection 38): New Zealand, South Island: Otago, Fiordland National Park, Tutoko River Track east of Milford Sound, 44°39' S, 167°58' E, 20-150 m alt., in part closely associated with *Potridiscus polymorphus*, 7 Feb. 1985, H. Mayrhofer 5753 & H. Hertel (GZU, holotype).

Etymology: *disciformis* (Latin) = disc-like; refers to the aspect of the ascomata seen from above.

Perithecia 90-200  $\mu\text{m}$  diam, circular or slightly irregular in outline, when mature often apically depressed and broader than the base, uncoloured except for the brownish



Figs 7-17: *Bryonectria disciformis* on *Dendrologotrichum dendroides*. 7. Ascomata on the adaxial side of lower and upper leaf parts. 8. Ascomata in outline. 9. Ascomata in longitudinal section. 10. Empty asci, spores discharged. 11. Ascospores. 12. Ascospores. 13. Pycnidia in longitudinal section. 14. Pycnidia in outline. 15. Sterile cells (of the hymenium). 16. Conidiogenous cells. 17. Conidia. Figs 7-11: Collection 38 (type). Figs 12-17: Collection 30. Scale in 7 = 0.5 mm. Scale in 8, 9, 14 = 100  $\mu$ m. Scale in 10 = 15  $\mu$ m. Scale in 11, 12 = 10  $\mu$ m. Scale in 13 = 50  $\mu$ m. Scale in 15-17 = 10  $\mu$ m.



hymenium lining the interior, glabrous, surface coarsely verruculose, verrucae up to 10  $\mu\text{m}$  high. Ostiole punctiform, ostiolar canal lined with periphyses. Excipular wall strongly gelatinous, in section up to 50  $\mu\text{m}$  thick in the apical and lateral regions, considerably thinner at the base, composed of *textura irregularis* with hyphal lumina very delicate, not always discernible. Interascal hyphae absent (but 1.5  $\mu\text{m}$  wide filaments observed in collection 30). Asci 35-50(-55)  $\times$  5-7.5  $\mu\text{m}$ , cylindrical, eight-spored, apical opening pore-like. Iodine-negative. Ascospores 8-11(-12)  $\times$  2.5-4  $\mu\text{m}$ , narrowly ellipsoidal to almost spindle-shaped, two-celled, uncoloured, often with one large oil droplet per cell. Hyphae typical for the genus, 1-3  $\mu\text{m}$  wide, thick-walled, preferring the anticlinal cell walls of the leaves. Appressoria and conidiogenous cells not observed. (Hyphal characters are hard to study as the very low leaf lamellae scarcely detach.)

Presumed anamorph pycnidial. Pycnidia narrowly elliptical, rarely almost circular, uncoloured, partly immersed between the lamellae, partly erumpent with a wedge-like base, (60-)75-110(-120)  $\mu\text{m}$  long, 25-85  $\mu\text{m}$  wide. Ostiole punctiform, often not recognizable in surface view. Excipulum as in teleomorph, apically up to 30  $\mu\text{m}$  thick, at the base 5-8  $\mu\text{m}$  and composed of elongated cells. Conidiogenous cells lining the whole interior of the excipulum, ellipsoidal, about 4  $\mu\text{m}$  wide, the fertile cells interspersed with sterile ones, about 3  $\mu\text{m}$  wide, with a delicate, up to 10(-15)  $\mu\text{m}$  long and 0.5  $\mu\text{m}$  wide hair-like filament. Conidia 4-5(-5.5)  $\times$  1(-1.5)  $\mu\text{m}$ , rod-shaped, sometimes slightly curved, one-celled, uncoloured.

Host: *Dendrologotrichum dendroides*.

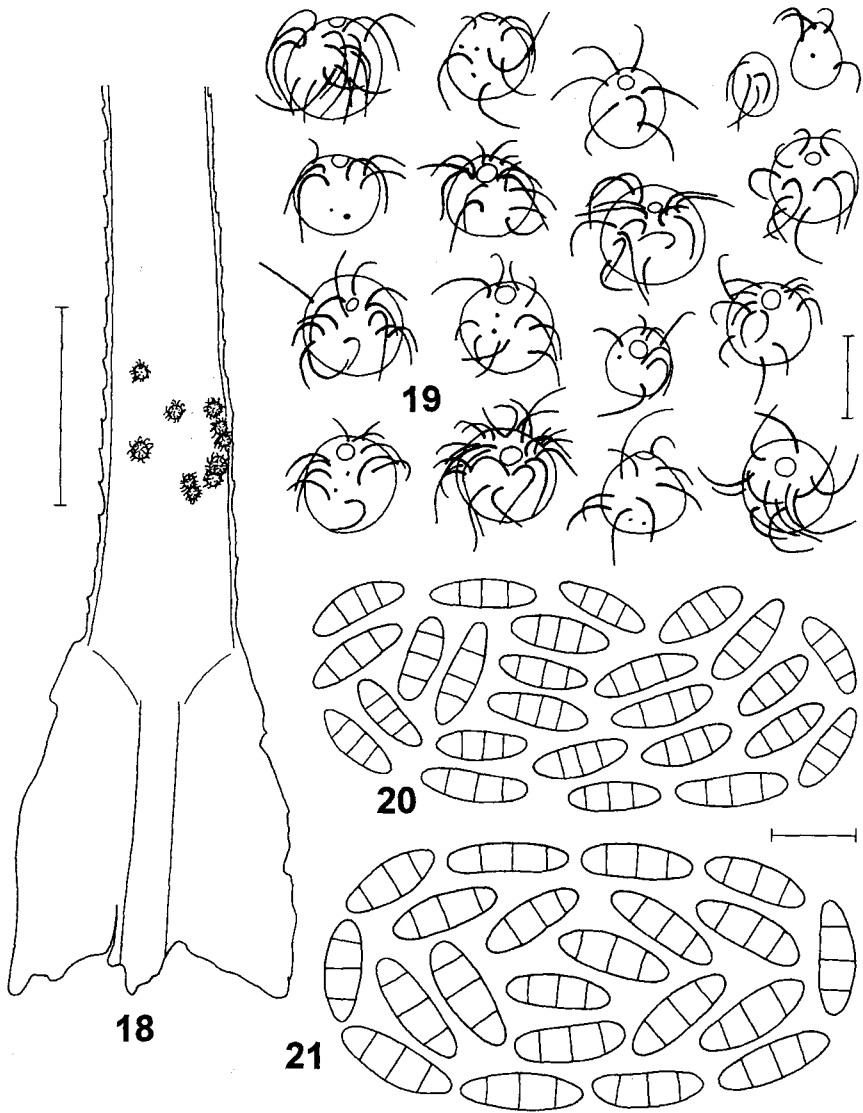
Known distribution: New Zealand.

Specimens examined: 30 (ascomata and pycnidia), 31 (only pycnidia), 34 (only pycnidia), 37 (only ascomata), 38 (only ascomata).

Solitary ascomata develop sparsely on the adaxial surface of the lower leaves. They are easily detachable and basally bear ridge-like structures (appearing as teeth in transverse sections) corresponding to the rows of lamellar end-cells on which they sit. Usually just one pycnidium develops per leaf, generally in the mid-proximal region of lower leaves.

The species is present in the teleomorphic or presumed anamorphic state on five of the 12 New Zealand collections cited. Ascomata and pycnidia are difficult to detect at lower magnification and may be easily confused with globose gelatinous colonies of green and blue-green algae and even with tiny liverworts growing on *Dendrologotrichum*. Perithecia and pycnidia sometimes develop in close proximity on the same host leaf. Up to now this type of pycnidia has not been recorded in connection with *Bryonectria*, but the excipular characters of both ascomata and pycnidia as well as the hymenial features are typical of the genus.

*Bryonectria disciformis* is the eighth species described in a genus comprising hepaticolous and muscicolous representatives. Half of the species are restricted to Polytrichaceae. *Bryonectria phyllogena* Döbbeler on *Polytrichum juniperinum* Hedw. from Chile and Poland deviates by conical or pyriform, brown ascomata (Döbbeler 1999c). The colourless *B. biseptata* (Döbbeler) Döbbeler is distinguished by three-



Figs 18-20: *Epibryon elegantissimum* on *Dendrologotrichum dendroides*. 18. Ten ascomata on the adaxial surface of the lower leaf region, infection density and position of fruit-bodies at some distance from the transition zone between lamina and sheath - untypical (collection 27). Scale = 1 mm. 19. Ascomata, the two above right immature (collection 19). Scale = 50  $\mu$ m. 20. Ascospores (collection 9). Scale = 10  $\mu$ m.

Fig. 21: *E. elegantissimum* on *Dawsonia superba*, ascospores (New Zealand, South Island, Westland, Paringa-Haast-Track, 18 Jan. 1959, U. Schweinfurth; M, type). Scale = 10  $\mu$ m.

celled spores formed within four-spored asci. It has been recorded from *Dawsonia grandis* Schlieph. & Geh. in New Guinea and from *Polytrichum* sp. in Nepal (Döbbeler 1978, 1981). Likewise colourless perithecia occur in *B. cuneifera* (Döbbeler) Döbbeler (Döbbeler 1978) which is more closely related to *B. disciformis*. *Bryonectria disciformis* is distinguished by perithecia developing separately upon the lamellae. The perithecia are often apically depressed and broader above than the base, measuring 90-200 µm diam. Perithecia of *B. cuneifera* are more or less globose or ellipsoidal, and up to 130 µm diam, arising from a wedge-like base inserted into the spaces between leaf lamellae. Gregariously formed ascomata typically tend to fuse laterally. Small differences among the species can also be found in the outer excipular structures of ascomata and in the size and form of asci and spores. The more than 15 European collections of *B. cuneifera* were invariably found on *Polytrichastrum formosum* (Hedw.) G.L. Sm. (Döbbeler, unpubl.).

#### 5. *Epibryon elegantissimum* Döbbeler (Döbbeler 1978)

Figs 18-21

Ascomata (45-)50-90(-100) µm diam, globose, pale brown. Setae up to 80(-120) µm long, dark brown to black, septate, in most cases arising in the upper third of the ascomata and curved to the substratum. Excipulum with *textura angularis*, cells (3-) 5-9(-13) µm diam, thin-walled. Interascal filaments absent. Asci (31-)35-49 × 10-15(-17) µm, narrowly to broadly ellipsoidal, eight-spored. Iodine reaction: hymenial jelly reddish. Ascospores (10.5-)11.5-15(-16) × 3.5-5.5(-6) µm, ellipsoidal, with 3 transverse septa, pale brown, without hyaline appendages.

Hosts: *Dendroligotrichum dendroides* (and *Dawsonia superba* Grev., Döbbeler 1978, 1981).

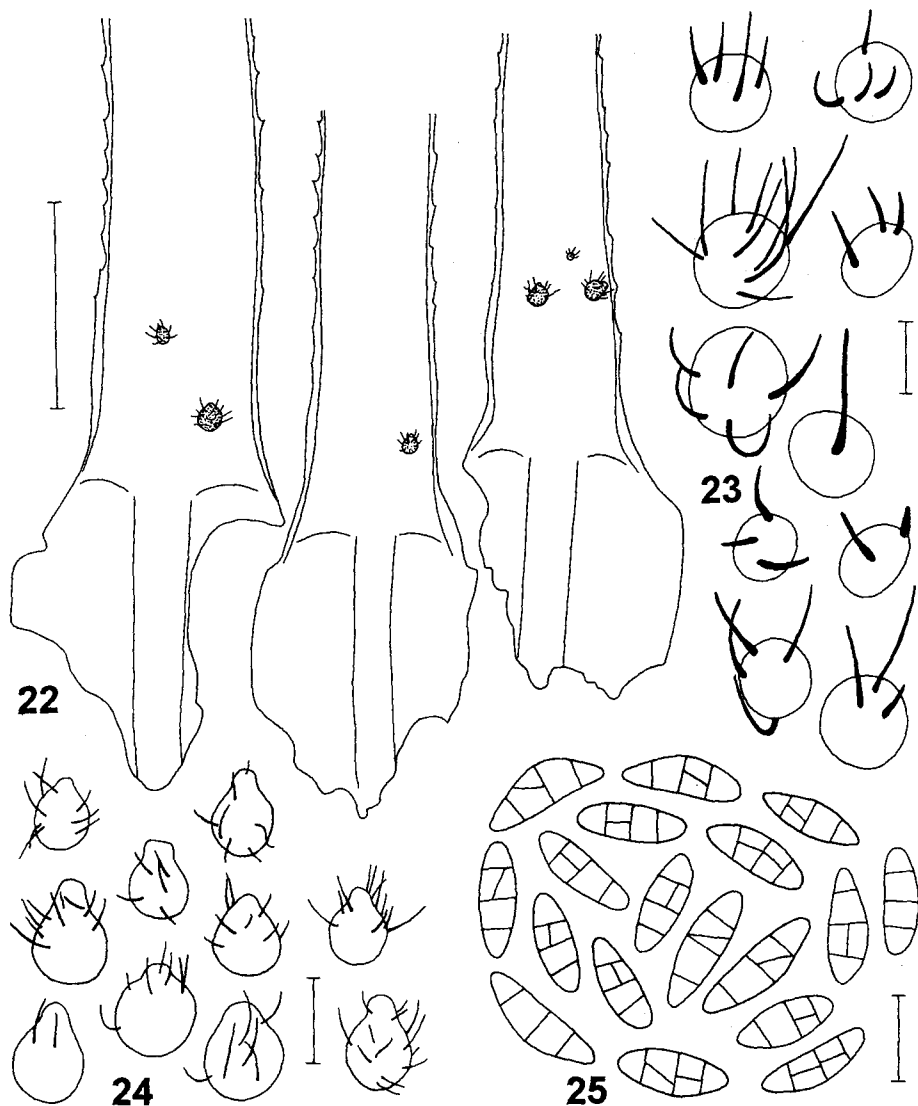
Known distribution on *Dendroligotrichum dendroides*: Chile, Juan Fernández Islands, Argentina (on *Dawsonia superba* recorded from New Zealand).

Specimens examined: 9, 11, 13, 19, 20, 22, 25, 26, 27.

Ascomata are formed individually and sporadically on the adaxial leaf side in the transition zone between sheath and lamina, or in the lower leaf part. Sometimes ascomata can be found in the middle or even upper leaf parts, with a clear preference for the leaf margin.

The following slight differences in spore size correlated with hosts and geographical regions were observed in *Epibryon elegantissimum*: Populations on *Dendroligotrichum dendroides* from South America: ascospores 3.5-4.5(-5) µm wide (Fig. 20). Populations on *Dawsonia superba* from New Zealand including the type: ascospores 4-5.5(-6) µm wide (Fig. 21).

*Epibryon elegantissimum* and the related *E. pulchellum* and *E. eremita* possess two types of setae on the same ascoma. Some are acute, thick-walled and bristle-like while others have truncate, thin-walled, light coloured apices that look as if their tips had been broken off (Döbbeler 1999b, Fig. 4b).



Figs 22-25: *Epibryon eremita* on *Dendroligotrichum squamosum*.:22. Ascomata on the adaxial side of lower leaf parts. Scale = 1 mm. 23. Primordia of ascomata. Scale = 20  $\mu$ m. 24. Mature ascomata. Scale = 100  $\mu$ m. 25. Ascospores. Scale = 10  $\mu$ m. Figs 22, 23: Collection 43. Figs 24, 25: Collection 49.

6. *Epibryon eremita* Döbbeler (Döbbeler 1999b)

Figs 22-25

Ascomata (60-)70-120(-150)  $\mu$ m high, (40-)55-90(-100)  $\mu$ m diam, subglobose with an apical papilla, more rarely ovoid, light to dark brown. Setae up to 60(-80)  $\mu$ m

long, dark brown, septate, straight or curved, present even on very young asomata. Excipulum with *textura angularis*, cells 4-8(-10)  $\mu\text{m}$  diam, thin-walled. Interascal filaments absent. Asci ca. 35-60(-65)  $\times$  20-27  $\mu\text{m}$ , in most cases eight-spored, but collections with some 16- or about 32-spored asci exist. Iodine reaction: hymenial jelly reddish. Ascospores (10-)12-15.5(-17)  $\times$  (3-)4-5(-6)  $\mu\text{m}$ , ellipsoidal, with 3 transverse and often 1 or 2 longitudinal septa, rarely only transversely septate, pale brown.

Hosts: *Dendroligotrichum squamosum* (and *Polytrichadelphus magellanicus*, Döbbeler 1999b, 2001).

Known distribution: Chile, Argentina.

Specimens examined: 43, 44, 45, 47, 48, 49, 50, 51, 53.

Scattered ascomata develop sparsely on the adaxial leaf side to which they are more or less laterally attached. Often they prefer the transition zone between sheath and lamina. More rarely the fruit-bodies occur in the lower leaf third and only exceptionally in the middle or even apical leaf parts. Generally, only one or two ascomata are found on a single leaf. Setae arise at all parts of the ascoma wall and are oriented upwards. Even primordial ascomata 25  $\mu\text{m}$  diam are provided with well-developed setae of both types (see *E. elegantissimum*).

#### 7. *Epibryon interlamellare* (Racov.) Döbbeler (Döbbeler 1978) Figs 26, 30, 31

Ascomata (30-)35-50(-60)  $\mu\text{m}$  diam, globose, light or dark brown, with setae. Ostiole 8-10  $\mu\text{m}$  diam, pore-like. Setae to 30(-35)  $\mu\text{m}$  long, dark brown to black, rigid, straight or slightly curved, often present even on very young ascomata. Excipulum composed of small angular cells. Interascal hyphae absent. Asci (15-)17-25(-28)  $\times$  5-7(-8)  $\mu\text{m}$ , narrowly ellipsoidal, thin-walled, eight-spored. Iodine reaction: hymenial jelly reddish. Ascospores (6-)7-8.5(-9.5)  $\times$  (2-)2.5(-3)  $\mu\text{m}$ , narrowly ellipsoidal, two-celled, septum very delicate, uncoloured.

Hosts: *Dendroligotrichum dendroides*, *D. squamosum* (and other Polytrichaceae, especially frequent on *Polytrichastrum formosum* and *Polytrichum commune* Hedw. (Döbbeler 1978), also recorded on *Dawsonia* spp. (Döbbeler 1981) and *Polytrichadelphus magellanicus* (Döbbeler 1999b, 2001)).

Known distribution on *Dendroligotrichum*: Chile, Juan Fernández Islands, Argentina, New Zealand (on other Polytrichaceae presumably cosmopolitan).

Specimens examined: 1, 3, 4, 5, 6, 7, 9, 12, 13, 14, 15, 16, 17, 18, 19, 23, 27, 28, 31, 32, 36, 43, 44, 45, 46, 47, 48, 49, 50, 51.

Ascomata are scattered on the middle and lower leaves of plants. The leaves often begin to decompose. Ascomata tend to be formed on the distal leaf half, especially the uppermost region and the leaf border. Normally only one or very few ascomata develop on each leaf. An exceptionally heavily infected leaf of *D. dendroides* yielded 25 fruit-bodies. On *D. dendroides* with low lamellae, ascomata are usually formed upon these lamellae, whereas in *D. squamosum* with high lamellae, ascomata are

often immersed in the interspaces and may even be laterally compressed. The species is certainly more frequent than the records suggest.

Comparing ascomata from different collections reveals considerable variation. Fruit-bodies may be small and light brown with few short setae arising near the ostiolar region, especially in deeply immersed specimens. When formed upon the substratum, ascomata may be larger, darker brown and ornamented with many setae on the apical and medullary regions. These features may be influenced by the microniche occupied and may therefore have no systematic importance. However, small differences also exist between ascus and spore sizes and spore form. For example, ends of spores may be more rounded or less so. Further studies will show if these differences are correlated with host affinity and geographical distribution (see also remarks under *Epibryon* spp.). Though *E. interlamellare* infects different genera of Polytrichaceae, it is not present on all species of certain genera. For example, despite extensive investigation there are no records for *Polytrichastrum sexangulare* (Döbbeler 1987) and *Polytrichadelphus innovans* (Müll. Hal.) A. Jaeger (Döbbeler 2001).

#### 8. *Epibryon pulchellum* Döbbeler, sp. nov.

Figs 26, 27

Species *E. elegantissimo* similissima sed ab eo characteribus sporarum et hospite alio differt. Sporae nonnihil longiores ((14-)15-19(-22) × (3-)3.5-4.5(-5) μm) et duabus guttulis mucilaginis ornatae. Habitat parasitice in foliis musci *Dendroligotrichum dendroides*.

Type (collection 32): New Zealand, North Island: Mt Egmont, 3000-4000 ft alt., Aug. 1929, A. Meebold (M, holotype).

Etymology: *pulchellus* (Latin) = beautiful (diminutive of *pulcher*), in reference to the beautiful ascomata.

*Epibryon pulchellum* differs from the similar *E. elegantissimum* by the following characters:

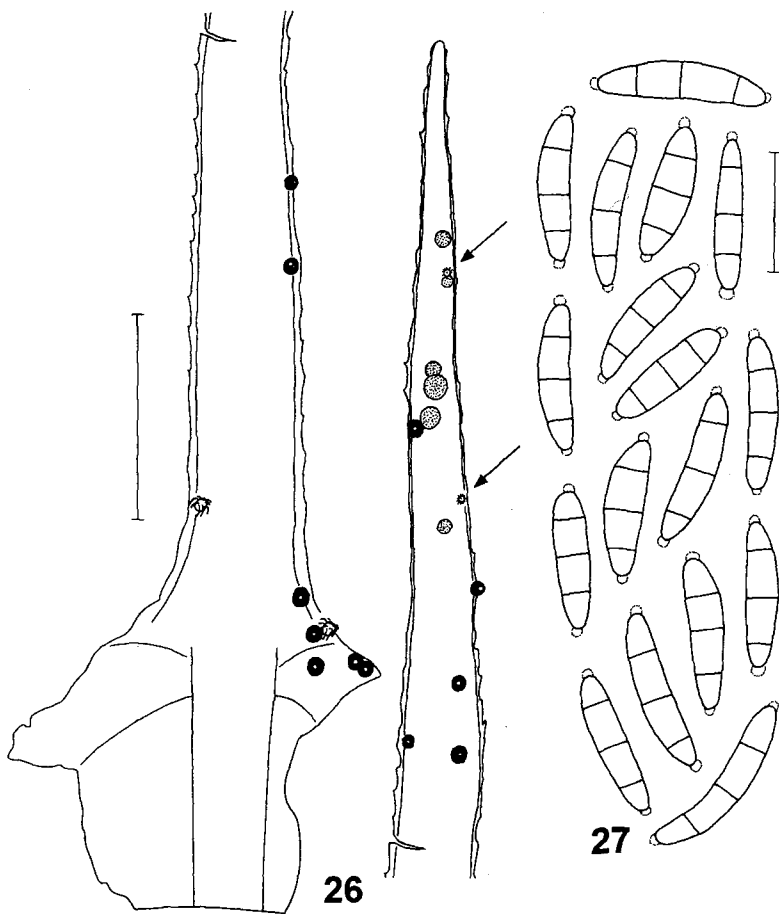
Ascomata (50-)60-80(-100) μm diam. Setae up to 100 μm long. Asci (31-)35-49 × 10-15 μm. Ascospores (14-)15-19(-22) × (3-)3.5-4.5(-5) μm (measured without appendages), narrowly ellipsoidal to subcylindrical, with a small, hyaline, mucilaginous drop-like appendage at each spore end-cell.

Host: *Dendroligotrichum dendroides*.

Known distribution: New Zealand.

Specimens examined: 28, 30, 31, 32, 33, 36, 39.

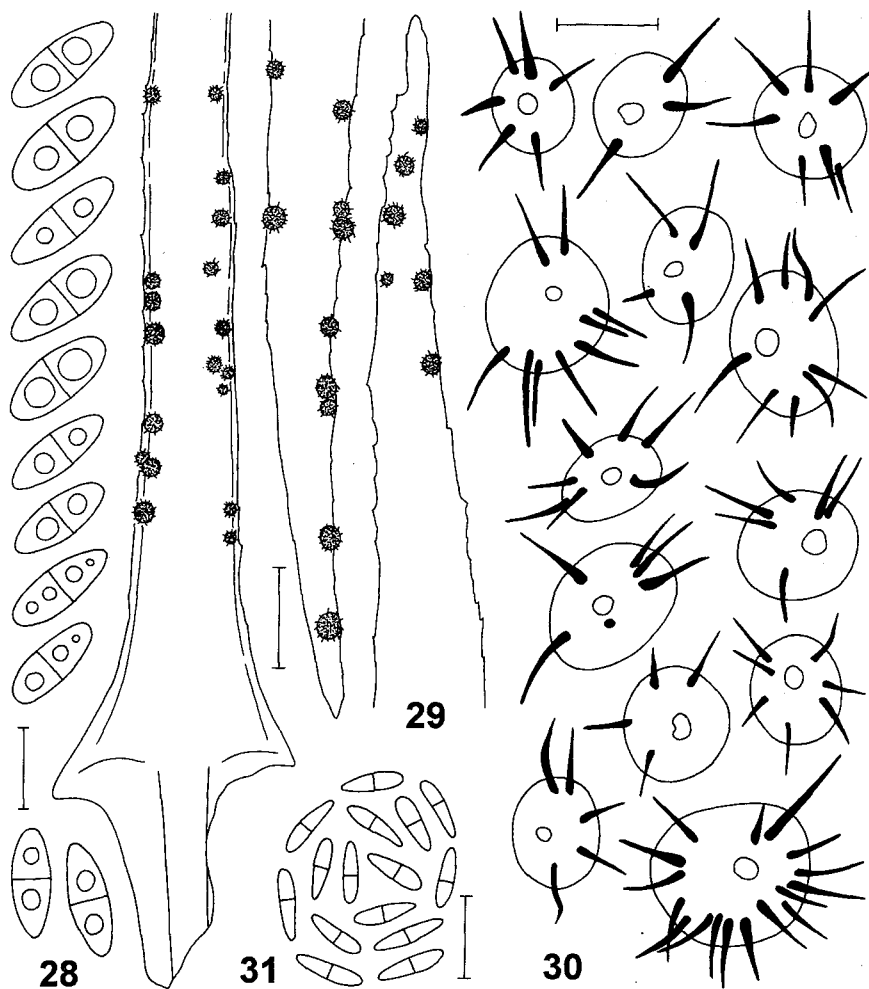
*Epibryon pulchellum* and *E. elegantissimum* are closely related but differ in their spore characters (size and presence or absence of appendages). Paradoxically, spore characters suggest closer relationships between populations of *E. elegantissimum* on *Dawsonia* in New Zealand and those on *Dendroligotrichum* in South America than between populations of *Epibryon* on the same host in New Zealand (*E. pulchellum*) and America (*E. elegantissimum*).



Figs 26, 27: *Epibryon pulchellum* on *Dendroligotrichum dendroides* (collection 32, type). 26. Two ascomata on the adaxial side of the lowermost leaf lamina. Associated species are: *Bryomyces* sp., 12 ascomata, black; *Potridiscus polymorphus*, six ascomata in the upper leaf half, stippled; *E. interlamellare*, two ascomata (arrows) in the upper leaf half. Scale = 1 mm. 27. Ascospores. Scale = 15  $\mu$ m.

### 9. *Epibryon* spp.

At least three additional species related to *E. interlamellare* occur on *Dendroligotrichum*. They are not formally described here, but are briefly characterized. These species considerably enlarge the distribution area of the genus *Epibryon* to some subantarctic islands. Ascomycetes with globose, dark and setose fruit-bodies and two-celled, ellipsoidal ascospores are among the most frequently observed fungi on bryophytes. They are associated with a great number of diverse hepatics and mosses including Polytrichaceae. Species delimitation is critical because the degree of variation in anatomical characters, host ranges and geographical distributions is



Figs 28, 29: *Epibryon* sp. 3 on *Dendrologotrichum dendroides* (collection 40). 28. Ascospores. Scale = 10  $\mu$ m. 29. Ascomata on the adaxial leaf side. Scale = 0.5 mm.

Figs 30, 31: *E. interlamellare* on *D. dendroides*. 30. Ascomata (collection 19). Scale = 30  $\mu$ m. 31. Ascospores (collection 1). Scale = 10  $\mu$ m.

unknown to a large extent. Type studies using modern methods have not been undertaken. To introduce new species names now based on ascoma size, spore size and occurrence on a hitherto unrecorded host would not be a step forward, particularly for a 'waste basket' genus like *Epibryon* (Döbbeler 1997).

Species 1: Ascomata 50-90  $\mu$ m diam, superficial on the adaxial leaf side; ascospores 8-10  $\times$  (2.5-)-3-3.5(-4)  $\mu$ m. - On *D. dendroides*, New Zealand (collection 33, B); on *D. squamosum*, Falkland Islands (collection 54, B), South Georgia (collection 59, AAS).



Species 2: Ascomata 60-90  $\mu\text{m}$  diam, superficial on the adaxial leaf side; ascospores 9-13  $\times$  3-3.5  $\mu\text{m}$ . - On *D. dendroides*, Argentina (collection 26, B).

Species 3: Ascomata 90-120  $\mu\text{m}$  diam, superficial on the adaxial leaf side; ascospores 12.5-16  $\times$  5-7  $\mu\text{m}$ . - On *D. dendroides*, together with a smaller-spored species of *Epibryon*, both incompletely developed, Auckland Islands (collection 40, MSC). Figs 28, 29

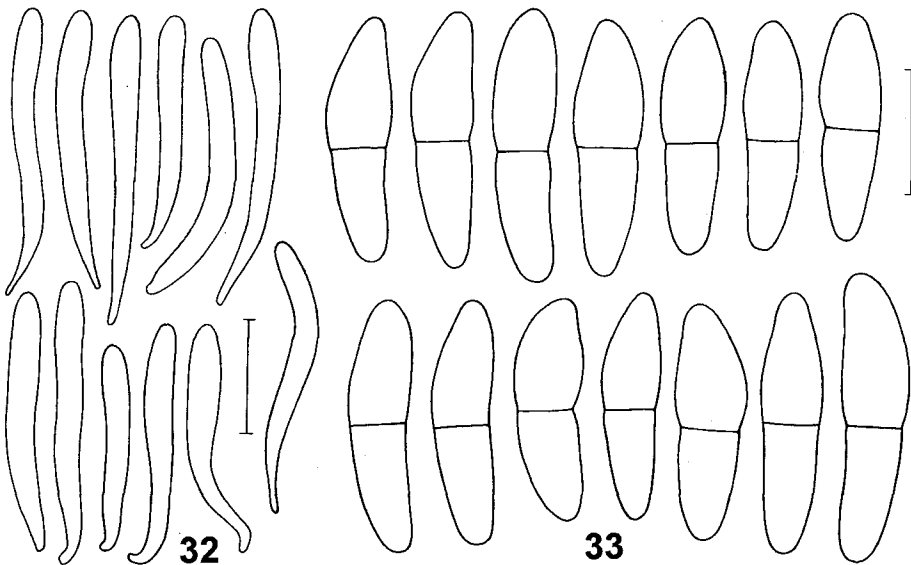
10. *Lizonia baldinii* (Piroz.) Döbbeler (Döbbeler 1978) subsp. **dendroligotrichi**  
Döbbeler, subsp. nov. Figs 32, 33

Differt a *Lizonia baldinii* subsp. *baldinii* ascis sporisque longioribus (26-34  $\times$  7-8.5  $\mu\text{m}$ ) et hospite alio. Habitat parasitice intra folia gametangia masculina circumdantia musci *Dendroligotrichum dendroides*.

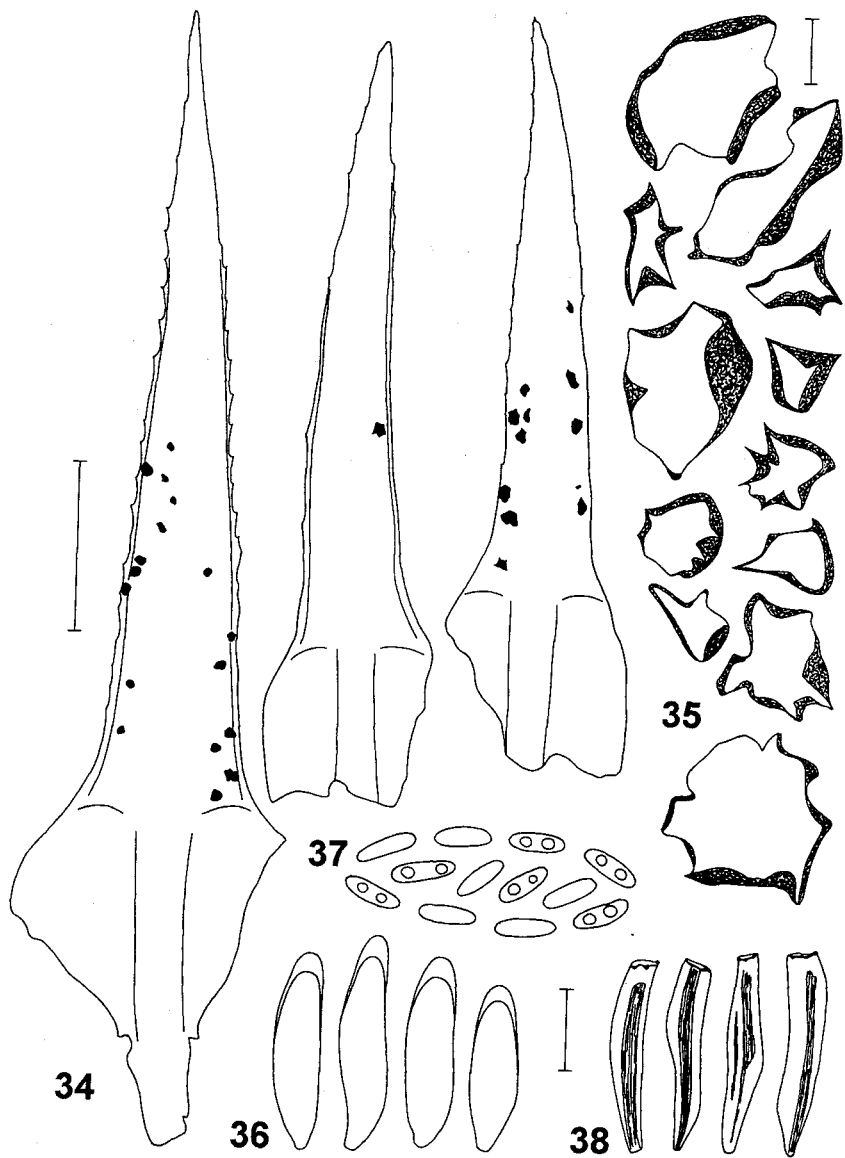
Type (collection 7): Chile, Prov. de Valdivia: Cordillera Pelada, road from La Unión to El Mirador, 800 m alt., 12 Dec. 1985, F. Hellwig (M, holotype).

Ascomata 200-350  $\mu\text{m}$  diam, globose, black, carbonaceous, glabrous. Excipulum (in longitudinal section) composed of several layers of rectangular cells. Interascal filaments in mature fruit-bodies inconspicuous. Asci (115-)130-180(-197)  $\times$  (15-)16-19(-21)  $\mu\text{m}$ , cylindrical to slightly claviform, 16-spored. Iodine-negative. Ascospores (24.5-)26-34  $\times$  (6.5-)7-8.5(-9.5)  $\mu\text{m}$ , ellipsoidal, one-septate, brown.

Host: *Dendroligotrichum dendroides*.



Figs 32, 33: *Lizonia baldinii* subsp. *dendroligotrichi* on *Dendroligotrichum dendroides* (collection 7, type). 32. Asci. Scale = 70  $\mu\text{m}$ . 33. Ascospores. Scale = 15  $\mu\text{m}$ .



Figs 34-38: *Malvinia endoderma* on *Dendroligotrichum squamosum* (collection 54, type). 34. Ascomata on the abaxial side of leaves. Scale = 1 mm. 35. Ascomata seen from above in outline. Scale = 40  $\mu$ m. 36. Mature asci. 37. Ascospores. 38. Empty asci, spores discharged. Scale in 36-38 = 10  $\mu$ m.

Known distribution: Chile. - *Lizonia baldinii* subsp. *baldinii* infects mainly *Polytrichastrum formosum* in Scandinavia and Central Europe, where it is locally abundant, as well as in Rumania, Italy, and Alaska (Parriat & Moreau 1954, Racovitza 1959, Döbbeler 1978).

Specimens examined: 6, 7.

Ascomata are exclusively formed within the antheridial cups of male plants. They are densely aggregated and often laterally fused, forming a pseudostromatic black structure. Infected plants begin to die off from the apex. Presumably a distinct necrotic zone may be seen in fresh material.

Collection 13 harbours very few incompletely developed ascomata of *Lizonia* sp. They grow on the uppermost region of sterile or female plants destroying their apices. The ascomata measure ca. 400  $\mu\text{m}$  diam, the eight-spored asci 132-140  $\times$  19-24  $\mu\text{m}$ , and the ascospores (35-)40-49  $\times$  9-12.5(-14)  $\mu\text{m}$ . It is hard to imagine that this specimen belongs to *Lizonia baldinii* (with 16-spored asci), particularly since antheridial cups are present but show no signs of infection. Further collections are needed to reveal if two species of *Lizonia* are present on *Dendrologotrichum dendroides*. Female (or sterile) plants have only rarely been observed to be colonized by *Lizonia*, particularly in their apical regions (Racovitza 1959, Fig. 36; Döbbeler 1978: 306, 1987: 90), where archegonia develop.

Presently, at least four polytrichicolous species of *Lizonia* can be distinguished. (I regard the non-bryophilous species assigned to *Lizonia* as not congeneric.) All known hosts belong to the genera *Pogonatum*, *Polytrichastrum*, *Polytrichum* (Racovitza 1959, Döbbeler 1978, 1987), and *Oligotrichum* (Parriat & Moreau 1954). Many observations in Central Europe indicate that these parasites are host species-specific. The Chilean collections of *Lizonia* are the first obtained outside the holarctic region.

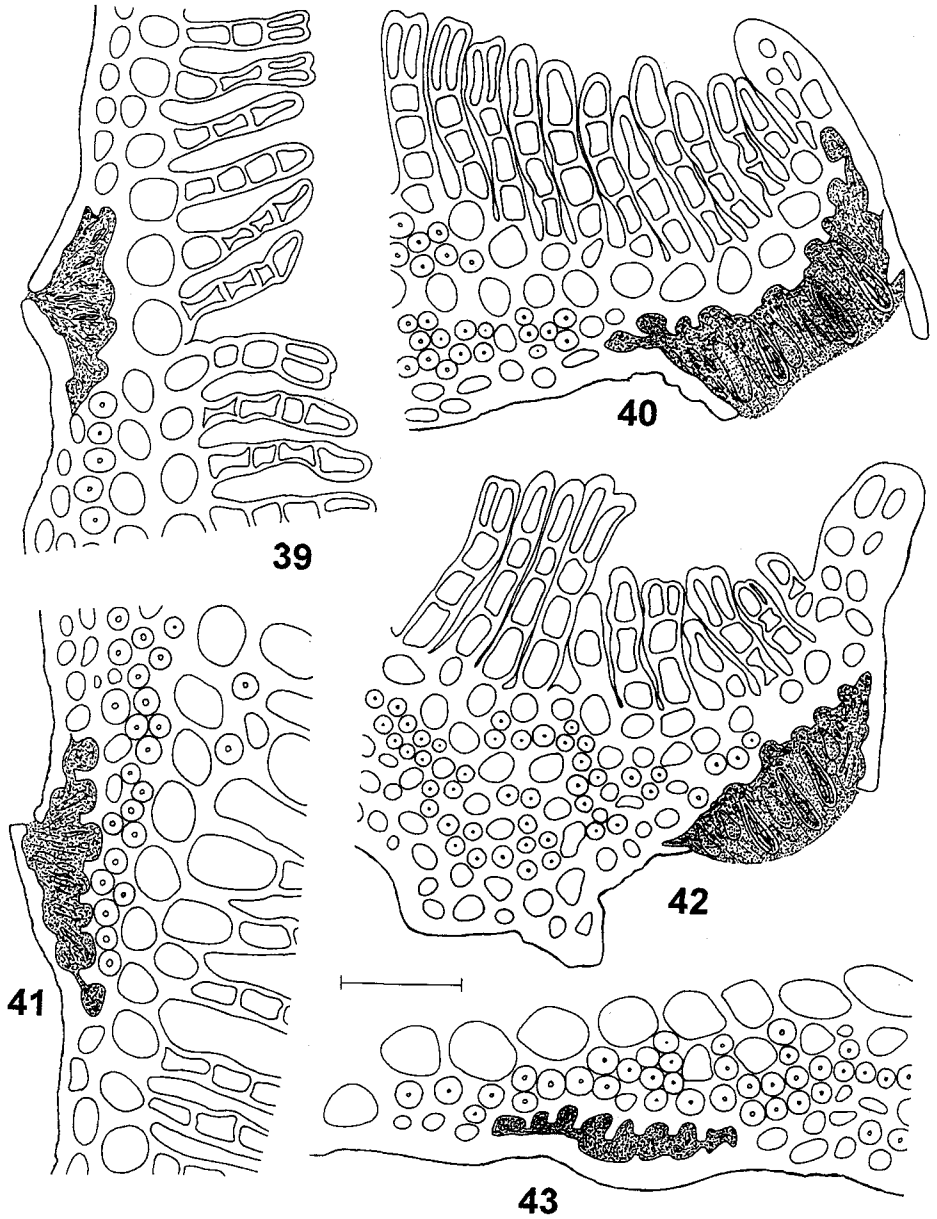
*Lizonia baldinii* seems to be infrequent on *Dendrologotrichum dendroides*, though it may be locally abundant on male plants. Many additional collections with antheridial cups have been examined in vain. To learn about the frequency of these highly-specialized ascomycetes, field observations should be made. *Dendrologotrichum squamosum* and other Polytrichaceae should also be taken into consideration in these investigations.

#### 11. *Malvinia endoderma* Döbbeler, gen. et sp. nov.

Figs 34-43

*Descriptio generico-specifica:* Genus Ostropalium. Ascomata apothecioidea, superne visa 65-120  $\mu\text{m}$  diam, usque ad 30  $\mu\text{m}$  alta, subcircularia, incolorata, glabra. apertura irregulari vel stellari. Excipulum valde reductum. Paraphyses 1.5  $\mu\text{m}$  latae, filiformes. Asci unitunicati, 22-26  $\times$  6-7  $\mu\text{m}$ , subcylindrici vel anguste ellipsoidei, octospori; reactio iodi negativa. Sporae 6.5-8  $\times$  2.5  $\mu\text{m}$ , ellipsoideae, incoloratae, unicellulares. Hyphae minus quam 0.5  $\mu\text{m}$  latae, incoloratae, in parietibus cellularum hospitis crescentes, inconspicuae. Habitat parasitice intra cellulas epidermidis abaxialis foliorum inferiorum veteriorum musci *Dendrologotrichum squamosum*.

Type (collection 54): Falkland Islands, West Falklands: Mt Adam, Cliffs on east side of summit ridge, 2200-2297 ft alt., 25 Jan. 1968, J.J. Engel 3016A (B, holotype; AAS, MSC, isotypes).



Figs 39-43: *Malvinia endoderma* on *Dendrologotrichum squamosum*, infected leaves transversely sectioned (collection 54, type). 39, 41: Developing ascomata lifting up the periclinal walls of epidermal cells. 40, 42: Mature ascomata. 43. Primordium of ascoma still enclosed within epidermal cells. Scale in 39-43 = 30  $\mu$ m.

Etymology: *Malvinia*: The genus is recorded from Las Islas Malvinas (Spanish name for the Falkland Islands). - *Endoderma*: *endo* (Greek) = within, *derma* (Greek) = skin, refers to the ascomata formed within the epidermis.

Genus of Ostropales. Ascomata apothecioid, (50-)65-120(-140)  $\mu\text{m}$  diam, up to 30 (-35)  $\mu\text{m}$  high, roundish, uncoloured, glabrous, aperture stellate or irregular. Lateral excipulum strongly reduced, of some paraphysis-like cells, basal part with some irregular, short-celled hyphae. Paraphyses filamentous, about 1.5  $\mu\text{m}$  wide, not ramified, often difficult to detect. Asci unitunicate, (20-)22-26(-28)  $\times$  (5.5-)6-7  $\mu\text{m}$ , subcylindrical or narrowly ellipsoidal, without apical structures, eight-spored. Iodine reaction negative, also after pretreatment with KOH. Ascospores (6-)6.5-8(-8.5)  $\times$  about 2.5  $\mu\text{m}$ , ellipsoidal, one-celled, uncoloured. Hyphae uncoloured, very delicate, less than 0.5  $\mu\text{m}$  wide, growing irregularly within the walls of the leaf cells.

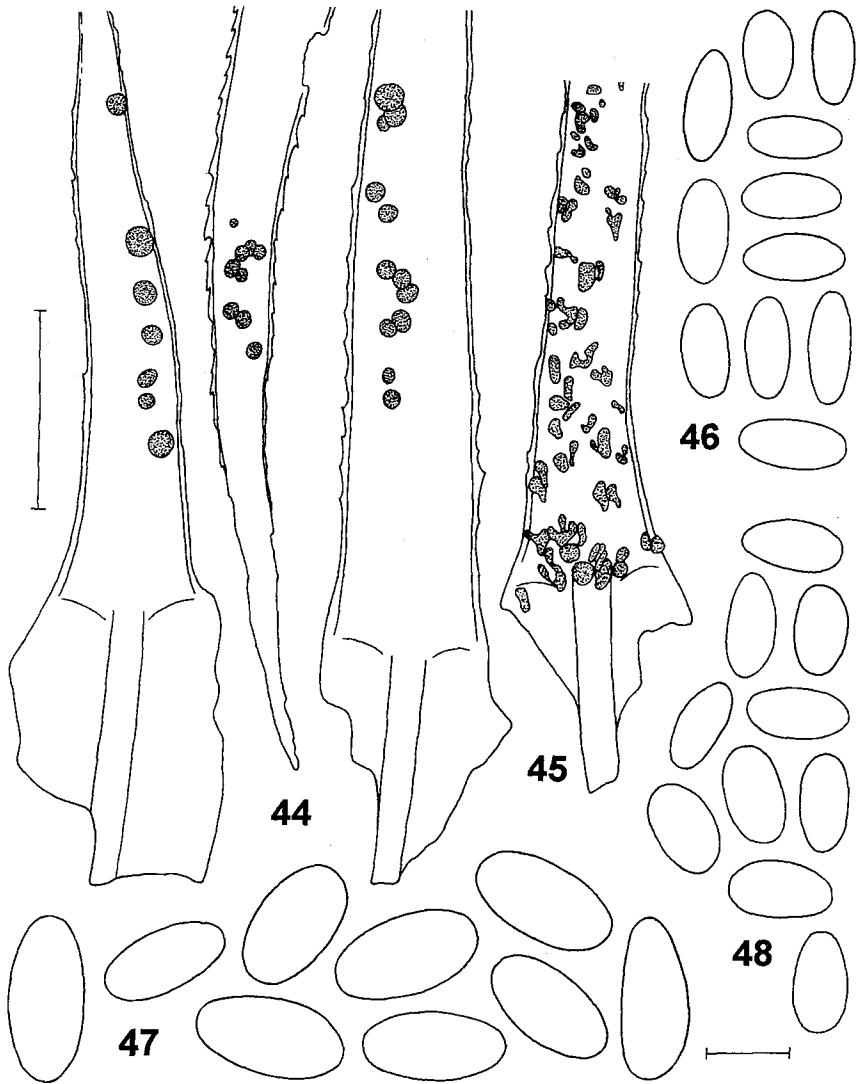
Host: *Dendrologotrichum squamosum*.

Known distribution: Falkland Islands.

Specimens examined: 54, 55.

Infection is mainly seen in the leaves of the lower stem, often those already showing incipient decomposition. Fruit-bodies never occur on young plants or upper stem leaves. Ascomata are scattered on the abaxial side from basal to apical leaf regions. Up to 19 fruit-bodies have been observed on single leaves. Sporulation preferentially occurs in the marginal regions at both sides of the nerve where the lamina consists of just two cell layers, the abaxial and the adaxial epidermis. Cells of the latter, called 'Bauchzellen' by Lorentz (1868) and 'ventral cells' by Smith (1971: 8), bear the longitudinal photosynthetic leaf lamellae on its entire surface except for its small outermost border. Ascomata begin to develop within the abaxial epidermal cells. While expanding they lift up the periclinal cell walls which finally burst, forming straight and well-defined slits or teeth. Seen from above, this appears as a primary stellate irregular opening. Sections reveal that the anticlinal walls of the colonized cells are split in the midregion, resulting in a dentate inner (adaxial) row of epidermal half cells and a corresponding raised outer (abaxial) row of counterpart half cells. Sometimes the periclinal parts of the cell-walls simply separate from the anticlinal walls entirely. The tooth-like flaps of periclinal wall covering the hymenium are often triangular and their reddish brown borders can be clearly seen using microscopic magnification. This contrasts with the lighter-coloured uncovered parts of the hymenium and the unaffected epidermis surrounding the areas of fruit-body formation. The slight colour changes are very useful in detecting the ascomata of this extremely inconspicuous species. Sections reveal that the uplifted periclinal walls are not darker coloured. The apparent colour change is an artefact caused by the uplifted walls absorbing more light than the walls lying in the plane of the epidermal surface. Apertures may later expand and the flaps may then fall off, but decomposition of host wall material apparently does not play a role.

The extremely delicate hyphae are not easy to trace, especially as host leaves have a complex structure and consist of coloured, thick-walled cells. Furthermore, old leaves are almost indiscriminately infected by sterile ascomycetes or conidial fungi whose hyphae can be confused with those of species forming fructifications. I am not sure



Figs 44-48: *Potridiscus polymorphus* on *Dendroligotrichum dendroides*. 44: Ascomata on the adaxial side of leaves (collection 1). 45: Primordia and immature ascomata on the adaxial side of a heavily infected leaf (collection 40). 46: Ascospores (collection 1). 47: Ascospores (collection 33). 48: Ascospores (collection 40). Scale in 44, 45 = 1 mm. Scale in 46-48 = 10  $\mu$ m.

whether the mycelium is restricted to the cell walls. Fine hyphal perforations are visible as with intracellularly growing species whose hyphae perforate the walls when crossing from one cell to another, but here the existence of intracellular hyphae is hard to verify.

Many ascomata contain empty asci that do not disappear after spore release. These asci are cylindrical and slightly longer than mature but still-closed asci. Their cord-like plasmatic content is very characteristic. Apically they reveal a broad opening with a border that is often slightly folded back (Fig. 38). Undischarged spores or spores lying on the leaves have not been observed, in contrast to what is seen in *Potridiscus polymorphus* and some other infections. Spore liberation and distribution seems to be effective.

*Malvinia endoderma* may be related to the ostopalean, also unispecific, *Rogellia nectrioidea* Döbbeler recorded on *Polytrichadelphus magellanicus* in southern South America (Döbbeler 1999b, 2001). In both cases, fruit-bodies develop endobiotically within the abaxial leaf side. The differences among systematically important characters such as excipular structure, spore-type and iodine reaction are so distinct that separating the two species generically seems to be justified.

## 12. *Potridiscus polymorphus* Döbbeler & Triebel (Döbbeler & Triebel 2001)

Figs 26, 44-51, 62

Ascomata (50-)70-150(-200)  $\mu\text{m}$  diam, apothecioid, often irregularly shaped and laterally confluent, sometimes with a small stipe formed on the leaf lamellae, light to dark brown or rarely black, glabrous. Excipulum of elongated cylindrical to slightly club-shaped cells and typically with dark brown transversely segmented cell contents. Paraphyses filamentous, also with dark cell inclusions. Asci (40-)43-70(-90)  $\times$  (10-)11-15(-16)  $\mu\text{m}$ , ellipsoidal to cylindrical, eight-spored. Iodine-negative. Ascospores (10-)11-14(-15.5)  $\times$  (4-)5-6.5(-7)  $\mu\text{m}$ , ellipsoidal, aseptate, brown; overmature spores often slightly rough.

Hosts: *Dendroligotrichum dendroides*, *D. squamosum* (additional hosts: *Polytrichadelphus magellanicus* (Döbbeler 2001); *Polytrichum commune*, *P. juniperinum*, *P. strictum* (Döbbeler & Triebel 2001)).

Known distribution on *Dendroligotrichum*: Chile, Juan Fernández Islands, Argentina, Falkland Islands, South Georgia, New Zealand, Auckland Islands (on other Polytrichaceae also recorded from Australia and Tasmania, Döbbeler & Triebel 2001), (Fig. 67).

Specimens examined: 1, 2, 3, 5, 6, 7, 8, 11, 12, 13, 17, 19, 20, 21, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 42, 45, 46, 47, 48, 49, 50, 51, 52, 54, 56.

Ascomata usually develop on mid-level and lower brown leaves, which often show signs of incipient decomposition. The adaxial leaf surface is the site where nearly all ascomata are formed. Normally, the infection rate is low. Single leaves of a plant may yield ten or more ascomata, whereas others are free of them.

*Potridiscus polymorphus* typically forms light to dark brown, relatively thick, irregular hyphae, which always accompany apothecia. They arise from the interlamellar spaces, cross one or few lamellae transversely or obliquely and disappear between lamellae. These hyphae are also often visible in the absence of, or prior to, ascoma formation. Very characteristic and rarely missing (e.g., in collection 40 from the Auckland

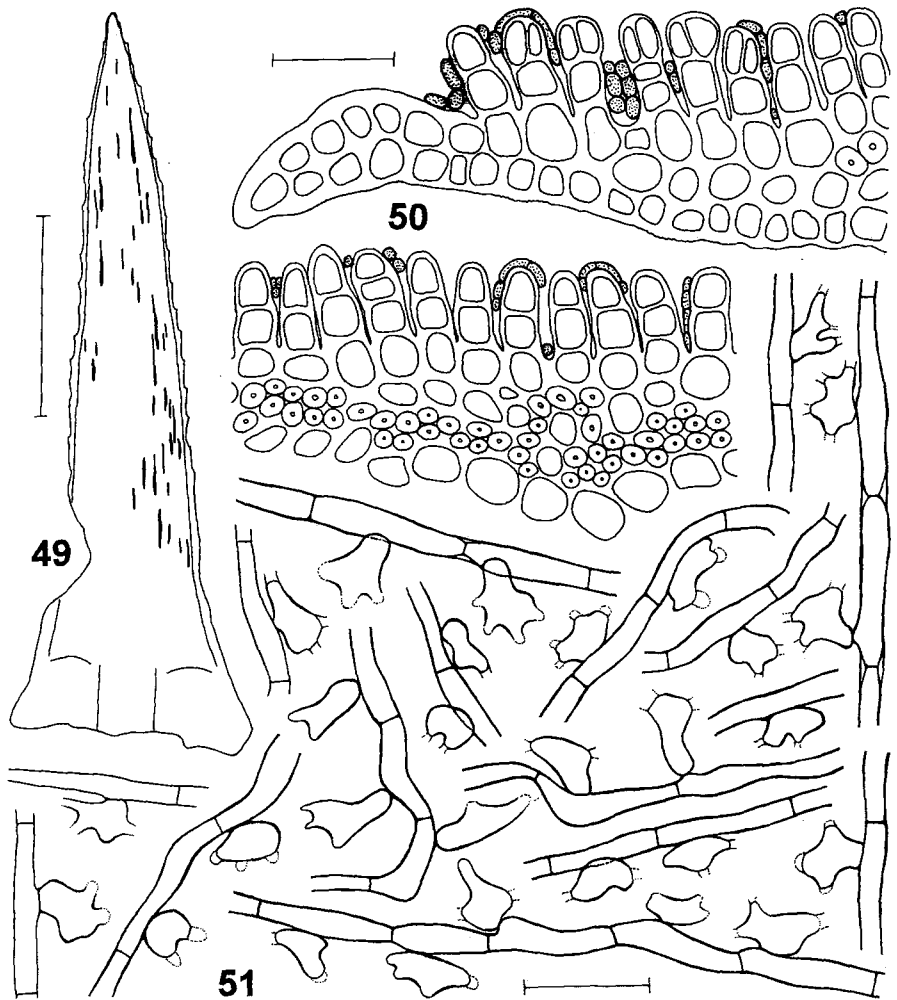


Fig. 49: *Potridiscus polymorphus* on *Dendroligotrichum squamosum* (collection 56), line-shaped hyphal plates in the interlamellar spaces of a leaf seen from above. Scale = 1 mm.  
 Figs 50, 51: *P. polymorphus* on *D. dendroides* (collection 38). 50. Host leaf in transverse section with hyphae growing between and above the leaf lamellae. Scale 30 =  $\mu\text{m}$ . 51. Appressoria. Scale = 15  $\mu\text{m}$ .

Islands) are the dark brown, granular or segmented contents of the excipular cells and paraphyses. These inclusions are normally present even in primordia giving them an unmistakable aspect. Discharged spores lying on the lamellae can regularly be observed.

An interesting type of appressorium is especially well-represented in collection 38 (Fig. 51). The sessile appendages arise laterally on the hyphae, and in surface view they are irregularly sinuous and 8-13  $\mu\text{m}$  diam. One to four blunt apices are formed



which have an extremely thin and almost colourless wall, thus contrasting with the normally brown, and thicker walls of the appressoria and hyphae. These delicate protrusions might have a haustorial function. In several other specimens of this species the same kind of appressorium is occasionally present. The only mycelial structures within the bryophilous ascomycetes that resemble these curious appressoria are the club-shaped appendages of the unrelated *Hypobryon insigne* Döbbeler & Menjívar, which grows on epiphyllous hepatics (Döbbeler & Menjívar 1992, Fig. 3.4). These appendages are also provided with fine finger-like protrusions, the function of which can hardly be haustorial as the species already forms intracellular haustoria. In collection 56, line-shaped hyphal plates were observed developing immersed between the leaf lamellae (Fig. 49).

Ascomata of *P. polymorphus* reveal a considerable range of variation, but extended linear fruit-bodies more or less completely immersed between the leaf lamellae, as recorded for this species in *Polytrichum commune*, were not detected. Four collections (33, 48, 51, 56) merit special mention for the apparent correlation of deviating anatomical characters and ecological preferences. Ascospores are significantly larger, measuring 15-20(-21) × 7-10 µm (Fig. 47), the asci about 65-90(-95) × 15-20 µm. Interestingly, the ascomata arise from hyphae colonizing the upper green leaves. Ascomata with normal spore sizes were also observed on the lower leaves of the same specimens.

Like *Potriphila epiphylla*, *Potridiscus polymorphus* occupies the whole distribution area of its host genus (Fig. 67). It is by far the most frequent ascomycete found on *Dendroligotrichum*. It is especially common on *D. dendroides* from New Zealand, where it was found on all 12 specimens cited, and on *D. squamosum* from the Fuegian region. *Polytrichadelphus magellanicus* occurring within the American range of *D. dendroides* was only once observed as host. The australasian *Polytrichadelphus innovans* was never found to be infected even though a reasonable number of New Zealand specimens were investigated (Döbbeler 2001). Additionally, *Potridiscus polymorphus* was not noted on *Dawsonia superba* from New Zealand, or on *D. longiseta* Hampe or *D. polytrichoides* R. Br. from southeastern Australia (Döbbeler 1981).

### 13. *Potriphila epiphylla* Döbbeler, sp. nov.

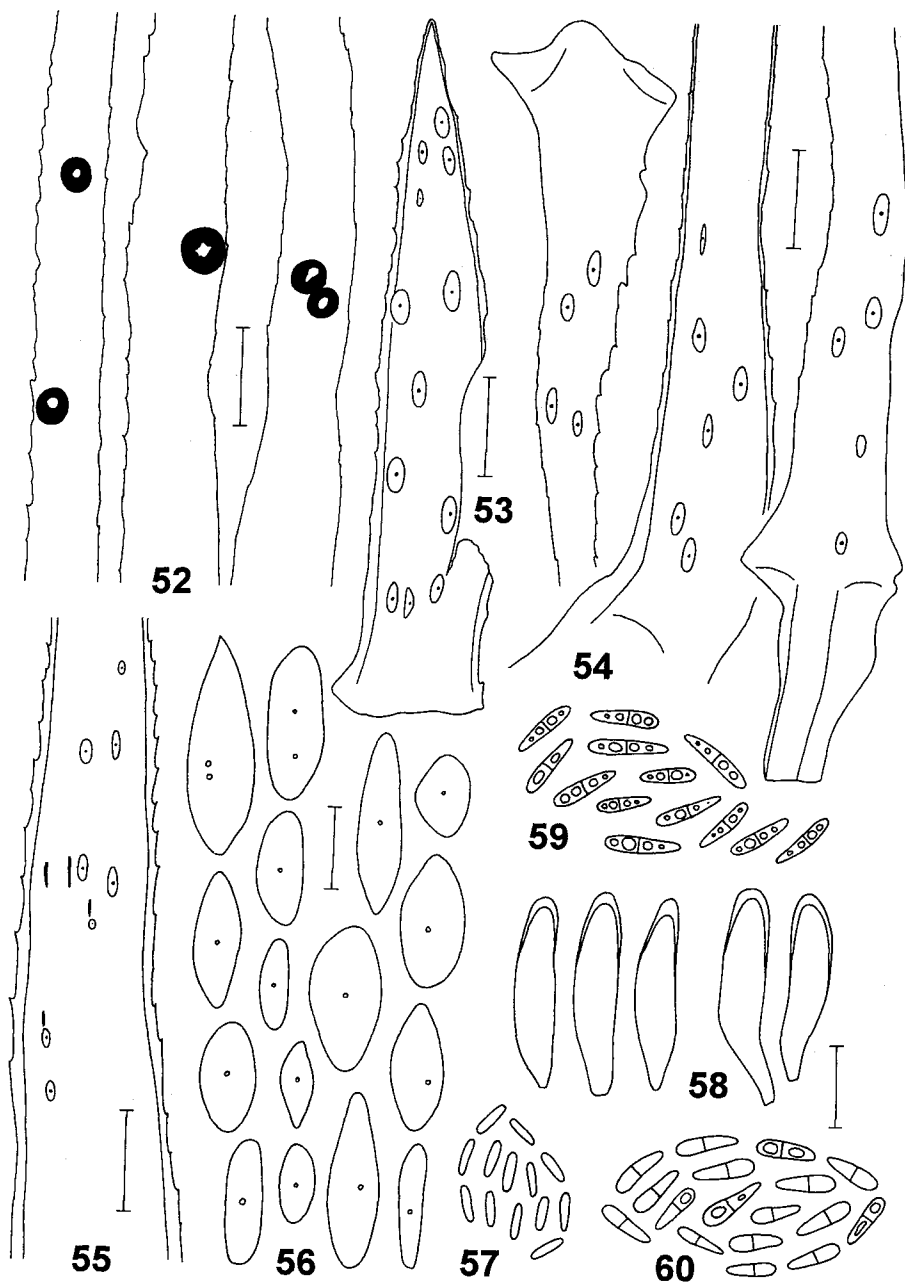
Figs 52-60, 62

*Potriphila epiphylla* speciei *Potriphila navicularis* similis sed ab ea differt ascomatibus superficialibus et (sub)globosis, sporis minoribus, pycnidii superficialibus, superne visa ambitu late elliptico usque ad circulari, conidiis minoribus (4-5 × 1-1.5 µm). Habitat parasitice in parte adaxiali foliorum mediorum inferiorum veteriorumque ambarum specierum generis *Dendroligotrichum*.

Type (collection 16): Chile, Prov. de Palena: 22 km southeast of Chaitén on gravel road to Pto Cárdenas, 90 m alt., 8 March 1985, on *Dendroligotrichum dendroides*, T. Stuessy, J. Furlow, E. Ruiz & N. Bustos 7082 (B, holotype).

Etymology: *epiphylla*: *epi* (Greek) = upon, *phyllon* (Greek) = leaf, lamella, refers to the ascomata formed both on the adaxial leaf surface and upon the lamellae.

Ascomata superficial on the leaf lamellae, (70-)100-200(-250) µm diam, globose to depressed globose, black, opening 45-100 µm diam, circular or irregularly toothed,



Figs 52, 54, 56-60: *Potriphila epiphylla* on *Dendroligotrichum dendroides*. 52. Ascomata on the adaxial side of leaves (collection 16, type). 54. Pycnidia on the adaxial leaf side (collection 40). 56. Pycnidia in outline (collection 40). 57. Conidia (collection 40). 58. Asci (collection 16, type). 59. Ascospores (collection 30). 60. Ascospores (collection 16, type). Scales in 52, 54 = 0.5 mm. Scale in 56 = 100  $\mu$ m. Scale in 57-60 = 10  $\mu$ m.

when overmature very fragile. Excipulum carbonized. Paraphyses filamentous, wide. Asci (19-)23-32(-37) × (4-)4.5-6 μm, narrowly ellipsoidal to cylindrical or subclaviform, eight-spored. Iodine reaction: ascus walls reddish, colouration sometimes preceded by a blue front. Ascospores (5.5-)6-8.5(-9.5) × 1.5-2.5 μm, ellipsoidal to clavate, two-celled, uncoloured.

Pycnidia broadly elliptical to almost circular in outline, oriented in the longitudinal direction of the leaf, (50-)100-160(-230) × (25-)40-80(-160) μm, black, carbonized, erumpent from the interlamellar spaces, often apically keeled. Ostiole seen in transmitted light as a small clear spot, sometimes bluntly projecting. Conidia 4-5 (-5.5) × 1-1.5(-2) μm, narrowly ellipsoidal to rod-shaped, one-celled, uncoloured.

Hosts: *Dendrologotrichum dendroides*, *D. squamosum*.

Known distribution: Chile, Juan Fernández Islands, Argentina, Falkland Islands, South Georgia, New Zealand, Auckland Islands (Fig. 67).

Specimens examined: 1, 5, 6, 7, 8, 11, 16, 17, 19, 20, 23, 24, 26, 27, 28, 29, 30, 31, 33, 34, 36, 40, 42, 44, 45, 47, 51, 53, 54, 56, 58.

Ascomata and pycnidia prefer the lower older leaves which often show signs of incipient decomposition. Pycnidia were only encountered a few times in the upper green leaves. The density of fruit-body formation mostly is low. All collections contain pycnidia with two or three ostioles. Sometimes this seems to be the result of fusion of two or more developing pycnidia. In five collections (44: Brunswick Island, 56, 58: South Georgia, 31: New Zealand, 40: Auckland Islands) only pycnidia were observed.

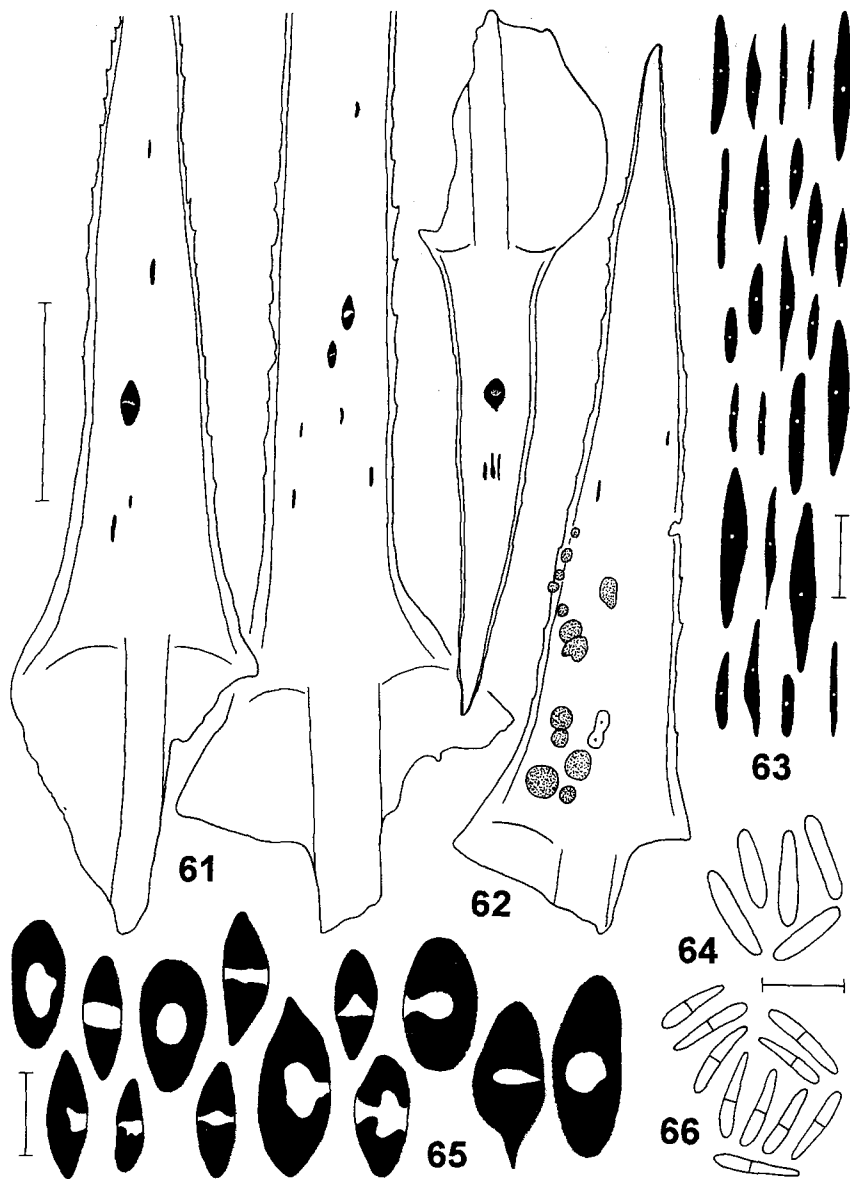
#### 14. *Potriphila navicularis* Döbbeler (Döbbeler 1996)

Figs 55, 61-66

Ascomata elliptical, 110-160(-180) μm long, (40-)55-90(-100) μm wide, black, glabrous, more or less deeply immersed between the leaf lamellae, initially closed, finally breaking open irregularly. Excipular cells extremely thick-walled and carbonized. Paraphyses filamentous. Asci 24-38 × 5-6 μm, ellipsoidal to club-shaped, eight-spored. Iodine reaction: hymenium bluish after pretreatment with KOH. Ascospores (8-)9-11(-12) × (2-)2.5 μm (13-16 μm long on *Polytrichastrum alpinum*), ellipsoidal to club-shaped, two-celled, uncoloured. Hyphae very delicate, forming intracellular haustoria within the distal cells of the lamellar hairs.

Pycnidia seen from above narrowly elliptical, fusiform to almost linear, (60-) 80-160 (-210) μm long, 10-35(-50) μm wide, completely immersed between the leaf lamellae. Ostiole always visible as a small pale spot. Conidia (7.5-)8.5-11(-12) × 2-3 μm, rod-shaped, one-celled, uncoloured.

Figs 53, 55: *P. epiphylla* on *D. squamosum*. 53. Pycnidia on the adaxial leaf side (collection 56). 55. Pycnidia on the adaxial leaf side associated with four pycnidia (black) of *P. navicularis* (collection 53). Scales in 53, 55 = 0.5 mm.



Figs 61-66: *Potriphila navicularis* on *Dendroligotrichum squamosum*. 61. Ascomata and pycnidia on the adaxial leaf side (collection 41). 62. Two pycnidia on the adaxial leaf side, associated species are: *Potridiscus polymorphus*, 13 ascomata, stippled; *Potriphila epiphylla*, two laterally fused pycnidia (collection 56). 63. Pycnidia in outline (collection 41). 64. Conidia (collection 41). 65. Ascomata in outline (collection 41). 66. Ascospores (collection 52). Scale in 61, 62 = 1 mm. Scales in 63, 65 = 100  $\mu$ m. Scale in 64, 66 = 10  $\mu$ m.

Hosts: *Dendrologotrichum squamosum* (and other Polytrichaceae, especially *Polytrichastrum alpinum* (Hedw.) G.L. Sm., Döbbeler 1996, 2001).

Known distribution on *D. squamosum*: Chile, Argentina, Falkland Islands, South Georgia (on other Polytrichaceae of bipolar distribution).

Specimens examined: 41, 45, 46, 52, 53, 55, 56, 57.

*Potriphila navicularis* is the only species treated that is regularly found on the young and green leaves. Infections are apparently systemic. With the exception of collections 53 and 56 where only pycnidia occur, both morphs were often present even on the same leaf.

The species is widely distributed in the northern and southern hemisphere excluding the tropical zones. It is present throughout the range of *Dendrologotrichum squamosum*, but it was not observed on *D. dendroides*, though genera like *Polytrichadelphus*, *Polytrichastrum*, and *Polytrichum* are among its hosts. All host species hitherto recorded have well-developed hairs formed by the leaf lamellae (see Döbbeler 1999a). These hairs are attacked by intracellular haustoria typical of *Potriphila navicularis*. Hairs are present in *D. squamosum* but lacking in *D. dendroides*. Interestingly, *Polytrichadelphus magellanicus* is a frequent host of *Potriphila navicularis* in southern South America, whereas the vicariant *Polytrichadelphus innovans* in Australasia is not attacked (Döbbeler 2001). The latter species has few, and when present, reduced lamellar hairs. It is possible that Polytrichaceae with poorly developed or missing lamellar hairs do not offer an adequate nutritional basis for growth of *Potriphila navicularis*.

*Potriphila navicularis* and the related *P. epiphylla* were encountered together three times in the same collection on the same plant and even on the same leaf (collections 45, 53, 56, Figs 55, 62). The characters distinguishing the two species are drawn up in Table I.

Table I: Differences between the two species of *Potriphila*

Characters	<i>P. navicularis</i>	<i>P. epiphylla</i>
Ascomata	immersed between the lamellae or protruding, more or less elliptical in outline	always superficial, (depressed) globose
Ascospores	9-11 × 2.5 µm	6-8.5 × 1.5-2.5 µm
Pycnidia	narrowly elliptical, fusiform to almost linear, completely immersed	broadly elliptical to almost circular, superficial on the lamellae
Conidia	8.5-11 × 2-3 µm	4-5 × 1-1.5 µm
Hosts	<i>D. squamosum</i> and other Polytrichaceae	<i>D. dendroides</i> , <i>D. squamosum</i>
Ecology	on the upper green leaves	normally on lower old leaves

### The host species *Dendroligotrichum dendroides* and *D. squamosum*

*Dendroligotrichum dendroides* and *D. squamosum* are typical dioecious Polytrichaceae, characterized by an unbranched, orthotropically growing stem that bears an apical cluster of branches, giving the impression of a dendroid plant. The Spanish common name 'palmita', meaning small palm, was recorded on one of the herbarium labels. Most Polytrichaceae are unbranched or sparingly branched. *Pogonatum sinense* (Broth.) Hyvönen & Wu is also dendroid (Hyvönen & Wu 1993).

The species are very distinctive and normally easy to distinguish by their habit. *Dendroligotrichum dendroides* 'is undoubtedly the largest moss of the Americas, almost equalling the largest *Dawsonia* species' (Smith 1971: 62). I have seen a sterile herbarium plant (collection 10) reaching 45 cm length. This extraordinary size allows these mosses to act as phorophytes for other bryophytes (Herzog 1926: 180, Malcolm & Malcolm 2000: 76). Some Lejeuneaceae have only been found on *D. dendroides* (Glenny 1996). Whereas even small individuals of *D. dendroides* are normally longer than 15 cm, *D. squamosum* is up to 10 cm long, though exceptionally large gametophytes in the material studied reached 15 or even 18 cm. The smaller and more densely formed leaves give rise to the condensed habit of *D. squamosum*. The leaf lamellae of this species are four to six cells high and have often paired marginal cells covered with conspicuous granular wax. Lamellae of *D. dendroides* are two or three cells high and form neither paired cells nor wax. The marked differences between the marginal cells may indicate that the species have only a superficial similarity of growth-form in common (Clayton-Greene et al. 1985). However, undivided end-cells frequently occur in *D. squamosum* (Figs 39, 40, 42) and longitudinally divided end-cells have been observed in *D. dendroides* (Fig. 50). An additional distinguishing leaf character is the presence of conspicuous lamellar hairs only in *D. squamosum* (Döbbeler 1999a). The two species of *Dendroligotrichum* were not genetically differentiated from each other at enzyme encoding loci in an electrophoretic study (Derda et al. 1999). Several anatomical, ultrastructural and karyological studies dealing with *D. dendroides* have been published (e.g., Ono 1972, Scheirer 1972, 1973, 1975, Héban & Berthier 1972, Héban 1973, 1975, 1977, Clayton-Greene et al. 1985, Rodríguez de Sarmiento & Schiavone 1988, Henseler & Frahm 2000).

*Dendroligotrichum dendroides* occurs in southern South America (especially Chile, south of about 40° S latitude down to the Fuegian region), Juan Fernández Islands, New Zealand and Auckland Islands (Fig. 67; Beever et al. 1992, Calabrese & Matteri 1999, Fife 1995, D.M. Greene 1986, He 1998, Robinson 1975, Schiavone 1993, Schiavone & Hyvönen 1993, Smith 1971, Vitt 1979). The record 'in Peruvia' cited in the checklist of the mosses of Peru by Menzel (1992) is very unlikely (doubted also by Churchill et al. 2000, Gradstein et al. 2001). Smith (1971) treated the New Zealand taxon as distinct, *D. dendroides* subsp. *microdendron* (Müll. Hal.) G.L. Sm.

In South America and New Zealand *Dendroligotrichum dendroides* occupies similar forest floor habitats. The species apparently share a common origin in Gondwanaland (Schofield 1985: 355). Frey et al. (1999) interpreted the modern disjunctions of these austral 'genoelements' as having derived from the break-up of Gondwana. Even today Lorch's statement (1908: 542) holds true: the distribution of the *Dendroligotricha* is of highest phytogeographical interest.

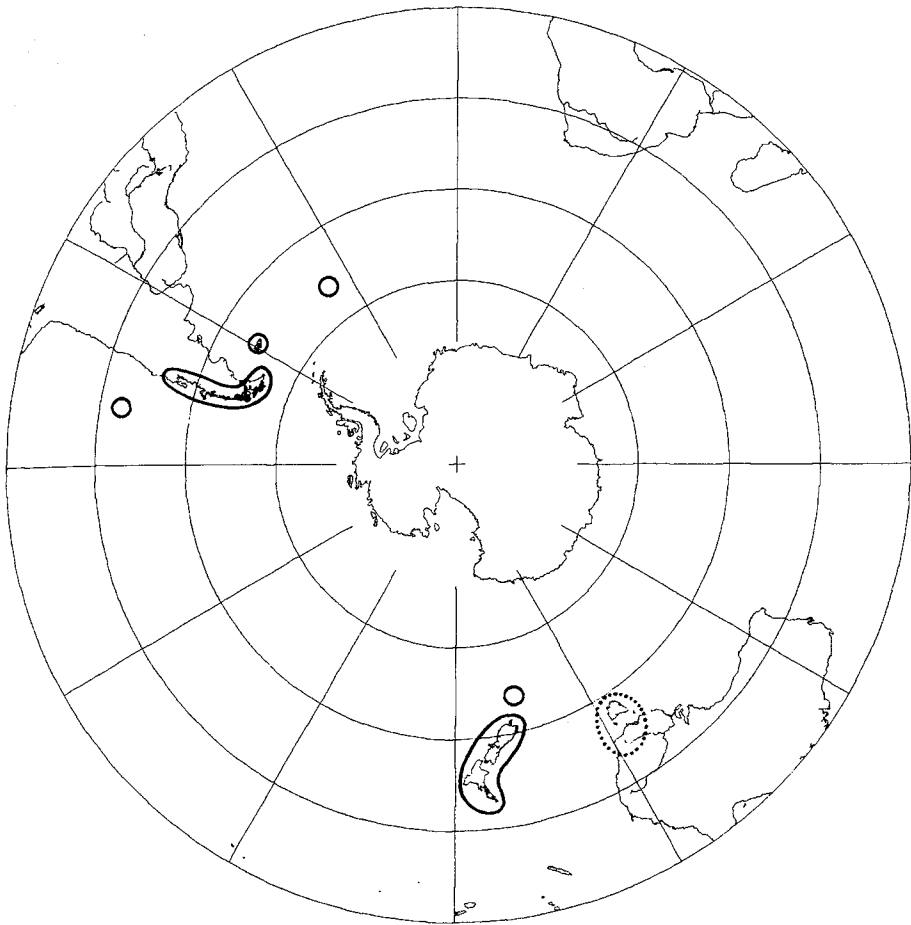


Fig. 67: Distribution map of *Dendroligotrichum* (solid lines). *Potridiscus polymorphus* and *Potriphila epiphylla* occur in the whole area of the host genus. *Potridiscus polymorphus* is additionally recorded from southeastern Australia and Tasmania (stippled line).

The second species, *D. squamosum*, is relatively restricted in distribution and is known only from southern South America (especially Fuegia), the Falkland Islands and South Georgia (Fig. 67, D.M. Greene 1986, S.W. Greene 1974, He 1998, Schiavone 1993, Schiavone & Hyvönen 1992, Smith 1971).

Dendroid mosses are generally intolerant of sites in which the humidity becomes low for extended periods (Schofield 1981: 153). They prefer damp and shady sites (Mägdefrau 1969: 294, 1982: 54, Schofield 1985: 318). *Dendroligotrichum dendroides* may grow in dense populations, as indicated by Herzog (1926: 180), Schiavone & Hyvönen (1993) and annotated on several labels. In New Zealand it is mainly

distributed in the upper montane and subalpine *Nothofagus* forest, according to Frey & Beever (1995), who considered genera like *Dendroligotrichum* to be remnants of the Gondwana flora. These mountain plant communities reflect the ecological conditions of Gondwana forests.

### Host selection, specificity and frequency

Altogether 59 collections of *Dendroligotrichum*, 40 of *D. dendroides* and 19 of *D. squamosum*, were identified as infected by one or up to five species of ascomycetes. Sixteen fungal species, including three undetermined species of *Epibryon*, have been recorded as associated with *Dendroligotrichum*. Eleven grow on *D. dendroides* and nine on *D. squamosum* (Table II). Four species have not yet been encountered on other bryophytes. These are: *Bryonectria disciformis*, *Epibryon pulchellum*, *Malvinia endoderma* and *Potriphila epiphylla*. The parasites of the two species of *Dendroligotrichum* are quite different though the hosts occur sympatrically in Fuegia. Excluding undetermined *Epibryon* species, the two host species only share three ascomycetes, *E. interlamellare*, *Potridiscus polymorphus* and *Potriphila epiphylla*. The first two species are also known from various other genera of Polytrichaceae, whereas the frequent and widespread *Potriphila epiphylla* is the only fungal parasite that seems to be restricted to *Dendroligotrichum*, although, admittedly, few austral Polytrichaceae have been checked. Bryomycological evidence shows that these two mosses are probably only distantly related.

Interestingly, the American and New Zealand *D. dendroides* populations harbour a relatively homogeneous set of fungal parasites. Eight named ascomycetes are present within the whole host range (plus three undetermined *Epibryon* species). Four species (*Bryomyces* sp., *Epibryon interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*) occur in both areas. *Epibryon elegantissimum* in southern South America and *E. pulchellum* in New Zealand are only separable by minor spore characters. The two collections of *Lizonia baldinii* from Chile and the few records of *Bryonectria disciformis* from New Zealand do not counterindicate a close relationship between the highly disjunct populations of *D. dendroides*.

Within the range of *Dendroligotrichum* as a whole, only a small number of Polytrichaceae and their parasitic fungi have been studied well enough to allow a comparison. These mosses are *Polytrichadelphus magellanicus* in southern South America, from which nine ascomycetes have been recorded (Döbbeler 2001), *Dawsonia superba* in New Zealand with eight (Döbbeler 1981), and *P. innovans* in New Zealand with only two known ascomycetes (Döbbeler 2001). *Dendroligotrichum dendroides* and *P. magellanicus* share only the ubiquitous *Epibryon interlamellare* and *Potridiscus polymorphus*, the latter being frequent on *D. dendroides* but rare on *Polytrichadelphus magellanicus*. Both parasites also occur on *D. squamosum*, together with *Bryochiton perpusillus*, *Epibryon eremita* and *Potriphila navicularis*, all of which attack *Polytrichadelphus magellanicus*. *Epibryon eremita* is so far known exclusively from *D. squamosum* and *P. magellanicus*. The New Zealand population of *D. dendroides* does not share any parasites with *P. innovans*, and *Dendroligotrichum*



Table II: Ascomycetes on *Dendroligotrichum* and their frequency by number of specimens recorded

on <i>D. dendroides</i>		on <i>D. squamosum</i>	
<i>Bryomyces</i> sp.	8	<i>Bryochiton heliotropicus</i>	1
<i>Bryonectria disciformis</i>	5	<i>Bryochiton perpusillus</i>	1
<i>Epibryon elegantissimum</i>	9	<i>Epibryon eremita</i>	9
<i>Epibryon interlamellare</i>	21	<i>Epibryon interlamellare</i>	9
<i>Epibryon pulchellum</i>	7	<i>Epibryon</i> sp. 1	2
<i>Epibryon</i> sp. 1	1	<i>Malvinia endoderma</i>	2
<i>Epibryon</i> sp. 2	1	<i>Potridiscus polymorphus</i>	11
<i>Epibryon</i> sp. 3	1	<i>Potriphila epiphylla</i>	9
<i>Lizonia baldinii</i>		<i>Potriphila navicularis</i>	8
subsp. <i>dendroligotrichi</i>	2		
<i>Potridiscus polymorphus</i>	32		
<i>Potriphila epiphylla</i>	22		

and *Dawsonia* are colonized by separate groups of fungi except that *E. interlamellare* is recorded on both hosts. It should be noted, however, that *E. pulchellum* on *Dendroligotrichum* and *E. elegantissimum* on *Dawsonia* are closely related.

The diversity of fungal parasites is often concentrated in very small areas, in single collections, single plants or even individual leaves. Five of the six Chilean species growing on *Dendroligotrichum dendroides* are present in collection 6, and five of the seven New Zealand species colonizing this host are found in collection 31. All four species in collection 32 from New Zealand were detected on a single leaf (Fig. 26). Collection 45 yielded five of the six Fuegian species recorded on *D. squamosum*. Three of the four species that occur on the same host in South Georgia were present on a single leaf (collection 56, Fig. 62).

As mentioned previously, Polytrichaceae are excellent hosts. Individual *Dendroligotrichum* plants lacking fungal fruit-bodies do exist, but mature or older plants appear universally to support ascomata of polytrichicolous ascomycetes. A high percentage of the *Dendroligotrichum* specimens in bryological herbaria harbour one or more fertile fungal parasites. On average, around three species are present on a specimen. However, the asymptomatic infections and the sporadic, concealed occurrence of ascomata and pycnidia make study of these fungi time-consuming and difficult.

### Geographical distribution of the ascomycetes on *Dendroligotrichum*

Table III summarizes the known distribution of ascomycetes on both species of *Dendroligotrichum*. *Potridiscus polymorphus* and *Potriphila epiphylla* are recorded in the whole distribution area of the host genus (New Zealand, southern South America,

Table III: Countries and islands in which ascomycetes were recorded on *Dendrologotrichum*

**Chile:**

*Bryomyces* sp.  
*Epibryon elegantissimum*  
*Epibryon eremita*  
*Epibryon interlamellare*  
*Lizonia baldinii*  
     subsp. *dendrologotrichi*  
*Potridiscus polymorphus*  
*Potriphila epiphylla*  
*Potriphila navicularis*

**Juan Fernández Islands:**

*Bryomyces* sp.  
*Epibryon elegantissimum*  
*Epibryon interlamellare*  
*Potridiscus polymorphus*  
*Potriphila epiphylla*

**Argentina:**

*Bryochiton perpusillus*  
*Epibryon elegantissimum*  
*Epibryon eremita*  
*Epibryon interlamellare*  
*Epibryon* sp.  
*Potridiscus polymorphus*  
*Potriphila epiphylla*  
*Potriphila navicularis*

**Falkland Islands:**

*Bryochiton heliotropicus*  
*Epibryon* sp.  
*Malvinia endoderma*  
*Potridiscus polymorphus*  
*Potriphila epiphylla*  
*Potriphila navicularis*

**South Georgia:**

*Epibryon* sp.  
*Potridiscus polymorphus*  
*Potriphila epiphylla*  
*Potriphila navicularis*

**New Zealand:**

*Bryomyces* sp.  
*Bryonectria disciformis*  
*Epibryon interlamellare*  
*Epibryon pulchellum*  
*Epibryon* sp.  
*Potridiscus polymorphus*  
*Potriphila epiphylla*

**Auckland Islands:**

*Epibryon* spp.  
*Potridiscus polymorphus*  
*Potriphila ephipylla*

some islands; Fig. 67). *Epibryon interlamellare* is also very common though not encountered on the (sub)antarctic islands. A special effort was made to detect *Malvinia endoderma* outside of the Falkland Islands. Apart from the 17 *D. squamosum* collections cited, more than 15 collections from Fuegia and South Georgia were carefully screened in vain. Whereas New Zealand and the Fuegian region once formed part of the Gondwana continent, the Auckland Islands, South Georgia and Juan Fernández Islands are of volcanic origin. Mas Afuera is the only island of the Juan Fernández archipelago where *D. dendroides* occurs (Robinson 1975). Radiometric dating reveals the island to be only 1-2.4 million years old, while the other two islands are about 4 and 5.8 million years old (Stuessy et al. 1984). Establishment of host populations within this period by long-range spore dispersal and subsequent infection by airborne ascospores is difficult to imagine, though possible spore sources in continental America are not too distant. Distribution of both partners of the association by movement of whole infected host segments is much easier to envisage. Specialized vegetative propagules are very rare in the Polytrichaceae, and are not known in *Dendrologotrichum*. Plant fragments including individual leaves may, however, serve as diaspores. Fragility of gametophytic structures in the moist and dry condition was repeatedly observed. Mycelia of one or more species may weaken the host's tissue structure and perhaps even facilitate detachment of dispersible fragments. In

*Pogonatum dentatum* (Brid.) Brid., unspecialized vegetative fragments play an important role in dispersal (Hassel 2000). McDaniel & Miller (2000) suggested that reproduction of bryophytes, including Polytrichaceae, by gametophytic fragments may be particularly efficient in arctic and alpine regions. Wyatt & Derda (1997: 268) indicated that members of the Polytrichaceae can easily regenerate from fragments. I presume that long-range dispersal and establishment of moss-fungus associations on volcanic islands has occurred through passive distribution of hyphal-infected fragments.

### Ecological remarks

As far as can be observed in herbarium material, none of the species encountered except *Lizonia baldinii* cause visible symptoms on the host plants. Formation of sporophytes is not impeded. *Lizonia baldinii* is a necrotroph that destroys the growing points and the antheridial cups of male plants. In fresh material an apical necrotic yellowish zone often reveals the presence of the parasite. Young plants are poor hosts and are not worth screening. Only few species are able to form ascomata within the upper green leaves. *Potriphila navicularis* commonly does this, while *P. epiphylla* and *Potridiscus polymorphus* do so rarely. Various species prefer lower older leaves often showing incipient decomposition. Examples are both species of *Bryochiton*, *Epibryon interlamellare* and *Malvinia endoderma*. However, green and young leaves in the upper part, adult ones in the medium part, and older withering leaves in the lower less illuminated part of a branch or plant are not sharply delimited from each other. As stems elongate, these zones also move upwards. It is therefore often difficult to be certain about the substrate type preferred by a given species.

Infections of *Potriphila navicularis* are apparently systemic though this can hardly be proved using microscopic surveys. Hyphae of various fungi within a moss are often difficult to distinguish from one another unless special characters can be seen. Adult Polytrichaceae free of hyphae do not exist. It is possible that systemic infections may spread through the often extensive underground rhizome system by which colonies of *Dendrologotrichum* proliferate. In one of the two *Potriphila epiphylla* collections from the Auckland Islands and in both specimens from South Georgia only pycnidia were present. As was previously seen with *P. navicularis* on *Polytrichastrum alpinum*, extreme environmental conditions favour occurrence of the anamorph alone (Döbbeler 1996). Vitt (1974) indicated that many mosses on Campbell Island (52° S latitude) are small and atypical compared to the more northerly populations. Size reduction may also occur in the parasites of *Dendrologotrichum* growing under extreme environmental conditions.

Bryophilous ascomycetes that are restricted to particular hosts tend to form structures that reflect the ecological conditions in which they and their hosts occur. Comparing the fungal parasites of *Dendrologotrichum* with those of *Radula flaccida* Lindenb. & Gottsche, a rather well-studied epiphyllous hepatic of afro-american tropical lowland rainforests, yields remarkable insights. Perhaps the most typical parasite of *Dendrologotrichum* is *Potriphila epiphylla* with its relatively large, dark and carbonized

ascomata, its many asci and very small, two-celled spores, and its small conidia formed in pycnidia. It is quite different from *Epibryon deceptor* Döbbeler (Döbbeler 1998), one of the most characteristic fungal parasites of *Radula flaccida*. The small, hyaline ascomata of *E. deceptor* contain only few asci with relatively large, six-celled phragmospores. No anamorph is present. The two species diverge strongly in their morphology and in their reproductive strategies. The correlation of morphological characteristics with particular ecological conditions is one of the most exciting aspects of future bryomycological studies.

### Microniches occupied

In *Dendroligotrichum* most of the distinct microniches known among other Polytrichaceae (Döbbeler 1986, 2002) are also specifically occupied by ascomata of niche-adapted species. *Lizonia baldinii* occurs within the antheridial cups of male plants. *Bryochiton heliotropicus* and *B. perpusillus* grow subcuticularly on the abaxial leaf side. Most suitable are the lamellae-bearing adaxial leaf sides. Pycnidia of *Potriphila navicularis* remain completely immersed within the interlamellar spaces but the ascomata are more or less erumpent. *Epibryon interlamellare* may be immersed or superficial. *Potridiscus polymorphus* and *Potriphila epiphylla* develop their ascomata superficially on the leaf lamellae. *Epibryon elegantissimum*, *E. eremita* and *E. pulchellum* are restricted to the transition zone between blade and sheath, or at least to the lower leaf part, whereas *E. interlamellare* prefers the upper leaf half. Fruit-body formation of *Malvinia endoderma* within the abaxial epidermis may be regarded as a new type of microniche, further increasing the high number of microsites offered by polytrichalean leaves (Döbbeler 2002). In comparison to the situation found on other polytrichaceous hosts, remarkably few interlamellar species exist in *Dendroligotrichum*. This may be due to the limited space between the low lamellae in *D. dendroides*. In *D. squamosum* the lamellae form a very dense and compact mesophyll-like structure. It seems that the paired and therefore broadened end-cells efficiently close the interlamellar spaces. Species like *Potriphila neurogena* Döbbeler or *Rogellia nectrioidea* with ascomata immersed within the leaf nerve of *Polytrichadelphus magellanicus* (Döbbeler 1999b, 2001) have not been found in *Dendroligotrichum*. To date, no fungi fruiting on the potentially substrate-rich stems are known in the Polytrichaceae. Whether *Octospora* (Pezizales) species infecting subterranean rhizoids or above-ground parts of mosses are associated with *Dendroligotrichum* should be investigated by field studies. Several operculate discomycetes have been recorded in association with non-polytrichalean mosses in (sub)antarctic regions (Pegler et al. 1980, Schumacher 1986, Olech & Mleczko 2000).

Considering how easy it would be to overlook *Bryochiton heliotropicus*, *Lizonia baldinii*, or *Malvinia endoderma*, one wonders how many additional fungi may exist on *Dendroligotrichum*. More than ten additional species of ascomycetes have been sporadically detected, and on a few occasions also phycophilous species were seen growing on algae covering *Dendroligotrichum* leaves. Material was too scarce, however, for a careful investigation and documentation. To get a more complete idea of the fungi on *Dendroligotrichum* stereomicroscopic further investigation is

needed. Fresh material is desirable to apply Baral's vital taxonomy, which elucidates many features lost in dried specimens and in specimens mounted in reactive solutions (Baral 1992). In field studies, emphasis should be given to necrotic plants. Such plants are underrepresented in bryological herbaria, since bryologists prefer to collect healthy mosses. Most desirable would be bryologically interested mycologists and mycologically interested bryologists: the fungi on mosses and hepatics are excellent taxonomists.

### Host specimens examined and their parasites

(Included are also the specimens 17 and 47 of *Potridiscus polymorphus* reported by Döbbeler & Triebel 2001.)

#### *Dendrologotrichum dendroides* as host

##### Chile

- 1 Prov. de Arauco: West slope of the Cordillera de Nahuelbuta near Curanilahue, Fundo Riquelme, ca. 420 m alt., April 1981, J. Grau (M). - *Epibryon interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 2 Prov. de Arauco: Monumento Natural Contulmo, 130 m alt., 7 May 1998, M. Baeza 1681 (M). - *Bryomyces* sp., *Potridiscus polymorphus*.
- 3 Prov. de Malleco: Parque Nacional de Nahuelbuta, west of Angol, Piedra de Aguila, 12 Jan. 1995, C. Ehrhart (M). - *Epibryon interlamellare*, *Potridiscus polymorphus*.
- 4 Prov. de Valdivia: División Comunal Valdivia, Cuesta Sta. Elvira, ca. 5 km north of Valdivia, northside of the Río Calle Calle, 39°45'60"S, 73°10'W, ca. 200 m alt., 14 April 1998, L. Beenken 926 & C. Hahn (M). - *Epibryon interlamellare*.
- 5 Prov. de Valdivia: Corral, March 1904, C. Scheduling (HBG). - *Epibryon interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 6 Prov. de Valdivia: La Unión, Fundo Catamutún, Dec. 1934, O. Brandt. - *Bryomyces* sp. (HBG, M), *Epibryon interlamellare* (M), *Lizonia baldinii* subsp. *dendrologotrichi* (HBG), *Potridiscus polymorphus* (HBG), *Potriphila epiphylla* (HBG, M).
- 7 Prov. de Valdivia: Cordillera Pelada, road from La Unión to El Mirador, 800 m alt., 12 Dec. 1985, F. Hellwig (M). - *Epibryon interlamellare*, *Lizonia baldinii* subsp. *dendrologotrichi* (holotype), *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 8 Prov. de Valdivia: Road La Unión to Hueicolla, 40°14'21"S, 73°21'20"W, 604 m alt., 3 Feb. 2002, M. Weigend, H. Förther, N. Dostert & K. Weigend 7061 (M). - *Bryomyces* sp., *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 9 Prov. de Valdivia: Fundo Chivío east of Futrono at the Argentinian border, Feb. 1981, J. Grau (M). - *Epibryon elegantissimum*, *E. interlamellare*.
- 10 Prov. de Osorno: Puyehue, National Park, pass at the road Osorno - Bariloche, 1300 m alt., 9 March 1987, E. Albertshofer (M). - *Bryomyces* sp.
- 11 Prov. de Osorno: Volcán Osorno, W slope, path El Solitario, 41°10'26"S, 72°31'01"W, 316 m alt., 4 Feb. 2002, H. Förther (M). - *Bryomyces* sp., *Epibryon elegantissimum*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 12 Prov. de Osorno: Southern foot of the volcano Osorno, road to the Refugio Teski, 400 m alt., 15 Feb. 1999, T. Feuerer (HBG). - *Epibryon interlamellare*, *Potridiscus polymorphus*.
- 13 Prov. de Llanquihue: Los Lagos region, Ensenada at the Llanquihue Lake, 30 Jan. 1961, F. Mattick 1197 (B). - *Epibryon elegantissimum*, *E. interlamellare*, (*Lizonia* sp.), *Potridiscus polymorphus*.

- 14 Prov. de Llanquihue: Southern foot of Cerro Juliet above Ralún, ca. 100 m alt., 18 Feb. 1999, T. Feuerer (HBG). - *Epibryon interlamellare*.
- 15 Prov. de Chiloé: Island Chiloé, 32 km south of Ancud, 28 March 1984, A. Bresinsky & N. Garrido (M). - *Epibryon interlamellare*.
- 16 Prov. de Palena: 22 km southeast of Chaitén on gravel road to Pto Cárdenas, 90 m alt., 8 March 1985, T. Stuessy, J. Furlow, E. Ruiz & N. Bustos 7082 (B). - *Epibryon interlamellare*, *Potriphila epiphylla* (holotype).
- 17 Prov. de Aisén: Carretera Austral in the direction of Puerto Cisnes, ca. 20 km south of Puyuhuapi, 5 March 1997, R. Mues & U. Drehwald (M). - *Epibryon interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 18 Prov. de Aisén: Puerto Aisén, west of the village, 19 March 1984, A. Bresinsky & N. Garrido (M). - *Epibryon interlamellare*.
- 19 Prov. de Aisén: Quitalco, southwest of Puerto Aisén, ca. 20 m alt., 3 Jan. 1995, C. Ehrhart (M). - *Epibryon elegantissimum*, *E. interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 20 Prov. de Capitán Prat: Chacabuco, south-southeast of the village, 26 March 1984, A. Bresinsky & N. Garrido (M). - *Bryomyces* sp., *Epibryon elegantissimum*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 21 Prov. de Magallanes: Brunswick Peninsula, Puerto Cutter, stream in ravine at base of Monte Condor, 26 Dec. 1967, J.J. Engel 2328 (MSC). - *Potridiscus polymorphus*.

#### Juan Fernández Islands

- 22 Mas Afuera: 3000 ft alt., Nov. 1965, H. Robinson (MSC; Bryophytes of the Juan Fernández Islands 791). - *Epibryon elegantissimum*.
- 23 Mas Afuera: Near Camp Correspondencia, ca. 3800 ft alt., 4 Dec. 1965, R. Hatcher & J. Engel (Bryophytes of the Juan Fernández Islands 121). - *Epibryon interlamellare* (AAS), *Potridiscus polymorphus* (AAS), *Potriphila epiphylla* (AAS, MSC).
- 24 Mas Afuera: Near Camp Correspondencia, ca. 3800 ft alt., 4 Dec. 1965, R. Hatcher & J. Engel (MSC; Bryophytes of the Juan Fernández Islands 118). - *Bryomyces* sp., *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 25 Mas Afuera: Near Camp Correspondencia, ca. 3800 ft alt., 4 Dec. 1965, R. Hatcher & J. Engel (MSC; Bryophytes of the Juan Fernández Islands 429). - *Epibryon elegantissimum*, *Potridiscus polymorphus*.

#### Argentina

- 26 Prov. de Río Negro, Dep. Bariloche, Puerto Blest - Puerto Alegre (Lago Frias), 820 m alt., 13 Jan. 1951, H. Sleumer 1687 (B). - *Epibryon elegantissimum*, *Epibryon* sp. 2, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 27 Prov. de Tierra del Fuego, Bahía Buen Suceso, Monte Noroeste, 54°47'S, 65°17'W, 25 Jan. 1986, Matteri-Schiavone (M ex herb. Frahm; Musci Fueg. Exs. 2, sub *D. dendroides*). - *Epibryon elegantissimum*, *E. interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.

#### New Zealand

- 28 North Island: Mt Manuoha, near Lake Waikaremoana, ca. 3000 ft alt., Jan. 1948, G.F. Jardine & G.O.K. Sainsbury (B). - *Epibryon interlamellare*, *E. pulchellum*, *Potridiscus polymorphus*, *Potriphila epiphylla*.

- 29 North Island: Gisborn district, Lake Waikaremoana, along road from Taupeupe Saddle to Maungapohatu, ca. 1000 m alt., 4 Sept. 1968, B.O. van Zanten 681986 (B). - *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 30 North Island: Tongariro National Park, *Nothofagus*-forest below the Château, 1 Nov. 1981, R. Mues (M). - *Bryonectria disciformis* (ascomata and pycnidia), *Epibryon pulchellum*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 31 North Island: Mt Ruapehu, *Nothofagus cliffortia*-forest near 'The Chalet', 3700 ft alt., 7 March 1959, H. & E. Walter (M). - *Bryonectria disciformis* (only pycnidia), *Epibryon interlamellare*, *E. pulchellum*, *Potridiscus polymorphus*, *Potriphila epiphylla* (only pycnidia).
- 32 North Island: Mt Egmont, 3000-4000 ft alt., Aug. 1929, A. Meebold (M). - *Bryomyces* sp., *Epibryon interlamellare*, *E. pulchellum* (holotype), *Potridiscus polymorphus*.
- 33 South Island: Subalpine bog and *Nothofagus* forest along Route 7, 0-4 mi west of Rahu Summit (5.3 miles west of Springs Junction), 42°25'S, 172°10'E, 2200 ft alt., 3 Dec. 1972, D.H. Vitt 8380 (B). - *Epibryon pulchellum*, *Epibryon* sp. 1, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 34 South Island: Arthur Valley, ca. 280 m alt., 23 Feb. 1914, R. Endlich 145 (HBG). - *Bryonectria disciformis* (only pycnidia), *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 35 South Island (Insula australis): Martin's Bay, 1874, Capt. Hutton (HBG). - *Potridiscus polymorphus*.
- 36 South Island: Diamond Lake, Jan. 1892, W. Bell (M). - *Epibryon interlamellare*, *E. pulchellum*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 37 South Island: Tutoko Valley, Darran Mountains, Fiordland National Park, ca. 150 m alt., 44°39'S, 167°58'E, 8 Feb. 1981, M. Priester (B). - *Bryonectria disciformis* (only ascomata), *Potridiscus polymorphus*.
- 38 South Island: Otago, Fiordland National Park, Tutoko River Track east of Milford Sound, 44°39'S, 167°58'E, 20-150 m alt., 7 Feb. 1985, H. Mayrhofer 5753 & H. Hertel (GZU). - *Bryonectria disciformis* (holotype, only ascomata), *Potridiscus polymorphus*.
- 39 South Island: West Otago, Doubtful Sound Crack, 2000 ft alt., Feb. 1952, W. Martin (M). - *Epibryon pulchellum*, *Potridiscus polymorphus*.

#### Auckland Islands

- 40 Auckland Island: Mt Raynal, 2114 ft alt., 2 Jan. 1973, D.H. Vitt 9869 (MSC). - *Epibryon* sp. 3, *Potridiscus polymorphus*, *Potriphila epiphylla* (only pycnidia). - A second collection from MSC with identical data on the label but a different collecting number (D.H. Vitt 9872) harbours the same association of ascomycetes. *Potriphila epiphylla* forms very few apothecia apart from many pycnidia. *Epibryon* is poorly developed. Spores, only found once, are smaller than those of *Epibryon* sp. 3. Both host collections are cited by Vitt (1979).

#### *Dendrologotrichum squamosum* as host

##### Chile

- 41 Prov. de Última Esperanza: Patagonian Channels, low treeless island near glacier at head of Fiordo Peel, 50°57'S, 73°47'W, 1 Oct. 1969, J.J. Engel 5452B (MSC). - *Potriphila navicularis*.
- 42 Prov. de Última Esperanza: Western side of Puerto Toro, 51°25'S 73°06'W, 15 Jan. 1977, C.M. Matteri (AAS; Transecta Botánica de Patagonia Austral B2335). - *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 43 Prov. de Última Esperanza: Monte Alto, Rubens, 8 April 1975, E. Pisano V. 4485 (AAS). - *Epibryon eremita*, *E. interlamellare*.

- 44 Prov. de Magallanes: Brunswick Peninsula, Punta Arenas, 8 km west of Punta Arenas, 1000-2000 ft alt., 19 Dec. 1967, J.J. Engel 1971 (MSC). - *Epibryon eremita*, *E. interlamellare*, *Potriphila epiphylla* (only pycnidia).
- 45 Prov. de Tierra del Fuego: Fuegia media, Estancia Camerón, Puesto Medio, 13 Dec. 1928, H. Roivainen (AAS; Bryoph. Fueg. 1882, sub *D. squamosum*). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*, *P. navicularis*.

### Argentina

- 46 Prov. de Tierra del Fuego: Ushuaia, valley of the river Pipo, 54°46'S, 68°20'W, ca. 400 m alt., 24 Dec. 1969, H. Roivainen (B; Plantae Argentinae 1355, sub *D. dendroides*). - *Bryochiton perpusillus*, *Epibryon interlamellare*, *Potridiscus polymorphus*, *Potriphila navicularis*.
- 47 Prov. de Tierra del Fuego: 30 km east of Ushuaia, road to Paso Garibaldi, ca. 190 m alt., 27 March 1997, R. Mues & U. Drehwald (M). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 48 Prov. de Tierra del Fuego: Ruta Nacional 3, 30 km east of Ushuaia, 190 m alt., 22 March 1997, U. Drehwald 970079 (M). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*.
- 49 Prov. de Tierra del Fuego: Parque Nacional Tierra del Fuego, path to the viewpoint, 20 Feb. 1987, U. Drehwald P 177 (M). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*.
- 50 Prov. de Tierra del Fuego: Dep. Ushuaia, Cascada del Río Pipo, 8 km southeast of Ushuaia, 20 Feb. 1984, Matteri-Schiavone, (M ex herb. Frahm; Musci Fueg. Exs. s.n., sub *D. squamosum*). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*.
- 51 Prov. de Tierra del Fuego: Ruta Nacional 3, Paso Garibaldi, ca. 400-480 m alt., 18 Feb. 1986, U. Drehwald P46 (M). - *Epibryon eremita*, *E. interlamellare*, *Potridiscus polymorphus*, *Potriphila epiphylla*.
- 52 Prov. de Tierra del Fuego: Lago Escondido, Refugio, 54°40'S, 67°53'W, ca. 120 m alt., 2 Dec. 1969, C. Matteri (Plantae Argentinae 686, sub *D. dendroides*). - *Potridiscus polymorphus* (B), *Potriphila navicularis* (B, MSC).
- 53 Prov. de Tierra del Fuego: E side of Paso Garibaldi, Sierra Lucas Bridges, 54°42'S, 67°45'W, 550 m alt., 27 Nov. 1971, G. Crow 1749 (MSC). - *Epibryon eremita*, *Potriphila epiphylla*, *P. navicularis* (only pycnidia).

### Falkland Islands

- 54 West Falklands: Mt Adam, Cliffs on east side of summit ridge, 2200-2297 ft alt., 25 Jan. 1968, J.J. Engel 3016A. - *Epibryon* sp. 1 (B), *Malvinia endoderma* (B, holotype; AAS, MSC, isotypes), *Potridiscus polymorphus* (AAS, B, MSC), *Potriphila epiphylla* (AAS, B, MSC).
- 55 East Falklands: Mt Osborne summit area, 750 m alt., 3 Feb. 1985, R.I.L. Smith 5445 (AAS). - *Bryochiton heliotropicus*, *Malvinia endoderma*, *Potriphila navicularis*.

### South Georgia

- 56 East side of Undine Harbour, 3 April 1970, E.P. Wright (AAS). - *Potridiscus polymorphus*, *Potriphila epiphylla* (only pycnidia), *P. navicularis* (only pycnidia).
- 57 Behind beach at Bore, ca. 250 ft alt., 5 Jan. 1974, D.W.H. Walton (AAS). - *Potriphila navicularis*.
- 58 Area to south of Shallop Cove, 20-25 ft alt., 30 Dec. 1970, R.I.L. Smith 1222 (AAS). - *Potriphila epiphylla* (only pycnidia).
- 59 South of Henningsen Glacier, 31 Dec. 1972, C.J. Barrow (AAS). - *Epibryon* sp. 1.



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