

## A phylogenetic analysis of the lichen family *Sphaerophoraceae* (*Caliciales*); a new generic classification and notes on character evolution

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**Abstract:** A phylogenetic analysis of the family *Sphaerophoraceae* (*Caliciales*, lichenized ascomycetes) has resulted in a new generic classification. Notes on character evolution are given. The genera *Sphaerophorus* s. str., *Bunodophoron* and *Leifidium*, gen. nov., are accepted. *Pleurocybe* and *Pseudosphaerophorus* are considered synonyms of *Bunodophoron* and *Thysanophoron* is considered synonym of *Sphaerophorus*. The following new combinations are proposed: *Bunodophoron coomerense* (OHLSSON) WEDIN, *B. diplotypum* (VAIN.) WEDIN, *B. dodgei* (OHLSSON) WEDIN, *B. flaccidum* (KANTVILAS & WEDIN) WEDIN, *B. formosanum* (Z AHLBR.) WEDIN, *B. imshaugii* (OHLSSON) WEDIN, *B. insigne* (LAURER) WEDIN, *B. kinabaluense* (M. SATŌ) WEDIN, *B. macrocarpum* (OHLSSON) WEDIN, *B. madagascareum* (NYL.) WEDIN, *B. microsporum* (OHLSSON) WEDIN, *B. murrayi* (OHLSSON) WEDIN, *B. notatum* (TIBELL) WEDIN, *B. ohlssonii* (WEDIN) WEDIN, *B. patagonicum* (C. W. DODGE) WEDIN, *B. ramuliferum* (I. M. LAMB) WEDIN, *B. scrobiculatum* (C. BAB.) WEDIN, *B. tibellii* (WEDIN) WEDIN, *B. whakapapaense* (WEDIN) WEDIN, and *Leifidium tenerum* (LAURER) WEDIN.

The classification of the family *Sphaerophoraceae* (*Caliciales*, lichenized ascomycetes) has varied considerably. Although the family was recircumscribed and reclassified fairly recently (OHLSSON in TIBELL 1984), this was based on a ten year-old phenetic analysis, and the phylogenetic interrelationships of the family have remained unknown. A more natural classification, based on a hypothesis on the phylogeny of the family, is highly desirable and would enable discussions on the evolution of characters and species. It could also contribute towards a better understanding of the biogeographic history of the Southern Hemisphere, as several species show a disjunct distribution and occur in the *Nothofagus* forests of southernmost South America and Australia-New Zealand.

The present paper proposes a revised generic classification of the *Sphaerophoraceae*, based on a preliminary phylogenetic analysis. The analysis is “preliminary” in the sense that several problematic species-groups are not yet fully understood and that quite a number of species, particularly from the tropics, still remain to be investigated and described.

*Sphaerophoraceae* is presently classified in the order *Caliciales*, where originally all lichens with a mazaedium were placed. According to TIBELL (1984), *Caliciales* is not a monophyletic group but a heterogeneous assembly of families which have independently achieved passive spore dispersal. The families *Mycocaliciaceae*, *Sphinctrinaceae*, and *Caliciaceae* were suggested to form a monophyletic group. TIBELL (1984) used the family rank to distinguish presumably monophyletic groups with unknown relationships to other ascomycetes, but left several genera without family designation. He indicated that some genera of tropical *Caliciales* shared similarities with certain pyrenomycetes, and subsequent authors (HARRIS 1989, APTROOT 1991) have included in these in *Pyrenulaceae*. TIBELL (1984) considered *Sphaerophoraceae* not to be closely related to other families in *Caliciales*, including *Calycidiaceae*. In the present paper, however, *Calycidiaceae* is postulated to be the sister taxon to *Sphaerophoraceae*.

**Review of earlier classifications.** *Lichen fragilis* LINNAEUS (1753) is the only species today classified in the family *Sphaerophoraceae* to be found in Species Plantarum. Other species described in the mid-18th century include *Lichen globosus* HUDSON (1762) and *L. globiferus* LINNAEUS (1767). NECKER (1771) included *Lichen globiferus* (and  $\beta$ -*fragilis*) in the class *Musci*, ordo *Frondescentes*, together with liverworts and algae. Later, NECKER (1790) proposed the name *Syrigosis* as a "species naturalis" with diagnosing characters referring to two illustrations, representing one *Roccella* and one *Sphaerophorus* species. NECKER's "species naturalis" are to be treated as unitary designations according to Art. 20.4 (GREUTER & al. 1988) and are not validly published generic names. *Syrigosis* was not validated by KREMPELHUBER (1869) as cited by STAFLEU (in FARR & al. 1979) and accepted by ERIKSSON & HAWKSWORTH (1991) in their list of synonyms of *Sphaerophorus*. ERIKSSON & HAWKSWORTH also cited *Baeoderma* VAINIO (1922) among the synonyms on the bases of information from OHLSSON (see HAWKSWORTH & al. 1983: 305) but his is an error by ZAHLBRUCKNER (1932) corrected by JAHNS & V. D. KNAPP (1973). *Sphaerophorus* was conserved against *Syrigosis* (SPECIAL COMMITTEE FOR LICHENS 1954) but as *Syrigosis* is not validly published, this conservation is unnecessary and the rejected name has thus been omitted from later editions of the list of nomina generica conservanda et rejicienda (GREUTER & al. 1988). Instead, *Sphaerophorus* is conserved with *S. coralloides* PERS. as conserved type species.

HUMBOLDT (1793) included *Lichen fragilis* L. in *Verrucaria* which together with *Peltigera*, *Lichen*, *Opegrapha*, and *Lepra* constituted the *Algae*.

In Vol 2, fasc. 2 of his *Plantae Lichenosae* (1792), HOFFMAN included *Lichen globiferus* L. and *L. fragilis* L. in *Coralloides* HOFFM. When HOFFMAN (1789) originally described *Coralloides* in the first fascicle of the first volume of the same work, however, the only species included were *Coralloides paschale* (*Lichen paschalis*) L. and *C. aculeatum*. Thus *Coralloides* HOFFM. can not be listed among the synonyms of *Sphaerophorus*. *Coralloides* HOFFM. is a superfluous name antedated by *Coralloides* WOLF (1776) (= *Cladonia*). HOFFMAN later (1796) included *Lichen globiferus* L. in *Stereocaulon*.

The genus *Sphaerophorus* PERSOON (1794 a) included *S. fragilis* and *S. coralloides*, the latter name a nomenclatural synonym of *Lichen globiferus* L. The genus was characterized by the globose fruits, containing a black, powdery mass of "seeds". PERSOON (1794 a) classified *Sphaerophorus*, together with *Endocarpon*,

*Verrucaria*, and *Opegrapha* in his *Familia tertia*, which was characterized by closed fruitbodies. Later the same year PERSEON (1794 b) suggested that the gender of the name should be neuter, to conform to the spelling of other plant genera, and changed the spelling to *Sphaerophorum*. ACHARIUS (1803), finally, changed the name to *Sphaerophoron*, replacing the Latin neuter ending with a Greek one. As the genus was first validly published as *Sphaerophorus*, this is the spelling that must

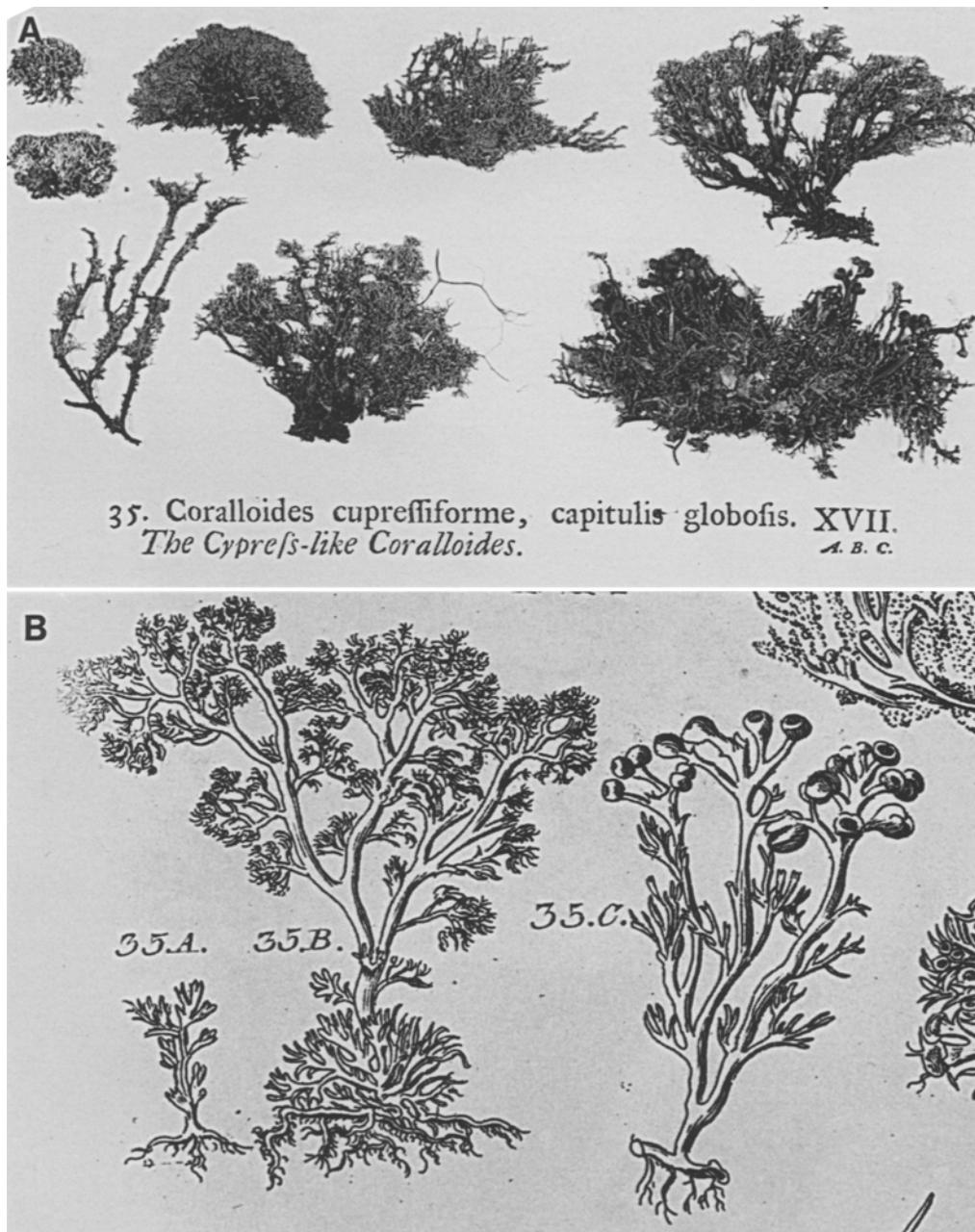


Fig. 1. *Sphaerophorus globosus*. A Material of “*Coralloides cupressiforme* . . .” in Herbarium DILLENII. B Illustration XVII: 35 from *Historia Muscorum*. 35 c is designated lectotype of *Lichen globosus* HUDS.

be used, and the neuter spellings should be treated as orthographic variants according to Art. 75 (GREUTER & al. 1988). Species names published with neuter spellings should be treated as if they were correctly (masculinum) spelled when

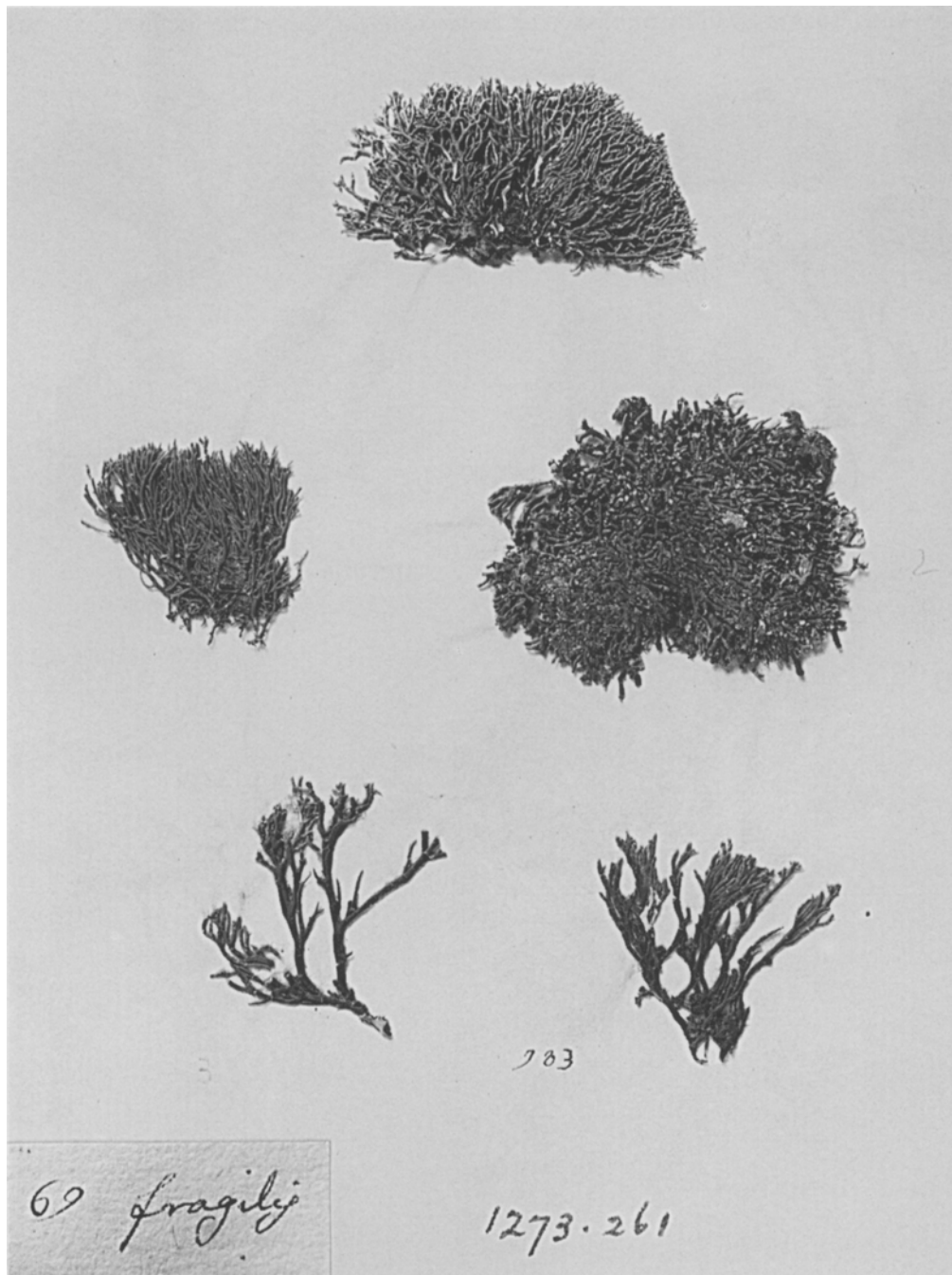


Fig. 2. *Sphaerophorus fragilis*. Sheet 1273: 261 from the LINNAEAN Herbarium. The uppermost specimen is designated lectotype of *Lichen fragilis* L. Inserted is LINNAEUS' annotation, found further down on the sheet

published (Art. 75.3), making all combinations from “*Sphaerophoron* ACH.” and “*Sphaerophorum* SCHRAD.” (never intended as new genera by their authors!) to *Sphaerophorus* superfluous.

LAURER (1827) described several new lichens from Australia, collected by the Austrian F. W. SIEBER during his stay in the vicinity of Sydney 1823. Among these were three species placed in *Sphaerophorus*; *S. australis*, *S. insignis*, and *S. tener*.

MASSALONGO (1861) introduced the genus *Bunodophoron* for species with a compressed thallus. He included *Sphaerophorus australis* LAURER, *S. compressus* ACH., and *S. insignis* LAURER in his new genus, but failed to make more combinations than *Bunodophoron australe*.

STIRTON (1883) described the genus *Thysanophoron* and considered the only species, *T. pinkertonii*, to be intermediate between *Sphaerophorus* and *Stereocaulon* due to the presence of cephalodia. Whether *Thysanophoron* should be regarded as a genus distinct from *Sphaerophorus* has been a frequent matter for conjecture.

FORSELL (1883) in his studies on cephalodia investigated the isotype of *Thysanophoron pinkertonii* in Uppsala and identified it as *Sphaerophorus stereocauloides* NYL. (NYLANDER 1869), a view supported by DU RIETZ (1925) who synonymized the two species.

The genus *Pleurocybe* described by MÜLLER ARGOVIENSIS (1884) was characterized by the hollow thallus and lateral apothecia. *Pleurocybe* was originally monotypic (*Pleurocybe hildenbrandtii* MÜLL. ARG.) and the only additional species described is *P. patagonica* C. W. DODGE (1966). The placement of this species in *Pleurocybe* is problematic, and DODGE (1966) gives no information on why he placed his species in this genus.

ZAHLBRUCKNER (1903) accepted five genera in the family *Sphaerophoraceae*; *Tholurna*, *Calycidium*, *Pleurocybe*, and *Sphaerophorus*. ZAHLBRUCKNER (1922) retained *Thysanophoron* but listed it as a “genus incertae sedis”. In 1932 ZAHLBRUCKNER listed *Thysanophoron* as a synonym of *Sphaerophorus*.

RÄSÄNEN (1943) accepted three genera in *Sphaerophoraceae*; *Sphaerophorus*, *Acroscyphus*, and *Pleurocybe*. *Thysanophoron* was listed as a synonym of *Sphaerophorus*. *Tholurna* and *Calycidium* were transferred to *Tholurnaceae*.

CHOISY (1957) listed *Sphaerophorus*, *Acroscyphus*, and *Pleurocybe* in *Sphaerophoraceae* which, together with *Tholurnaceae* and “*Caliciaceae*” (*Calycidium*), were classified in *Sphérophorales* in the *Protolichens* and not together with other lichens having a mazaedium.

MURRAY (1960), in his bewildering treatment of the New Zealand *Coniocarpineae*, included *Calycidium cuneatum* in *Sphaerophorus*.

SATŌ (1966), who explicitly stated that cephalodia are an essential generic character, combined *Sphaerophorus stereocauloides* in *Thysanophoron*. Later SATŌ (1967) described the monotypic genus *Pseudosphaerophorus*, characterized by laminal apothecia and 2-celled spores. OHLSSON (1973) pointed out that SATŌ’s spore observations were incorrect and included the single species in *Sphaerophorus* (in TIBELL 1987).

HENSSEN & JAHNS (1973) accepted *Calycidium*, *Pleurocybe*, and *Sphaerophorus* in *Sphaerophoraceae*. The family was characterized by the highly differentiated fruticose or foliose thallus and by the raised hemispherical columella.

POELT (1974) included *Calycidium* in *Sphaerophorus* but accepted *Pleurocybe*, *Pseudosphaerophorus*, and *Thysanophoron*, together with *Acroscyphus* in the family.

He stated that the family was not homogeneous as currently circumscribed and considered *Acroscyphus* to be strongly isolated and *Pleurocybe* also quite different from the other three genera.

The most complete treatise was OHLSSON (1973) in his unpublished thesis, where he revised the family on a world-wide basis. OHLSSON (1973) synonymized *Thysanophoron*, *Bunodophoron*, *Pleurocybe*, and *Pseudosphaerophorus* with *Sphaerophorus* and excluded *Calycidium*, *Acroscyphus*, and *Tholurna* from the family *Sphaerophoraceae*. He also subdivided *Sphaerophorus* in four subgenera, validated by TIBELL (1984). OHLSSON's (1973) subgenera do, to a large extent, correspond to the groups here given generic rank. HALE (1983) followed OHLSSON (1973), recognizing only *Sphaerophorus* in the family.

GALLOWAY (1985) argued that cephalodia and the distinct holdfast were sufficient to retain *Thysanophoron* distinct from *Sphaerophorus*. GALLOWAY (1985) was, in my opinion, correct in his assertion that this species is very distinct from the other species present in New Zealand. In the present work it is treated in *Sphaerophorus* s. str. It is, in fact, the only member of this genus present in Australasia.

### Material and methods

The study is based on my own collections and on herbarium specimens in AK, ANUC, BM, CBG, CHR, FH, GZU, H, HO, LINN, MEL, MSC, NSW, OXF, S, UPS, US, and W. Field studies have been carried out in Scandinavia, in Chile and Argentina (1989), New Zealand and Australia (1990, 1992), and Hawaii (1989). The 27 now accepted species of *Sphaerophoraceae*, including three undescribed, fairly well-investigated species, are included in the analysis.

**Parsimony analysis.** The data matrix (Table 1) was analysed by parsimony analysis using the program Hennig 86 version 1.5 (FARRIS 1988) with the options "mhennig\*" and "bb\*" specified. Fitch parsimony (all multistate characters treated as unordered) was preferred as no a priori assumptions on the direction of evolution is included in the analysis, following the discussion in HAUSER & PRESCH (1991).

Character polarizations were determined by outgroup comparison using *Calycidium cuneatum* (the monotypic family *Calycidiaceae*) as outgroup, as this is the only species presently known with some similarities with the *Sphaerophoraceae*. *Calycidium cuneatum* is in gross morphology similar to the more flattened *Bunodophoron*-species, and one chemotype has sphaerophorin (WEDIN, unpubl.). Other genera suggested as possible relatives in the literature (e.g., *Tholurna*, *Acroscyphus*) have been shown to be members of *Caliciaceae* (TIBELL 1984).

Autapomorphies, and synapomorphies for the ingroup, were deactivated in the analysis (with the exception of some multistate characters), but are indicated on the cladogram in Fig. 6. Successive weighting of characters (FARRIS 1969) with subsequent analyses in order to choose among equally parsimonious cladograms (CARPENTER 1988) was also performed. A strict consensus tree was calculated from the original most parsimonious cladograms using the nelsen command.

### Characters used in and considered for the matrix

**Thallus morphology.** The fruticose and foliose concepts are not always easy to apply to some species in *Sphaerophorus* and *Bunodophoron*. The thalli (CHAR 1) of *Sphaerophorus* s. str. (Figs. 1, 2) and *Leifidium tenerum* (Fig. 3 C) are as a rule radially symmetric, but in *Sphaerophorus stereocauloides* and in some populations of *S. globosus* in British Columbia,

Table 1. Character matrix used to construct the cladogram in Fig. 6. – Variability, ? unknown character states

	5	10	15	20	25	29
<i>Calycidium cuneatum</i>	000000000		0000000??–		0000?0000	
<i>Sphaerophorus globosus</i>	201000001		1111101000		010000001	
<i>S. fragilis</i>	200000001		1111101100		010000000	
<i>S. stereocauloides</i>	1010010001		1111101000		000000001	
<i>Leifidium tenerum</i>	2000101000		1100011000		000–00000	
<i>Bunodophoron diplotypum</i>	1100000–00		1100011210		00100?010	
<i>B. madagascareum</i>	110000?200		1100011??0		0010010?0	
<i>B. dodgei</i>	1001000100		1100011310		000001010	
<i>B. formosanum</i>	100100?100		1100011210		00100?0?0	
<i>B. australe</i>	1000000100		1100011210		–01001010	
<i>B. microsporum</i>	100000?–00		1100011210		000101000	
<i>B. kinabaluense</i>	100100?100		1100011210		0010010?0	
<i>B. ramuliferum</i>	1010000101		1101011110		10–001010	
<i>B. whakapapaense</i>	1000000–00		1100011110		1010010?0	
<i>B. notatum</i>	200000?111		1102021211		101000110	
<i>B. macrocarpum</i>	–00000?111		1101021210		101000010	
<i>B. scrobiculatum</i>	000000?211		11020–1211		100100110	
<i>B. ohlssonii</i>	1000000110		1102021200		0010000?0	
<i>B. patagonicum</i>	0000000200		1102021121		000010000	
<i>B. murrayi</i>	0000000200		1102021111		000110000	
<i>B. flaccidum</i>	0000000200		1102021121		000110000	
<i>B. insigne</i>	00000002–2		1102021??0		000110000	
<i>B. tibellii</i>	0000000212		1102021120		000110000	
<i>B. imshaugi</i>	000000?110		11000–1110		000110000	
<i>B. coomerense</i>	100000?1?0		1?00021??0		?00110000	
<i>B. spec. A</i>	100000?110		110?011??0		00100??0?	
<i>B. spec. B</i>	000000?210		11020211–0		000110000	
<i>B. spec. C</i>	000000?2–2		110?021??0		000110000	

there is a tendency of the algae to aggregate on one side of the thallus and for the branches of lower order to branch in one plane. In *Bunodophoron* (Fig. 3 A, B), the thalli are more or less flattened in all species except *B. notatum* and (as a rule) *B. ramuliferum*. In *B. macrocarpum*, the branches carrying apothecia are commonly terete but develop from a foliose basal thallus. Several species of *Bunodophoron* and *Calycidium cuneatum* have a clearly foliose growth form with the algal layer restricted to the upper side of the thalli.

Some variation in branching pattern can be distinguished. Three species of *Bunodophoron* have the same type of palmate branching from the base of the thallus (CHAR 4). This is a character that should be investigated further.

**Cortex.** The cortex (CHAR 5) is composed of thick-walled, gelatinized, fused hyphae covered by a thin epicortex in all species. The cortex thickness of *Sphaerophorus* varies between c. 60–200 µm. In *Bunodophoron*, the cortex (the upper cortex in species with a prominently dorsiventrally flattened thallus) is between 45–130 µm. *Bunodophoron diplotypum*, *B. dodgei*, *B. formosanum*, *B. madagascareum*, *B. microsporum*, and *B. murrayi* have a thinner cortex (ca. 45–80 µm) and the rest of the species have a cortex thickness between 60–130 µm. *Leifidium tenerum* has a remarkably thin cortex, only 30–45 µm thick. The

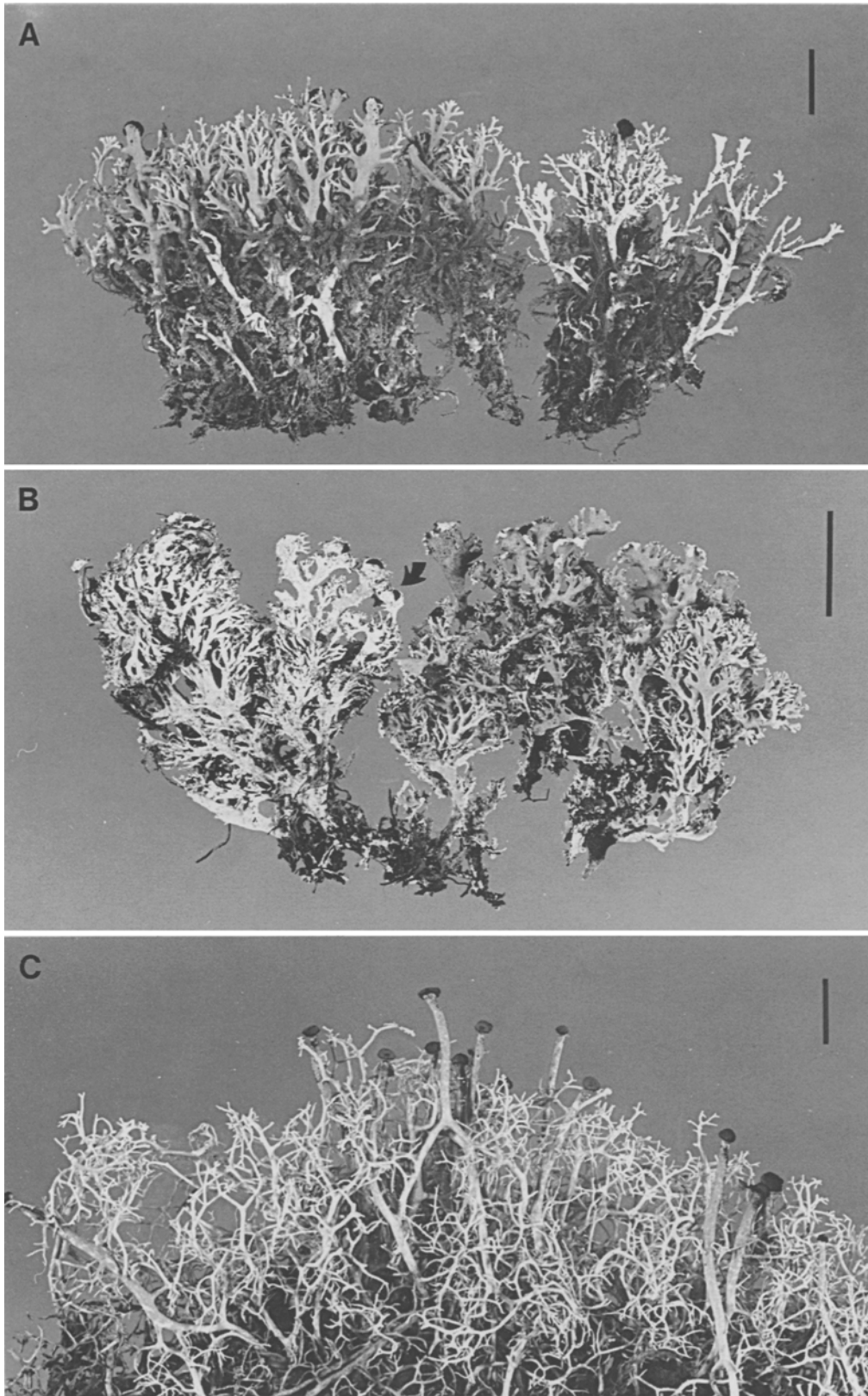


Fig. 3. *A* *Bunodophoron australe*. WEDIN 2736. *B* *Bunodophoron insigne*. Note the crack-like rupturing of thalline receptacle (arrow). WEDIN 2997. *C* *Leifidium tenerum*. WEDIN 2857. All specimens in UPS. Bar: *A-B*: 10 mm, *C*: 5 mm



Table 2. Character descriptions. The numbers correspond to those in Table 1

Nr	Character	Plesiomorphy (0)	Apomorphies (1–3)
1.	Thallus	broadly flattened	narrowly flattened (1); terete (2)
2.	Thallus	solid	hollow
3.	Branchlets	non-coralloid	coralloid
4.	Branching	other	palmately
5.	Cortex	thick (45–200 $\mu\text{m}$ )	thin (35–45 $\mu\text{m}$ )
6.	Cephalodia	absent	present
7.	Exipulum	disintegrating	persisting
8.	Mazaedia	apically exposed	subapically (1); ventrally (2)
9.	Ascoma base	smooth	wrinkled
10.	Receptacle	missing	globose/hemisphaerical (1); veil-like (2)
11.	Asci	clavate	cylindrical
12.	Spore wall	pigmented	non-pigmented
13.	Spores	globose	ellipsoidal
14.	Spore size	4–9 $\mu\text{m}$	9–12 $\mu\text{m}$ (1); 10–21 $\mu\text{m}$ (2)
15.	Ornamentation 1	missing	present
16.	Ornamentation 2	missing	grey (1); brown (2)
17.	Paraphyses	non-carbonized	carbonized
18.	Conidia	3–3.5 $\mu\text{m}$	3.5–4.5 $\mu\text{m}$ (1); 4–5.5 $\mu\text{m}$ (2); 5.5–8 $\mu\text{m}$ (3)
19.	Conidia	ellipsoidal	rodshaped (1); rodshaped with thick ends (2)
20.	Sphaerophorin	present	absent
21.	Isousnic	absent	present
22.	Thamn/squamatic	absent	present
23.	Stictic-complex	absent	present
24.	Protocetraric	absent	present
25.	“Blue”	absent	present
26.	Blue pigment	absent	present
27.	“Notatus”	absent	present
28.	“Apothecium”	absent	present
29.	Medulla	I-	I+ violet

cortex in *Calycidium cuneatum* is 55–65  $\mu\text{m}$  thick. Even if this character to some extent is correlated with taxonomic groupings, it varies considerably within species and show a great overlap between species. This has made it very difficult to divide the size-ranges in discrete entities to be used in the matrix. I have consequently only used this character to show that *Leifidium tenerum* has a significantly thinner cortex than all other species.

**Medulla.** The medulla is composed of longitudinally arranged thick-walled hyphae in all species. In *Bunodophoron diplotypum* and *B. madagascareum* the medulla is more or less replaced by a cavity, making the thallus hollow (CHAR 2). The medulla in *Sphaerophorus globosus* and *S. stereocauloides* is I+ violet-blue (CHAR 29).

**Photobionts.** A detailed study of the photobionts of *Sphaerophoraceae* and *Calycidium* has not been performed by myself. Cephalodia (CHAR 6) containing *Scytonema* occur as bundles of small, sausage-like structures in *Sphaerophorus stereocauloides*. They have also been reported from *Sphaerophorus yangii* (most probably a *Bunodophoron* species) by WANG-YANG & LAI (1976) but this has not been confirmed by me, as material of this species has not been available for study.

**Asexual propagules.** Soredia do not occur in any of the species studied. True isidia (easily breakable outgrowths) probably do not occur either, but several species have branches, or bundles of coralloid branchlets (CHAR 3), that are brittle in the dry state and that might function as vegetative propagules despite their comparatively large size. In several species small outgrowths similar to phyllidia have been observed in connection with damaged parts of the thalli. These structures may be the "isidia" erroneously reported by OHLSSON (1973) and TIBELL (1987) in *B. microsporum*. In some tropical species, for example *B. coomerense* and *B. formosanum*, short, blunt outgrowths occur more or less regularly on the upper side of the thallus. These outgrowths are probably not easily detached in nature and their function is unknown, but they might possibly serve as condensation points for mist. Fragmentation is probably important for the dispersal of terricolous species, e.g., *Sphaerophorus fragilis*, *S. globosus*, and possibly also *Leifidium tenerum*. Otherwise, fragmentation is not believed to be of any major importance. Asexual reproduction is not considered important in the group.

**Ascomata.** The ascomata are apothecioid and are regularly produced by all species in favourable habitats. Most species produce ascomata abundantly and some species, e.g., *Bunodophoron scrobiculatum* and *B. macrocarpum*, have very large and conspicuous fruit-bodies. Several species have wrinkles or raised ridges around the ascoma base (CHAR 9). This is very pronounced in *B. scrobiculatum*, and has given the species its name.

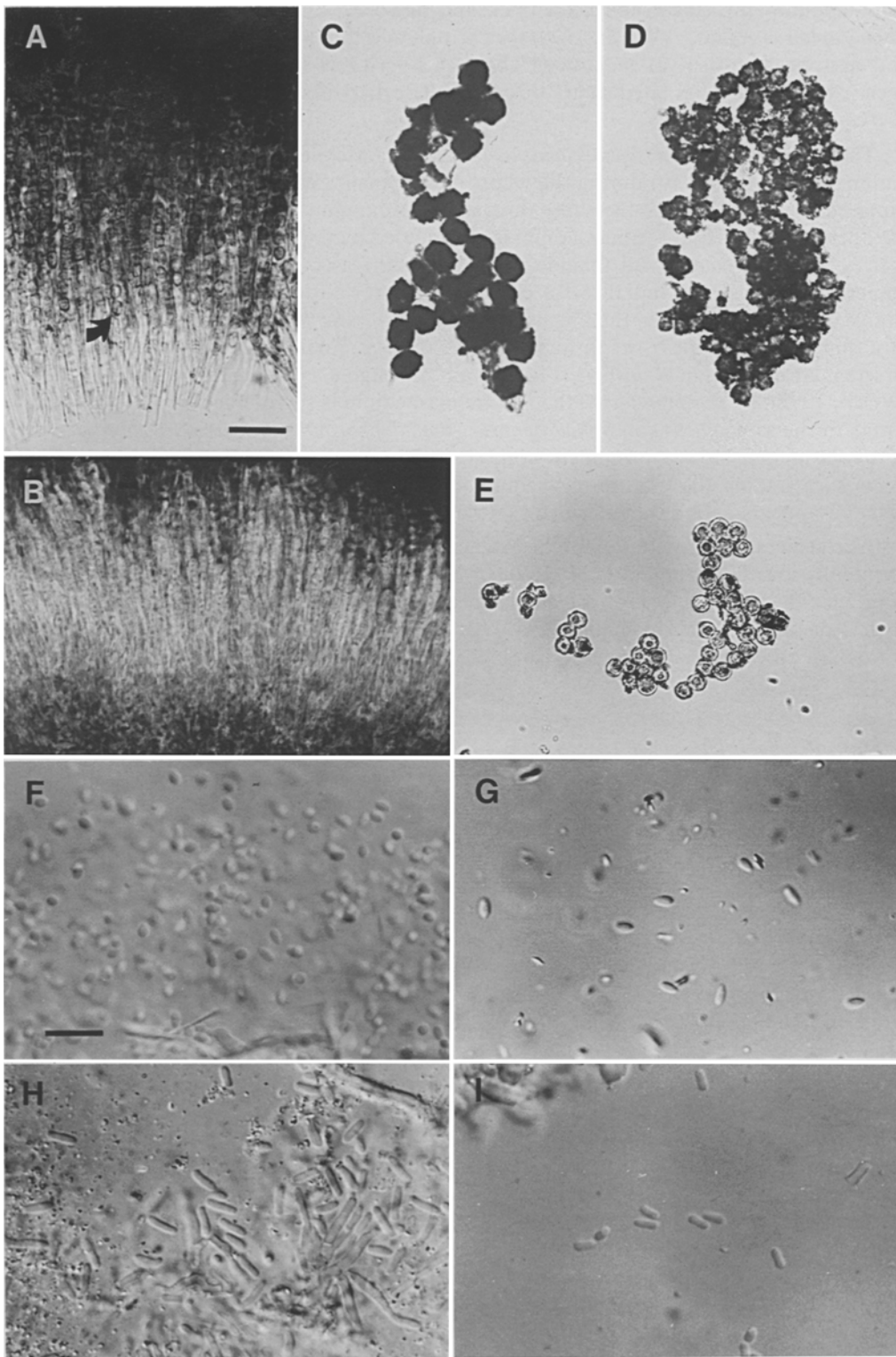
**Position.** Ascomata are as a rule produced terminally in the primary branches. In *Bunodophoron madagascareum*, however, they are produced on short stalks along the lower side of the branches. The same phenomenon, although not as obvious, is also present in *B. diplotypum*. In several other species of *Bunodophoron*, ascomata are often more or less lateral, as branchlets from the apothecium margin sometimes to continue to grow and produces new fruit-bodies.

**Ontogeny.** The ontogeny of the ascomata is angiocarpic in all investigated species of *Bunodophoron* and in *Leifidium tenerum*. Here "angiocarpic" is defined as a development where the excipulum ("primordium wall" sensu WEDIN 1990) is still enclosing the hymenium when a mazaedium has developed. In *Sphaerophorus* the development is regarded as hemiangiocarpic, e.g., the mazaedium is not developed to any extent when the excipulum is disintegrated. Asci may, however, have disintegrated and spores have been released in this stage, as shown by WEDIN (1990). *Calycidium* also has a hemiangiocarpic development.

**Excipulum.** In *Sphaerophoraceae*, the excipulum (primordium wall sensu WEDIN 1990) persists for a long time (CHAR 7). In *Leifidium*, the mazaedium is covered by the excipulum until very late in the development (WEDIN 1990). When the mazaedium is fully mature the stiff excipulum is shed, typically in one piece, as a cap. In the investigated species of *Bunodophoron*, the excipulum disintegrates during the development of the mazaedium, but

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Fig. 4. *A Sphaerophorus stereocauloides*. Section through hymenium showing asci with developing spores. Note dark ornamentation on the spore walls accumulated inside the asci (arrow). TIBELL 13514. *B Bunodophoron diplotypum*. Section through hymenium showing asci with developing spores. WEDIN 3697. *C Sphaerophorus stereocauloides*. The broadly ellipsoidal spores are completely black due to the ornamentation. WEDIN 2742. *D Bunodophoron diplotypum*. Globose spores with dark, irregular ornamentation. FARKAS & POCS 89119 A. *E Leifidium tenerum*. Almost smooth globose spores. WEDIN 2716. *F Sphaerophorus stereocauloides*. Ellipsoidal conidia. WEDIN 2252. *G Leifidium tenerum*. Ellipsoidal-obovate conidia. WEDIN 1592. *H Bunodophoron diplotypum*. Bacilliform conidia. FARKAS & POCS 89119 A. *I Bunodophoron tibellii*. Oblong conidia with thickened ends. WEDIN 2259. Bar: *A-E*: 20  $\mu$ m (same magnification), *F-I*: 10  $\mu$ m (same magnification). All specimens in UPS



still surrounds the mazaedium as a thick and powdery, but still compact, enclosure. In *Sphaerophorus globosus* (WEDIN 1990) the excipulum is thinner than in the other two genera and disappears earlier, as mentioned above. As very few species in *Bunodophoron* have been investigated, I hesitated to use this character otherwise than as an autapomorphy for *Leifidium tenerum*.

**Thalline receptacle.** In *Sphaerophorus* (Fig. 1) the ascoma is more or less enclosed by thalline tissue (CHAR 10) during the whole development (WEDIN 1990). The thalline wall ruptures at approximately the same time as the excipulum disintegrates. In later stages, the opening widens and the mazaedium is surrounded by flaps of thalline tissue. In several species of *Bunodophoron*, all thalline tissue above the ascoma disappears early in development, or the ascoma initializes so close to the lower cortex surface that the ascoma is almost never surrounded by thalline tissue. In *B. insigne* and *B. tibellii* the ascoma is covered by a thin veil of thalline tissue throughout development, finally becoming exposed through an irregular opening in *B. insigne* (Fig. 3 B) and through a small, circular hole in *B. tibellii* (WEDIN 1992). In *B. ramuliferum* the mature mazaedium is surrounded by flaps of thalline tissue, in the same way as in *Sphaerophorus*. *Bunodophoron macrocarpus*, *B. notatum*, and *B. scrobiculatum* have a prominent cone-shaped or hemispherical receptacle of thalline tissue surrounding the mature mazaedium. In *Leifidium tenerum*, the enclosing thalline tissue disappears early in development (WEDIN 1990).

**Mazaedium.** The orientation of the mazaedium varies considerably between species with terminally located ascomata (CHAR 8). In *Sphaerophorus* (Fig. 1) and *Leifidium tenerum* (Fig. 3 C), the mazaedium is directed apically (upwards). In several species of *Bunodophoron* with a distinctly flattened thallus (Fig. 3 B), the mazaedium is directed ventrally (downwards). In other *Bunodophoron* species (Fig. 3 A), the mazaedium is pointing slightly downwards ("sub-apically").

**Asci.** The asci (CHAR 11) are eight-spored, clavate in *Calycidium* and cylindrical in the genera of *Sphaerophoraceae* (Fig. 4 A, B).

**Ascospores.** The ascospores are broadly ellipsoidal (CHAR 13) and almost black (in water) in *Sphaerophorus* (Fig. 4 C), globose and hyaline, dark or pale grey, brownish grey or reddish brown in *Bunodophoron* (Fig. 4 D). *Leifidium* (Fig. 4 E) also has globose and hyaline to pale grey spores. These colours are most probably caused by spore ornamentation. *Calycidium* has globose (the basal spore in the ascus is, however, usually irregularly ellipsoid or pyriform), brown spores. This brown colour is caused by a pigmentation (CHAR 12) in the spore wall (TIBELL 1984), whereas in *Sphaerophoraceae* the spore wall is hyaline. The spore sizes (CHAR 14) in *Sphaerophorus* are c. 8–12 × 7–11 μm. In *Bunodophoron*, the spore sizes vary between 4–21 μm in diameter, but the within-species variation is rarely large. In *Leifidium*, the spores are (5.5–)6.5–8.5(–10) μm and the spores of *Calycidium* are ca. 5–8 μm in diameter.

**Spore ornamentation types.** All species of *Sphaerophoraceae* have ornamentated spores. The spore ornamentation in *Sphaerophorus* (CHAR 15) is caused of epiplasmatic material deposited on the spore wall inside the asci (TIBELL 1981, 1984; WEDIN 1991). The ornamentation in *Bunodophoron* and *Leifidium* (CHAR 16) is formed by an electron-dense amorphous substance which adheres to the spore wall when the spores are released into the mazaedium (TIBELL 1981, 1984, 1985; WEDIN 1990, 1991, 1992; WEDIN & TIBELL 1991; KANTVILAS & WEDIN 1992). This mazaedial material probably originates from the disintegration of the asci and the processes causing the carbonization of the paraphyses. The amount of deposited ornamentation is very variable between species, and the spores in old and over-mature ascomata often completely lack ornamentation. In *Leifidium*, as a rule, only a very small amount of ornamentation seems to be produced. *Calycidium* has no ornamentation of this kind, but the surface of the spore wall appears smooth or has irregular cracks, as seen in SEM (TIBELL 1984).

**Paraphyses.** The paraphyses of all species of *Sphaerophoraceae* are strongly carbonized (CHAR 17). The paraphyses of *Calycidium* are not carbonized.

**Conidiomata.** Pycnidia were observed in *Leifidium*, in all species of *Sphaerophorus*, and in all species of *Bunodophoron* with the exception of *B. madagascareum*. The pycnidia are primarily located in tips of terminal branchlets, but when the branchlets continue to grow the pycnidia are also often found along the lower sides. Pycnidia have not yet been found in *Calycidium*.

**Conidiophores.** The conidiophores are branched with terminal and intercalary conidiogenous cells, corresponding to VOBIS' type V or VI (VOBIS 1980).

**Conidia.** The conidia (CHAR 18, 19) are short (3.0–3.5  $\mu\text{m}$ ) and ellipsoidal to obovate in *Sphaerophorus globosus*, *S. sterocauloides*, and *Leifidium tenerum* (3.0–4.0  $\mu\text{m}$ ) (Fig. 4 F, G). In *Sphaerophorus fragilis* and *Bunodophoron ohlssonii* the ellipsoidal conidia are slightly longer, 3.5–4.5  $\mu\text{m}$ . In *Bunodophoron* (Fig. 4 H, I) the conidia are bacilliform (4.0–6.0  $\mu\text{m}$ ; 5.5–8.0  $\mu\text{m}$  in *B. dodgei*) or oblong (4.0–4.5  $\mu\text{m}$ ). One group of species in *Bunodophoron* has oblong conidia with a strong tendency for the ends to be thickened (Fig. 4 I). All species have conidia with a thickness between 1.5–2.0  $\mu\text{m}$ , with the exception of *Bunodophoron dodgeii*, where the thickness can be up to 2.5  $\mu\text{m}$ .

**Chemistry.** The secondary chemistry of *Sphaerophoraceae* is quite diverse. Sphaerophorin (CHAR 20) occurs in most of the species, and in one chemotype of *Calycidium* (WEDIN, unpubl.), and the absence of sphaerophorin is regarded as an advanced state. Isousnic acid (CHAR 21) occurs as a major substance in three, and frequently as a minor one in several *Bunodophoron* species. The  $\beta$ -orcinol depsides thamnolic and squamatic acids (CHAR 22) in *Sphaerophorus fragilis* and *S. globosus* occur in chemical strains of the substitution or the additive type and, in *S. globosus*, hypothamnolic acids also occur in the same way. The  $\beta$ -orcinol depsidones stictic, constictic, norstictic, and cryptostictic acids (CHAR 23) occur in several *Bunodophoron* species. In other *Bunodophoron* species, protocetraric acid (CHAR 24) occurs as a major substance. 4-O-methylhypoprotocetraric acid occurs in *Bunodophoron scrobiculatum* (HUNECK & TIBELL 1985). This substance is, with some hesitation, considered as biosynthetically more related to protocetraric acid than to stictic acid because of the presence of a lactone ring, and is coded as protocetraric acid in the analysis. Several not yet identified substances occur in various *Bunodophoron* species. One or several dibenzofuranes, visible as pale blue spots after charring, occur in the mazaedium of most of the species with protocetraric acid (CHAR 25). An unidentified blue pigment (CHAR 26) occur in apothecia of species with stictic acid. *Bunodophoron notatum* and *B. scrobiculatum* have a weak spot (CHAR 27) slightly below the sphaerophorin front in system C. Several *Bunodophoron* species have an unknown substance, probably related to usnic acid, present mainly in the apothecia (CHAR 28).

## Results

The analysis resulted in 20 equally parsimonious cladograms of 58 steps and with a consistency index of 0.53 and a retention index of 0.80. The strict consensus tree is shown in Fig. 5. Successive weighting of characters resulted in four cladograms, with topologies identical to four of the original 20 cladograms. Figure 6 shows the character state changes optimized on one of these four cladograms.

## Discussion

Natural groups are, in my opinion, synonymous to monophyletic groups, i.e., groups where all members share a common ancestor and where no extant offspring to this ancestor is excluded. Rigid hypotheses on monophyly can only be the result of a

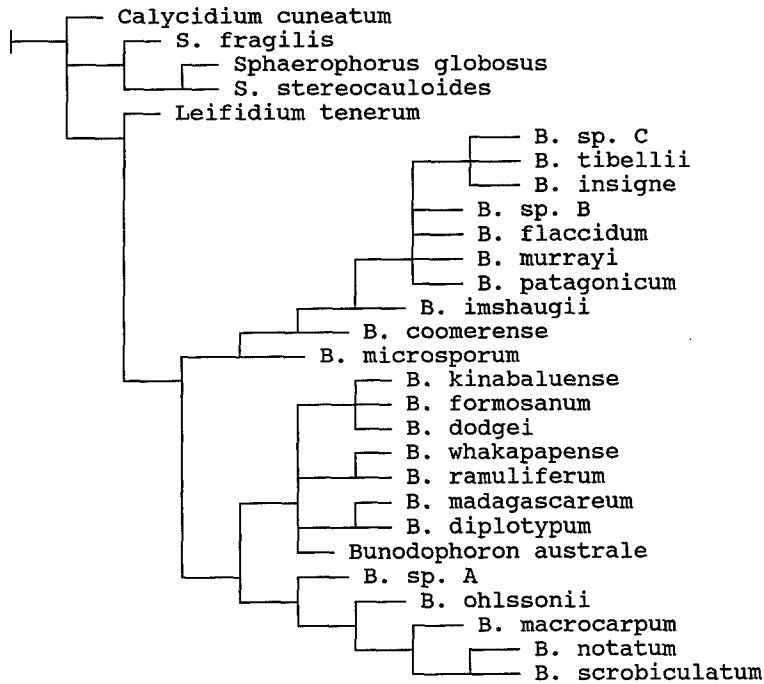


Fig. 5. Strict consensus tree of the 20 most parsimonious cladograms

phylogenetic analysis. Among the monophyletic groups identified, the level of generic rank should then, in my opinion, be chosen so that the genera are easily circumscribed and recognized. In the present investigation, generic rank is given to three such groups; *Sphaerophorus*, *Bunodophoron*, and *Leifidium*, as a result of the analysis presented.

The family *Sphaerophoraceae*, as presently circumscribed, has earlier been regarded as very uniform and homogeneous. In reality, however, *Sphaerophorus* s. str. has few characters in common with *Bunodophoron* and *Leifidium*, a fact that has earlier been very much overlooked. The species in these genera share the characters 11: cylindrical asci (common in *Caliciales*), 12: non-pigmented spore-walls (also found in *Sclerophora*), and 17: carbonized paraphyses (also found in *Microcalicium* and *Tylophoron*), all features that are not present in the outgroup. In some cases these characters also occur outside *Caliciales*, and the hypothesis on the monophyly of the family is retained mainly because it has not yet been possible to demonstrate the opposite. *Sphaerophoraceae* and *Calycidiaceae* contain sphaerophorin (most species in *Sphaerophoraceae* and one chemotype in *Calycidium cuneatum*), a substance which within *Caliciales* is found only in these two genera, and which is very rare outside the order (CULBERSON & al. 1984, TÖNSBERG 1992). They also share a general similarity in the growth form, difficult to describe as discrete character states. The phylogenetic relationship between *Sphaerophoraceae-Calycidiaceae* and other families in *Caliciales* is obscure. TIBELL (1984), could not see any close relationship between *Calycidium* and other families in the order, including *Sphaero-*

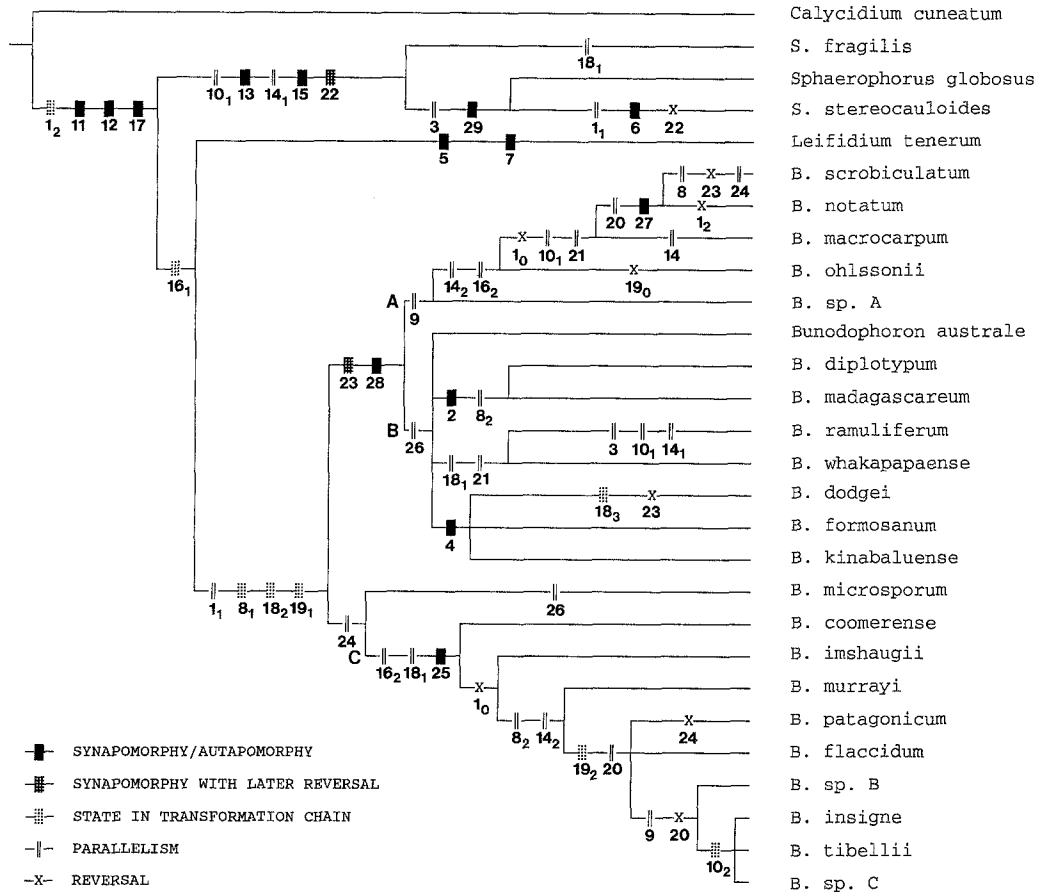


Fig. 6. One of four cladograms resulting from successive weighting of characters. A, B, C indicate nodes discussed in the text

*phoraceae*. In the future, my own studies will be extended to search for the natural placement of *Sphaerophoraceae* and *Calycidiaceae* in the *Ascomycetes*.

*Sphaerophorus* is distinguished by having broadly ellipsoidal spores (13), the unique spore ornamentation (15) and the production of thamnolic/squamatic acids (22). *Sphaerophorus* also has a globose thalline receptacle (10<sub>1</sub>) and medium-sized spores (14<sub>1</sub>). *Sphaerophorus stereocauloides* (“*Thysanophoron s.*”) is the sister species to *S. globosus*, both having a I+ violet medulla (29). I do not accept the genus *Thysanophoron* as *Sphaerophorus* becomes paraphyletic if *Sphaerophorus stereocauloides* is excluded.

*Bunodophoron* and *Leifidium* together form a monophyletic group characterized by the spore ornamentation type (16). *Leifidium* is characterized by the cap-like, persisting excipulum (7) and by the very thin cortex (5). *Bunodophoron* is characterized by having a more or less flattened thallus (1, with a reversal in *B. notatus*), subapical to ventrally exposed mazaedia (8) and by having rod-shaped (reversal in *B. ohlssonii*) conidia (19). The conidium length 4–4.5 μm (18<sub>2</sub>) is also a single evolutionary event achieved here. The genus *Pleurocybe*, with *P. madagascarea*, is

monophyletic if *Bunodophoron diplotypum* is included. These two species, however, are well-nested within *Bunodophoron*. Consequently, as *Bunodophoron* would become paraphyletic if *Pleurocybe* is excluded, the latter is listed as a synonym. Likewise, acceptance of the monotypic genus *Pseudosphaerophorus* M. SATŌ, with *P. kinabaluense*, would leave *Bunodophoron* paraphyletic.

As a result of the analysis, some hypotheses on character evolution can be made. A character widely used in classification of *Caliciales* at different taxonomic levels is the ontogeny of the spore ornamentation. In *Sphaerophoraceae*, the two ways of achieving spore ornamentation (characters 15 and 16) are in my opinion non-homologous, and are coded as such. The brown colour of the spores in certain *Bunodophoron*-species, obtained by spore ornamentation, is an advanced state, compared to the grey colour occurring in *Leifidium* and other *Bunodophoron*-species, and has evolved twice (16). This is, however, weakly supported as indicated by the amount of parallelisms between the two branches characterized by, e.g., gain of this character state. The quantitative multistate character 14 (spore size) is also very homoplasious, as might have been expected.

The evolution of conidium shape (19), together with conidium size (18) could also be commented upon. Short, ellipsoidal conidia is the primitive condition, and long, rod-shaped conidia has evolved once (18<sub>2</sub>, 19<sub>1</sub>). The ellipsoidal conidia are longer in *Sphaerophorus fragilis* (18<sub>1</sub>). The rod-shaped conidia become shorter twice (18<sub>1</sub>) and achieve thickened ends once (19<sub>2</sub>), as indicated by the optimization on the cladogram. Here one must bear in mind, however, that the state of character 19 is unknown in several of the species above the node defined by 19<sub>2</sub>.

It can be noted that the analysis does not support recognition of subgeneric taxa within *Bunodophoron*, corresponding to the subgenera suggested by OHLSSON (in TIBELL 1984). OHLSSON's subgenus *Aghimus* is polyphyletic as members are to be found above both nodes A and C, and his subgenus *Bunodophoron* is paraphyletic as *B. microsporum* is not among the species above node B (Fig. 6). It must be stressed, however, that the resolution within *Bunodophoron* is not very stable, and all statements here must be treated as very tentative. No subgeneric classification is suggested in *Bunodophoron* here, pending a more stable and definite result.

### Taxonomic treatment

***Sphaerophoraceae*** E. M. FRIES. Lich. Eur.: 7. 1831. [*"Sphaerophoraceae* FÉE", Essai Crypt. Écorc. LXXIX. 1824, nom. inval., Art. 32.1 (b).] – Type: *Sphaerophorus* PERS.

Lichenized ascomycetes. Thallus fruticose, terete or flattened. Apothecia sessile to subimmersed, rarely slightly stalked, terminal, subterminal or rarely laminal. Mazaedium black. Asci cylindrical, formed singly from ascogenous hyphae with croziers. Paraphyses strongly carbonized. Ascospores broadly ellipsoidal or globose, non-septate, dark violet, brownish, greyish or hyaline; spore wall hyaline. Spores with ornamentation of carbonized material originating either from the epiplasm of the asci or from mazaedial material added to the spore surface in the mazaedium. Pycnidia in tips of terminal branches or laminally along the lower sides. Conidia ellipsoidal or oblong to bacilliform.  $\beta$ -orcinol depsides and depsidones frequent as well as the orcinol depsidone sphaerophorin. Isousnic acid,



anthraquinones as well as several unidentified dibenzofuranes and other substances occur.

***Sphaerophorus*** PERS. Ann. Bot. (Usteri) 7: 23. 1794. — Type: *Sphaerophorus coralloides* PERS., nom. superfl. [= *Sphaerophorus globosus* (HUDS.) VAIN.] (Typ. cons.).

≡ *Sphaerophoronomyces* CIFERRI & TOMASELLI, Atti Ist. Bot. Lab. Critt. Univ. Pavia, Ser. 5, 10: 66. 1953. Nom. illeg. — Type: *Sphaerophoronomyces coralloidis* CIFERRI & TOMASELLI, nom. illeg. (≡ *Sphaerophorus coralloides* PERS.)

*Thysanophoron* STIRTON, Trans. Bot. Soc. Edinburgh 14: 359. 1883. — Type: *Thysanophoron pinkertonii* STIRTON (= *Sphaerophorus stereocauloides* NYL.)

Thallus slender; terete, or with a weak dorsiventral orientation of the branching system and of the algal layer; more or less richly branched, forming cushions or patches; brownish, greyish or almost white. Branching anisotomic to isotomic dichotomous, often with bundles of short coralloid branchlets. Cortex 60–200 µm thick. Medulla often I+ violet. Apothecia terminal, globose, opening through cracks in the thalline envelope; mazaedia more or less surrounded by irregular flaps of thalline tissue during spore dissemination. Ascospores broadly ellipsoidal, dark violet-blue, ca. 8–12 × 7–11 µm; almost completely covered by a thick, dark ornamentation added to spore wall inside the ascus. The ornamentation is at an early stage composed of tubular elements (TIBELL 1981, WEDIN 1991) and intensely green in KOH. Pycnidia in tips of terminal branchlets. Conidiophores branched with conidiogenous cells both terminally and intercalary, i.e., corresponding to VOBIS' type V or VI (VOBIS 1980). Conidia hyaline, simple, ellipsoidal to obovate, 3.0–4.5 × 1.5–2.0 µm.

**Chemistry.** Sphaerophorin occurs in all species. *Sphaerophorus globosus* and *S. fragilis* have several chemotypes of the substitution or additive types where one or several of the β-orcinol depsides thamnolic, hypothamnolic and squamatic acids occur.

**Ecology and distribution.** *Sphaerophorus globosus* is a bipolar species with a disjunction between boreal arctic and alpine areas, and southernmost South America and the Antarctic Peninsula. It grows on rocks or on the ground, but occurs also as an epiphyte in wet oceanic forests in Europe, the Azores, and western North America. *S. fragilis* is an epilithic circumboreal arctic-alpine species. *S. stereocauloides* is endemic to New Zealand, growing as an epiphyte in the canopy of *Nothofagus* forests.

1. ***Sphaerophorus fragilis*** (L.) PERS., Ann. Bot. (Usteri) 7: 23. 1794.

≡ *Lichen globiferus β-fragilis* (L.) NECK., Method. Muscor. 17: 67. 1771. *Verrucaria fragilis* (L.) HUMB., Flora Friburg Specim., 42. 1793. *Coralloides fragile* (L.) HOFFM., Descript et Adumbr. Plant Lich. 2: 34. 1794. *Stereocaulon fragile* (L.) HOFFM., Deutschl. Flora, 131, 1795. *Sphaerophorus coralloides β-fragilis* (L.) MUDD (as "*Sphaerophoron coralloide β-fragile*"), Man. Brit. Lich. 8: 264. 1861. *Lichen fragilis* L. Spec. Plant., 1154. 1753. — Type: LINN 1273.261!, the uppermost specimen (lectotype, selected here).

2. ***Sphaerophorus globosus*** (HUDS.) VAIN., Result. Voyage S. Y. Belgica, Botan., 35. 1903.

≡ *Lichen globosus* HUDS., Flora Anglica, 460. 1762. – Type: “Coralloides cupressiforme, capitulis globosis” DILLENIIUS’ Hist. Musc., fig. XVII: 35 c. 1742 (lectotype, selected here).

*Lichen globiferus* L., Mant. Plant., 133. 1767. – Type: LINN 1273.251! (lectotype, selected by HOWE 1912). *Coralloides globiferum* (L.) HOFFM., Descript. et Adumbr. Plant. Lich. Vol. II, fasc. II, 25. 1792. *Stereocaulon globiferum* (L.) HOFFM., Deutschl. Flora, 131. 1796. *Sphaerophorus globiferus* (L.) DC. in LAM. & DC., Fl. Franc. 3rd edn., Vol. II, 327. 1805.

≡ *Sphaerophorus coralloides* PERS., Ann. Bot. (Usteri) 7: 23. 1794, nom. superfl.

3. *Sphaerophorus stereocauloides* NYL., Flora 52: 69. 1869.

≡ *Thysanophoron stereocauloides* (NYL.) M. SATŌ, Misc. Bryol. Lichenol. 4: 48. 1966. – Type: New Zealand. 1867, KNIGHT s.n. (H-Nyl40395!, holotype; BM!, WELT-KNIGHT 13: 7, isotypes).

*Thysanophoron pinkertonii* STIRT., Trans. Proc. Bot. Soc. Edinburgh 14: 359. 1883. – Type: New Zealand. PINKERTON [labelled by STIRTON *Thysanocaulon Pinkertoni*], (GLAM lectotype selected by GALLOWAY 1985, not seen; BM!, UPS!, isolectotypes).

*Sphaerophorus nobilis* ZAHLBR., Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 104: 258. 1941. – Type: New Zealand. Southland. Stuart Mts, on tree trunks, THOMSON, no Z. A. 424 (CHR 162474, lectotype selected by GALLOWAY 1985, not seen; B!, isolectotype).

**Nomenclatural remarks.** *Lichen fragilis* L. The sheet 1273.261 in the LINNAEAN Herbarium is annotated by LINNAEUS and also carries the number in Flora Suecica, cited in the original description. This sheet most probably contains the specimens LINNAEUS studied when describing *Lichen fragilis*. The uppermost specimen, which is the best developed one, is here chosen as lectotype (Fig. 2). It contains sphaerophorin and hypothamnolic acid.

*Lichen globosus* HUDS. HUDSON’s own herbarium was lost in a fire in 1783 (DIXON 1959, 1963). Thus HUDSON names must be lectotypified from other syntypes cited in the original description. HUDSON cites three synonyms: “Coralloides cupressiforme, capitulis globosis” (DILLENIIUS 1742), “Muscus coralloides tunbrigen-sis, bracteolis nigerrimis” (PETIVER 1703) and “Lichenoides non tubulosum, ramis scutellis nigris terminatis” (RAY 1724), the last one only a new name for PETIVER’s (1703) “Muscus coralloides . . .” as the latter is cited as a synonym by RAY (1724).

DILLENIIUS’ (1742) illustrations in Historia Muscorum were based on material in his herbarium preserved in Oxford. Number 35 (*Coralloides cupressiforme* . . .) is to be found on the lower half of plate nr. 52 in the herbarium, and consists of eight specimens. The specimen in the lower right corner, the only fertile specimen (Fig. 1 A), has most probably been used to produce illustration XVII: 35 c. The illustration XVII: 35 c is consequently chosen as lectotype of *Lichen globosus* HUDS. (Fig. 1 B). A small fragment analysed by TLC revealed sphaerophorin and squamatic acid and the medulla reacts very faintly I+ violet, the faint reaction probably caused by the age of the specimen.

PETIVER’s collection is included in the SLOANE herbarium (BM-SL). Two numbers of “Muscus coralloides . . .” is preserved here, one in the PETIVER herbarium (HS-150) and one in the BUDDLE collection (HS-115), most probably a duplicate of the PETIVER material. This material is a species of *Bunodophoron* and a lecto-

typification on some of these collections would cause a reinterpretation of both the name and the genus. Consequently, they can be disregarded from this discussion.

In the description of *Lichen globiferus* L. LINNAEUS (1767) cites a specimen from Stenbrohult in Småland, Sweden, collected by his son. He also mentions "Lichen fruticosus coralloides non tubulosus, cinereus, ramosissimus, receptaculis sphaericis, concoloribus" (MICHELIUS 1729) and "Coralloides cupressiforme, capitulis globosis" (DILLENIIUS 1741) as synonyms.

In the LINNAEAN Herbarium, there are two specimens of *Lichen globiferus* preserved annotated by LINNAEUS fil. No material has been found in the LINNAEAN collections in Uppsala and Stockholm. Furthermore, no such material is to be found in the LINNAEAN collection in Helsinki (KUKKONEN & VILJAMAA 1973). JØRGENSEN and JAMES (pers. comm.), who are presently working on the typification of LINNAEAN lichens, have informed me of the earlier overlooked lectotypifications made by HOWE (1912), which they will accept in their forthcoming paper. The specimen 1273.251 in LINN, annotated "*Lichen globifer*" by LINNAEUS fil. was selected as lectotype by HOWE (1912) and I agree with JØRGENSEN and JAMES in accepting this choice. The specimen is fertile and contains sphaerophorin and squamatic acid (JAMES, pers. comm.). The other specimen in LINN, 1273.252, is sterile and thus does not agree with the protologue. The lectotype will be illustrated and fully discussed in the above mentioned paper by JØRGENSEN and JAMES.

***Bunodophoron*** A. MASSAL. Mem. Imp. Reale Ist. Veneto Sci. **10**: 76. 1876. – Type: *Sphaerophorus australis* LAURER, Linnaea **2**: 44. 1827 (as "*Sphaerophoron australe*") [≡ *Bunodophoron australe* (LAURER) A. MASSAL.].

≡ *Sphaerophorus* subg. *Bunodophorus* (A. MASSAL.) OHLSSON in TIBELL, Nova Hedwigia Beih. **79**: 682. 1984.

*Pleurocybe* MÜLL. ARG., Flora **67**: 613. 1884. – Type: *Pleurocybe hildebrandtii* MÜLL. ARG. [= *Bunodophoron madagascareum* (NYL.) WEDIN]. ≡ *Pleurocybomyces* CIFERRI & TOMASELLI, Atti Ist. Bot. Lab. Critt. Univ. Pavia, Ser. 5, **10**: 62. 1953. Nom. illeg.

*Pseudosphaerophorus* M. SATÔ, Misc. Bryol. Lichenol. **4**: 108. 1967. – Type: *Pseudosphaerophorus kinabaluensis* M. SATÔ [≡ *Bunodophoron kinabaluense* (M. SATÔ) WEDIN].

*Sphaerophorus* subg. *Aghimus* OHLSSON in TIBELL, Nova Hedwigia Beih. **79**: 682. 1984. – Type: *Sphaerophorus insignis* LAURER, Linnaea **2**: 45. 1827 (as "*Sphaerophoron insigne*") [≡ *Bunodophoron insigne* (LAURER) WEDIN].

Thallus more or less dorsiventrally compressed or, rarely, terete; often dimorphic. Cortex 45–130 µm thick, composed of thick-walled, fused hyphae. Medulla dense, lax or hollow; I–. Apothecia terminal, or (rarely) laminal on the underside of the primary branches. Ascomata ontogeny angiocarpic, the excipulum disintegrates but, as a rule, encloses the mazaedium until it is mature. Thalline receptacle lost early or remaining throughout development. Mazaedia oriented subapically or ventrally. Ascospores globose; 4–21 µm diam.; pale to dark grey, rarely almost hyaline, grey with a greenish tinge, dark brownish grey or reddish brown, with an irregular amount of a dark ornamentation consisting of an amorphous substance adhering to the wall after the spores have been released from the asci (TIBELL 1981, 1984, 1985; WEDIN 1990, 1991, 1992; WEDIN & TIBELL 1991; KANTVILAS & WEDIN 1992); greenish in KOH, reddish in HNO<sub>3</sub>, ornamentation

dissolving in KOH. Pycnidia in tips and along the lower side of terminal branchlets. Conidiophores branched with conidiogenous cells both terminally and intercalary, i.e., corresponding to VOBIS' type V or VI (VOBIS 1980). Conidia hyaline; simple; bacilliform to oblong;  $3.5\text{--}5.5(-8) \times 1.5\text{--}2.0(2.5)\ \mu\text{m}$ . In some species with oblong conidia, the ends tend to be thickened. In one species, the conidia are ellipsoidal.

**Chemistry.** Sphaerophorin and one or several  $\beta$ -orcinol depsidones occur in most species. Some species groups mainly characterised by their chemistry can be distinguished. One species group has protocetraric acid as major substance together with one or several unidentified dibenzofuranes restricted to the mazaedium (first reported by TIBELL 1987) and the other species group has stictic and constictic acids. Isousnic acid occurs as a major substance in three species and as a minor in two. Isousnic acid has never been found together with protocetraric acid. Several unidentified substances have been found, some very characteristic for single species or groups of species. A group of species has a pigment in the mazaedium, visible as a bright blue spot on TLC plates. The characteristic substance UN-“apothecium” occurs in the apothecia of several species. *Bunodophoron patagonicum* has a set of several unidentified substances.

**Ecology and distribution.** Most species of *Bunodophoron* are epiphytes, a few, however, occur also on rocks or on the ground. *Bunodophoron* is widely distributed in the temperate rainforest of the Southern Hemisphere, in highly oceanic areas in the Northern Hemisphere and in high-altitude rainforest in tropical and subtropical areas.

1. *Bunodophoron australe* (LAURER) A. MASSAL., Mem. Imp. Reale Ist. Veneto Sci. **10**: 76. 1876.

= *Sphaerophorus compressum* var. *australe* (LAURER) LINDS., Trans. Roy. Soc. Edinburgh **22**: 151. 1859. *Sphaerophorus melanocarpus* var. *australis* (LAURER) J. S. MURRAY, Trans. Roy. Soc. New Zealand **88**: 188. 1960. *Sphaerophorus australis* LAURER, Linnæa **2**: 44. 1827 (as “*Sphaerophoron australe*”). — Type: Australia. SIEBER s.n. [BM!, lectotype selected by OHLSSON in TIBELL 1987; BM, PC, isolecototypes (not seen)]. Non *Sphaerophorus australis* HOOK. f. & T. TAYLOR (nom. illeg.) = *Leifidium tenerum* (LAURER) WEDIN.

2. *Bunodophoron coomerense* (OHLSSON in TIBELL) WEDIN, comb. nova

Basionym: *Sphaerophorus coomerensis* OHLSSON in TIBELL, Symb. Bot. Upsal. **27(1)**: 219. 1987. — Type: Australia. Queensland, on the way to Coomer River, McPherson Range, 1951, MORRIS (MEL!, holotype).

3. *Bunodophoron diplotypum* (VAIN.) WEDIN, comb. nova

Basionym: *Sphaerophorus diplotypus* VAIN., Hedwigia **37**: 36. 1898. — Type: Madagascar. “in silva Ivohimanitra”, FORSYTH-MAJOR 97 (BM!, holotype).

*Sphaerophorus digitatus* WANG-YANG & M. J. LAI, Taiwania **21(1)**: 84. 1976. — Type: Taiwan. Ilan, LAI 8108 (TAI, holotype, not seen).

4. *Bunodophoron dodgei* (OHLSSON in WEDIN) WEDIN, comb. nova

Basionym: *Sphaerophorus dodgei* OHLSSON in WEDIN, Lichenologist **24**: 121. 1992. — Type: Chile. Osorno. Forest around Lago Toro on road to Refugio Antillanca, IMSHAUG 42952 (MSC!, holotype).

5. *Bunodophoron flaccidum* (KANTVILAS & WEDIN) WEDIN, comb. nova

Basionym: *Sphaerophorus flaccidus* KANTVILAS & WEDIN. *Nova Hedwigia* **54**: 494. 1992. – Type: Australia. Tasmania. Truchanas Huon Pine Reserve, 42° 39' S 146° 58' E, 1985, KANTVILAS 185/85 (HO!, holotype; BM!, UPS!, isotypes).

**6. *Bunodophoron formosanum* (Zahlbr.) Wedin, comb. nova**

Basionym: *Sphaerophorus melanocarpus* ssp. *formosanus* ZAHLBR., *Repert. Spec. Nov. Regni Veg.* **31**: 206. 1933. – Type: Taiwan. Raisha, ASAHINA F 274 (W!, holotype; TNS, isotype, not seen). ≡ *Sphaerophorus formosanus* (Zahlbr.) Asah. in MITUNO, *J. Japan Bot.* **14**: 667. 1938.

**7. *Bunodophoron imshaugii* (Ohlsson in D. J. Galloway) Wedin, comb. nova**

Basionym: *Sphaerophorus imshaugii* OHLSSON in D. J. GALLOWAY, *New Zealand J. Bot.* **21**: 197. 1982. – Type: Argentina. Isla de Los Estados. Bahía Primera, IMSHAUG 52363 (MSC!, holotype).

**8. *Bunodophoron insigne* (Laurer) Wedin, comb. nova**

Basionym: *Sphaerophorus insignis* LAURER, *Linnaea* **2**: 45. 1827 (as “*Sphaerophoron insigne*”). – Type: Australia. Sieber s.n. (BM!, lectotype chosen by Ohlsson in Tibell 1987).

*Sphaerophorus ceranoides* HAMPE, *Linnaea* **28**: 217. 1856. – Type: Australia. Sealers Cove, Aug. 1854, HAMPE s.n. (MEL!, lectotype, selected here; MEL!, isolectotype).

*Sphaerophorus australis* var. *proliferus* F. WILSON, *J. Linn. Soc. Bot. (London)* **28**: 370. 1891 (as “*Sphaerophoron australe* var. *aut forma prolifera*”). – Type: Australia. Victoria. On trunk of trees, Black Spur. 21. III. 1885, WILSON s.n. (NSW L 4186!, lectotype, selected here; NSW!, two isolectotypes).

**9. *Bunodophoron kinabaluense* (M. Satô) Wedin, comb. nova**

Basionym: *Pseudosphaerophorus kinabaluensis* M. SATÔ, *Misc. Bryol. Lichenol.* **4**: 108. 1967. – Type: Borneo. Kinabalu Nat. Park, HALE 28656 (Holotype in Herb. Univ. Ibaraki, Japan, not seen; TNS, not seen, US, not seen, UPS!, isotypes) ≡ *Sphaerophorus kinabaluensis* (M. Satô) OHLSSON in TIBELL, *Symb. Bot. Upsal.* **27** (1): 228. 1987.

**10. *Bunodophoron macrocarpum* (Ohlsson in D. J. Galloway) Wedin, comb. nova**

Basionym: *Sphaerophorus macrocarpus* OHLSSON in D. J. GALLOWAY, *New Zealand J. Bot.* **21**: 197. 1983. – Type: New Zealand. Westland. Gillespies Cook River Road, between Tornado Creek and Whelan Creek, HARRIS 6241 (MSC!, holotype).

**11. *Bunodophoron madagascareum* (Nyl. in Cromb.) Wedin, comb. nova**

Basionym: *Sphaerophorus madagascareus* NYL. in CROMB., *J. Linn. Soc., Bot.* **15**: 409. 1876 (as “*Sphaerophoron madagascareum*”). – Type: Madagascar. Near Antanarin, POOL s.n. (H-Nyl 40407!, holotype; BM!, isotypes). ≡ *Pleurocybe madagascarea* (Nyl. in Cromb.) ZAHLBR., *Engler-Prantl: Natürl. Pflanzenfam. I Teil Abt. 1*: 86. 1903.

*Pleurocybe hildebrandtii* MÜLL. ARG., *Flora* **67**: 614. 1884. – Type: Madagascar. Imerina, Andragolvaka, HILDEBRANDT 2179 (FH!, isotype).

**12. *Bunodophoron microsporum* (Ohlsson in D. J. Galloway) Wedin, comb. nova**

Basionym: *Sphaerophorus microsporus* OHLSSON in D. J. GALLOWAY, New Zealand J. Bot. **21**: 197. 1983. – Type: New Zealand. Westland. W of Turiwhate, IMSHAUG 48120 (MSC!, holotype).

**13. *Bunodophoron murrayi* (OHLSSON in TIBELL) WEDIN, comb. nova**

Basionym: *Sphaerophorus murrayi* OHLSSON in TIBELL, Nordic J. Bot. **1**: 335: 1981. – Type: New Zealand. Westland. 8 miles W of Turiwhate, HARRIS 6343 (MSC!, holotype).

**14. *Bunodophoron notatum* (TIBELL) WEDIN, comb. nova**

Basionym: *Sphaerophorus notatus* TIBELL, Publ. Herb. Univ. Uppsala. **10**: 9. 1982. – Type: New Zealand. Otago. Mt Aspiring Nat. Park, 10 km NNE of Makaroa, close to Cameron Flat Campsite, TIBELL 10604 (UPS!, holotype, Tibell Calic. Exs. 73, isotypes).

*Sphaerophorus melanocarpus* var. *melanocarpus* f. *ramosissimus* MURRAY, Trans. Roy. Soc. New Zealand **88**: 188. 1960. – New Zealand. Southland, Secretary Island, Murray 4054 (BM!, holotype; BM!, isotype).

**15. *Bunodophoron ohlssonii* (WEDIN) WEDIN, comb. nova**

Basionym: *Sphaerophorus ohlssonii* WEDIN, New Zealand J. Bot. **29**: 290. 1991. – Type: New Zealand. Wellington. Tongariro Nat. Park, vicinity of Whakapapa Village, close to Whakapapanui Stream, TIBELL 13508 (UPS!, holotype; CHR!, isotype).

**16. *Bunodophoron patagonicum* (C. W. DODGE) WEDIN, comb. nova**

Basionym: *Pleurocybe patagonica* C. W. DODGE, Nova Hedwigia **16**: 484. 1969. – Type: Argentina. Rio Negro. Parque Nacional Nahuel Huapi, Rucumlen, on trail to Lagunilla Espejo Chico, C. W. & B. S. DODGE 700 (FH!, ?isotype, holotype in Herb. Dodge). ≡ *Sphaerophorus patagonicus* (C. W. DODGE) OHLSSON in D. J. GALLOWAY, New Zealand J. Bot. **21**: 197. 1983.

**17. *Bunodophoron ramuliferum* (I. M. LAMB) WEDIN, comb. nova**

Basionym: *Sphaerophorus ramulifer* I. M. LAMB, Farlowia **4**: 426. 1955. – Type: Argentina. Rio Negro. Near Lago Frias, LAMB 5977 (CANL, holotype, not seen; FH, not seen, H!, UPS!, isotypes).

**18. *Bunodophoron scrobiculatum* (C. BAB. in HOOK. f.) WEDIN, comb. nova**

Basionym: *Sphaerophorus australis* var. *scrobiculatus* C. BAB. in HOOK. f., Botany Antarctic Voyage **2** (2): 304. 1855 (as “*Sphaerophoron australe* var. *scrobiculatum*”). – Type: New Zealand. North Island, s. loc., COLENZO (BM!, selected by GALLOWAY 1985). ≡ *Sphaerophorus scrobiculatus* (C. BAB. in HOOK. f.) M. SATÔ, Misc. Bryol. Lichenol. **4**: 151. 1968.

*Sphaerophorus australis* var. *macrophyllus* ZAHLBR., Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. **104**: 259. 1941. – Type: New Zealand. Canterbury. Cass, base of trunk of *Nothofagus menziesii*, ZOTOV, no. Z. A. 475 (W no 1946!, lectotype, selected here).

**19. *Bunodophoron tibellii* (WEDIN) WEDIN, comb. nova**

Basionym: *Sphaerophorus tibellii* WEDIN, Lichenologist **24**: 129. 1992. – Type: New Zealand. Wellington. Tongariro Nat. Park, vicinity of Whakapapa Village, close to Whakapapanui Stream, TIBELL 13445 (UPS!, holotype; CHR!, isotype).

**20. *Bunodophoron whakapapaense* (WEDIN) WEDIN, comb. nova**

Basionym: *Sphaerophorus whakapapaensis* WEDIN, New Zealand J. Bot. **29**: 287. 1991. — Type: New Zealand. Wellington. Tongariro Nat. Park, along track to Silica Springs, 39° 12' S 175° 32' E, WEDIN 2322 (UPS!, holotype, AK, BM, CBG, CHR, HO, isotypes).

**Nomenclatural remarks.** *Bunodophoron australe* (LAURER) A. MASSAL. is the correct name for the species erroneously called *Sphaerophorus melanocarpus* (Sw.) DC., in the cool temperate areas of the Southern Hemisphere. The epithet “*melanocarpus*” refers to a species from tropical South America which belongs to a critical complex of tropical species related to *Bunodophoron formosanum*, that are at present under investigation.

*Sphaerophorus australis* var. *macrophyllus* ZAHLBR. The two syntypes mentioned in the protologue are preserved in the ZAHLBRUCKNER collection in W. Both collections are fertile and represent *Bunodophoron scrobiculatum* (C. BAB. in HOOK. f.) WEDIN. The slightly larger collection by ZOTOV is designated lectotype.

*Sphaerophorus australis* var. *proliferus* F. WILSON. In NSW, four syntypes, three duplicates collected March 21st 1885 and one March 23rd, are kept together in one envelope. WILSON has written “*prolifera*” with a pencil on all four specimens, and subsequently written the actual label data and the species name in ink. On one of the three duplicates, and on the syntype with another date, WILSON has later also added “var. *proliferum*” to the species name in ink. The specimen collected March 21st carrying the new variety name in ink is selected as lectotype, and the two duplicates are considered isolectotypes. All specimens represent *Bunodophoron insigne* (LAURER) WEDIN.

*Sphaerophorus ceranoides* HAMPE. OHLSSON (1973) apparently saw only one of the two isotypes present in MEL and assumed that this collection was the holotype. I consequently designate the collection carrying OHLSSON's annotations as lectotype. The collection represents *Bunodophoron insigne* (LAURER) WEDIN.

*Bunodophoron notatum* (TIBELL) WEDIN. Among the isotypes of *Sphaerophorus notatus* TIBELL was unfortunately some material of *Bunodophoron ramuliferum*, this was found in the isotypes in BM and MEL.

*Pleurocybe patagonica* C. W. DODGE. A relatively large part of the type collection is present in FH. This material does not, however, carry any annotations by OHLSSON who otherwise clearly annotated all types studied and I assume that it is not the holotype seen by him, but a duplicate.

***Leifidium* WEDIN, gen. novum**

≡ *Sphaerophorus* subg. *Sphaerocarpus* OHLSSON in TIBELL. Nova Hedwigia Beih. **79**: 682. 1984.

Thallus tenuis teres ramosissimus pulvinos vel tegetes formans. Rami principales crassi elongati, ascomatibus apicalibus. Cortex tenuis, 30–40 µm. Ascomatum ontogenesis angiocarpa. Ascosporae globosae, (5.5–)6.5–8.5(–10) µm diam., hyalinaecinerea. Conidia ellipsoideae-obovata, 3.0–4.0 × 1.5–2.0 µm.

Type: *Leifidium tenerum* (LAURER) WEDIN, comb. nova.

Basionym: *Sphaerophorus tener* LAURER, Linnaea **2**: 45. 1827 (as “*Sphaerophoron tenerum*”). — Type: Australia. SIEBER s.n. [PC, lectotype (not seen), selected by OHLSSON in TIBELL 1987: 225; FH!, isolectotype].

*Sphaerophorus taylorii* C. W. DODGE, Nova Hedwigia **19**: 489. 1970. ≡ *Sphaerophorus australis* HOOK. f. & T. TAYLOR (as “*Sphaerophoron australe*”), London

J. Bot. 3: 653. 1844 (non *Sphaerophorus australis* LAURER). — Type: Auckland Island, 1840 HOOKER s.n. (FH-Tayl. 246!, lectotype selected by OHLSSON in TIBELL 1987: 254; UPS!, syntype).

*Sphaerophorus curtus* HOOK. f. & T. TAYLOR, London J. Bot. 3: 654. 1844 (as “*Sphaerophoron curtum*”). *Sphaerophorus tener* var.  $\beta$ -*curtus* (HOOK. f. & T. TAYLOR) T. TAYLOR & HOOK. f., Fl. Antarct. 1: 195. 1844 (as “*Sphaerophoron tenerum* var.  $\beta$ -*curtum*”). *Sphaerophorus globosus* var. *curtus* (HOOK. f. & T. TAYLOR) ZAHLBR., Cat. Lich. Univ. 1: 692. 1922. — Type: Auckland Island, 1840 HOOKER s.n. (FH-Tayl. 153!, lectotype selected by OHLSSON in TIBELL 1987: 254; UPS!, isolectotype).

*Sphaerophorus tener* f. *compactus* CROMB., J. Linn. Soc. Bot. 15: 223. 1876 (as “*Sphaerophoron tenerum* f. *compactum*”). — Type: Puerto Gallant, Straits of Magellan, 1867, CUNNINGHAM s.n. (BM!, lectotype; BM!, isolectotype). The lectotypification proposed by OHLSSON 1973: 53 herewith validated.

*Sphaerophorus tener* f. *globosoides* J. S. MURRAY, Trans. Roy. Soc. New Zealand 88: 194. 1960. — Type: New Zealand. Otago. Near Pulpit Rock, Silver Peaks, MURRAY 4288 (BM!, isotype).

**Nomenclatural remarks.** *Sphaerophorus tener* LAURER. The lectotypification follows OHLSSON in TIBELL 1987. FILSON (1986) explicitly attempted to validate OHLSSON’s choice of lectotype but cited instead a specimen in BM, not seen by OHLSSON. FILSON (1986) also cited an isolectotype in M, not found there (HERTEL, in litt.) and not seen by OHLSSON. As the specimen in PC has not been available for study, I do not yet wish to make any statement on the correct lectotype.

*Sphaerophorus australis* HOOK. f. & T. TAYLOR. *Sphaerophorus curtus* HOOK. f. & T. TAYLOR. The labels of the TAYLOR herbarium in FH were retyped at some stage when the specimens have been remounted. The year shown on the labels is 1844, but this is the year when the names were published, not the year of collection. The herbarium numbers cited by OHLSSON are also not on the labels. Otherwise, the collections are clearly part of the original material and also carry OHLSSON’s annotations.

Thallus slender, terete, more or less richly branched, forming loose to compacted cushions or patches; pale grey to white, rarely somewhat brownish. Main branches stouter, elongated, very sparingly branched; up to 7 cm long and ca. 0.4–1.8 mm wide; carrying terminal ascomata conspicuously above the mass of the thallus. Cortex thin, 30–45  $\mu$ m, 2–3 hyphal layers thick. Medulla dense; I-, K-, Pd-. Apothecia strictly terminal, ca. 0.8–2.1 mm diam. Ascomata ontogeny angiocarpic, the excipulum covers the developing mazaedium until it is finally shed in one piece (WEDIN 1990). The thalline receptacle of the ascoma is normally completely lost early in development. Mazaedium oriented apically. Ascospores globose, (5.5–)6.5–8.5(–10)  $\mu$ m diam., hyaline to pale grey, with a comparatively small amount of an irregular ornamentation consisting of an amorphous substance adhering to the spore wall after the spores have been released from the asci (WEDIN 1990), or completely smooth; spores becoming more bluish-greenish grey in KOH, but no visible change in colour in HNO<sub>3</sub>, ornamentation dissolving in KOH. The amount of spore ornamentation is as a rule considerably smaller than in the species of *Bunodophoron*. Pycnidia in tips of terminal branchlets or sometimes also along the lower sides of the branchlets. Conidiophores branched with conidiogenous



cells both terminally and intercalarily, corresponding to VOBIS' type V or VI (VOBIS 1980). Conidia hyaline; simple; broadly ellipsoidal to obovate;  $3.0\text{--}4.0 \times 1.5\text{--}2.0 \mu\text{m}$ .

**Chemistry.** Sphaerophorin and unidentified accessory chemical substances.

**Ecology and distribution.** *Leifidium tenerum* has a very large ecological amplitude and grows both on the ground and on rocks in alpine and subantarctic areas, and on trunks, branches and twigs of various trees, tree-ferns, bushes, lianas, and bamboos in temperate rainforests.

*Leifidium tenerum* increases in abundance in wet and more open, well-lit habitats. The frequency of apothecia increases dramatically with increasing altitude (and increasing rainfall) in New Zealand and southernmost South America, according to my own observations. At lower altitude apothecia are often produced in open places with a high local humidity, as close to waterfalls. *L. tenerum* is widely distributed in the Southern Hemisphere, occurring from Cape Horn to Temuco, Chile in South America, New Zealand, from Tasmania to central New South Wales in Australia (the collection from Queensland reported by TIBELL 1987 is a sterile fragment of a *Bunodophoron* species), and on several of the subantarctic islands.

*Leifidium* is closely related to *Bunodophoron* A. MASSAL. *Leifidium* differs from *Bunodophoron* by the terete, cushion-forming, richly branched thallus, the extremely thin cortex, the almost smooth spores, the small, ellipsoidal conidia, and by the proper excipulum of the ascoma persisting until very late in the development of the fruitbody, when the whole excipulum is shed in one piece, as in lifting off a cap.

*Leifidium tenerum* is easily distinguished in the field by the pale, slender and richly branched thallus forming cushions or patches, and the terminally situated apothecia formed on stouter terete branches higher than the rest of the thallus. The branches carrying ascomata vary considerable in size and thickness, as does the compactness of the cushions. As in other species of the family, the apothecia persist after spore production has ceased, and often only the naked hypothecium remains and no mazaedium can be found. Superficially, sterile, corymbose and brownish specimens of *L. tenerum* can sometimes resemble *Sphaerophorus globosus* but are, in a sterile state, most easily distinguished by their distinctly thinner cortex.

**Exsiccata examined.** ARNOLD, Lich. exs. 1210 (B, BM, H, H-NYL, S-Vrang, UPS); MALME & SANTESSON, Lich. Austroam. 381 (B, BM, H, S, UPS); 404 (B, BM, H, S, UPS); TIBELL, Calic. exs. 97 (BM, GZU, H, MEL, UPS); WEBER, Lich. exs. 294 (B, BM, GZU, H, MEL, UPS); VEZDA, Lich. sel. exs. 2154 (BM, H, UPS).

**Selected specimens examined.** **Argentina, Nequen:** Nahuel Huapi Nat. Park, along the track from Pto Blest to Laguna los Cantaros,  $41^{\circ}01'S$   $71^{\circ}50'W$ , 840 m s.m., 1989, WEDIN 1830 (UPS). – **Australia, New South Wales:** 20 km SE of Braidwood, Monga State Forest, along Mongarlowe River,  $35^{\circ}38'S$   $149^{\circ}55'E$ , 730 m s.m., 1981, TIBELL 12148 (UPS); **Tasmania:** ca. 12.5 km WSW Zeehan, along Trial Harbour Road, slopes SW Cumberland Lake,  $41^{\circ}54'S$   $145^{\circ}11'E$ , 200 m s.m., 1992, WEDIN 4309 (UPS, HO). – **Chile, Osorno:** Puyehue Nat. Park, along the road to Refugio Antillanca, 7 roadkm from Park Administration, in valley of Rio Nauto,  $40^{\circ}45'S$   $72^{\circ}18'W$ , 590 m s.m., 1989, WEDIN 1667 (UPS); **Tierra del Fuego:** Isla Clarence, Southern Peninsula, 1987, STENROOS 2579 (H); Isla Navarino, 13 km S Pto Williams, in valley SE Diente de Navarino,  $56^{\circ}02'S$   $67^{\circ}35'W$ , 300 m s.m.,

1989, WEDIN 1230 (UPS); **Valdivia**: ca. 40 km SW Valdivia, Monumento Natural Alerce Costero, El Mirador, 40° 04' S 73° 33' W, 930 m s.m., 1989, WEDIN 1699 (UPS); – **New Zealand, South Auckland**: Pirongia State Forest Park, Track 1, 1984, WRIGHT 6255 (AK, UPS); **Otago**: Mt Aspiring Nat. Park, Makaroa River, Cameron Flat, along Cameron Hut Track, 44° 09' S 169° 17' E, 400 m s.m., 1989, WEDIN 2857 (AK, BM, UPS); **Taranaki**: Mt Egmont Nat. Park, Pouakai range, along Dover Track, 39° 17' S 174° 05' E, 860 m s.m., 1990, WEDIN 2135 (AK, BM, CBG, CHR, HO, UPS, US).

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