

Evolutionary trends in the *Physciaceae*

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Abstract: The current delimitation of the family *Physciaceae* has been generally accepted since detailed descriptions of ascus characters allowed for a more natural circumscription of lichenized ascomycetes. The generic relations within the family are, however, still controversial and depend on the importance different authors attribute to specific morphological or chemical characteristics. The aim of this paper is to describe ascospore ontogeny and to test the present taxonomic structure of the family against a parsimony-based cladistic analysis, which includes three different scenarios of *a priori* character weighting. A study of ascospore ontogeny revealed two distinct developmental lines. One line revealed a delayed septum formation, which clearly showed transitions from spores with apical and median thickenings to spores without apical, but still well developed median thickenings, and to spores without any thickenings. In the second developmental line with an early septum formation, again taxa with no thickenings, median thickenings, and both median and apical thickenings were found. Although these characters were constant at a species level, median wall thickenings especially varied among otherwise closely related taxa. In the cladistic analyses the current taxonomic structure of the *Physciaceae* was only obtained after the five character groups, namely morphology and anatomy of the vegetative thallus, conidiomata and conidia, morphology and anatomy of the apothecia, ontogeny of the ascospores, and secondary metabolites of the thallus, were given equal importance, and after a subjective *a priori* weighting further increased the weight of the three characters 'conidial shape', 'presence of apical thickenings', and 'spore septation delayed'. This structure was not supported by a cladistic analysis with equally weighted characters but reflected the biased character weighting of the present day *Physciaceae* taxonomy. The taxonomic importance of conidial characters and of anatomical and ontogenetical spore characteristics need, therefore, a careful reconsideration in future.

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Introduction

The current delimitation of the family *Physciaceae* has been generally accepted since detailed descriptions of ascus characters allowed for a more natural circumscription of lichenized ascomycetes (Hafellner 1979; Hafellner *et al.* 1979). Generic relationships

within the family are still controversial, however, depending on the importance different authors attribute to specific morphological or chemical characteristics. Nevertheless, there is a general agreement in all morphology-based concepts of the *Physciaceae*, that growth form has a much lower taxonomic value than it was given in former systems (e.g. Zahlbruckner 1926), when crustose taxa were distinguished from foliose and fruticose taxa even at a family level. Ascospore characteristics have been recognized as important in various genera of the *Physciaceae*. Arnold (1872) used internal wall thickenings of ascospores in his treatment of *Rinodina* from Central Europe. In a paper on South American *Rinodina* species,

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Malme (1902) subdivided this genus into sections and subsections based on spore types. Poelt (1965) presented a systematic revision of the spore types within the *Physciaceae* and he recognized seven different spore types based mainly on internal wall thickenings. Since then ascospore anatomy has been considered the most important character to group genera within the family (Hafellner *et al.* 1979; Mayrhofer 1982) and Mayrhofer showed the outstanding value of these thickenings in delimiting species in the genus *Rinodina* (e.g. Mayrhofer & Poelt 1979; Mayrhofer 1984). As already stated by these authors, internal wall thickenings are not always easy to observe and later studies on *Buellia* (Scheidegger 1988, 1993; Scheidegger & Ruef 1988) introduced a more dynamic concept of the internal wall thickenings and emphasized that wall thickenings may change during spore ontogeny. This is also true for *Rinodina colobina* (Ropin & Mayrhofer 1995). Furthermore, lateral and median spore wall thickenings may change among closely related taxa. Delayed septum formation during spore ontogeny also has been recognized as a new character earlier during these studies and has, since then, been discussed in a range of taxonomic papers (Giralt 1994; Giralt & Matzer 1994; Giralt & Mayrhofer 1994a, 1994b, 1995).

Conidia have been given less consideration in the literature, although Vainio (1890) used filiform conidia to delimit the taxon presently known as *Hyperphyscia*. Later the same type of conidia were found in *Buellia* (Choisy 1950) and used to delimit the genus *Amandinea* (Scheidegger 1993; Matzer *et al.* 1994; Sheard & May 1997; Mayrhofer *et al.* 1999) with long, filiform conidia. The same type of conidia are also present in the newly described genus *Australiaena* (Matzer *et al.* 1997a). An ellipsoid type of conidia was found to be characteristic of the genera *Phaeophyscia* (Moberg 1977) and *Mobergia* (Mayrhofer *et al.* 1992), whereas the bacillar conidial type is common in all other genera.

In a revision of European taxa of the genus *Buellia* (Scheidegger 1993), pycnoconidial characters proved to be more constant than

ascospore wall thickenings and were used to separate the genus *Amandinea*. Later, taxa previously treated under *Rinodina* were included in this same genus. The present concept of the genus *Amandinea* includes both species with and without median spore wall-thickenings, but this character is always constant at the species level (Scheidegger 1993; Matzer *et al.* 1994). Authors who considered the long filiform conidia of high taxonomic value hypothesize the foliose genus *Hyperphyscia* to be closely related to *Amandinea* (Scheidegger 1993), whereas authors who favoured the ascospore characters placed *Hyperphyscia* in the vicinity of *Physcia* and *Phaeophyscia* (Hafellner *et al.* 1979). The authors all agree that a more comprehensive treatment of the morphology-based taxonomy of the family can only be realized through a continuing co-operation where the experience from different taxonomic groups among the *Physciaceae* could be shared.

During the past decade character states of spore ontogeny have been discussed during workshops and selected taxa representing the major diversity of the family have subsequently been analysed. The aim of this paper is to test the present taxonomic structure of the family with a parsimony-based cladistic analysis, which included two scenarios of *a priori* character weighting, and one with unweighted characters.

Material and Methods

Specimens

One to several specimens were selected for each genus of the *Physciaceae* in this study. If available, fertile species, were selected, irrespective of the region and substratum and, in heterogeneous genera especially, more than one species was investigated. Most specimens analysed were herbarium specimens that were several years old. If possible well developed, luxuriant specimens were selected and cited as reference specimens in Table 1. For most species additional specimens not cited here were tested and checked for compatibility with the reference specimens.

Selection of characters

A total of 123 characters were evaluated. Forty-eight invariable characters were excluded, and

TABLE 1. List of specimens analysed and references for chemical analyses

Taxon	Specimen	Chemistry
<i>Amanidinea conitops</i> (Wahlenb. in Ach.) Scheideg. & Mayrhofer	Norway, Finnmark: Vardö, Ad scopulos maris glacialis circa Wardöc Finmarkiae orientalis. 1864, <i>Fries</i> , <i>Fries</i> , <i>Lichenes Scand.</i> 69 (W)	Scheidegger (1993)
<i>A. inasperata</i> (Nyl.) H. Mayrhofer & Ropin	Argentina, Buenos Aires: Zarate, 6 ix 1894, G. O. Malme (UPS)	Mayrhofer et al. (1999)
<i>A. petermannii</i> (Hue) Matzer, H. Mayrhofer & Scheideg.	Antarctica, South Georgia: on rocks by shore, near Koppen Point, Royal Bay GR 162 098, 1961, S.W. Graene 2230 (AAS), after Matzer et al. (1994)	Matzer et al. (1994)
<i>A. punctata</i> (Hoffm.) Coppins & Scheideg.	England, Cumberland: Borrowdale, c. 0.5 mile of Rostwaite, on <i>Fraxinus</i> in pasture by road. 30 vii 1970, Coppins & Rose (Edinburgh)	Scheidegger (1993)
<i>Anaptychia ciliaris</i> (L.) Körb.	Sweden, Uppland: 1959, <i>Santesson</i> 12757 (UPS)	This study
<i>Australiaena streimannii</i> Matzer, H. Mayrhofer & Elix	Australia, Northern Territory: Robin Falls, 13 km SSE of Adelaide River Township, dense vegetation on creek flats surrounded by <i>Eucalyptus</i> savannah. 1989, H. Streimann 42134 (CANB—holotype), after Matzer et al. (1997a)	Matzer et al. (1997a)
<i>Buellia aethalea</i> (Ach.) Th.Fr.	Sweden, Västergötland: Langared; Hällnäs, siliceous boulder along road. 13 viii 1949, <i>Degehus</i> (UPS)	Scheidegger (1993)
<i>B. disciformis</i> (Fr.) Mudd	Sweden: 'in Fago & c. obvia' E. Fries, 1826, Novae Schedulae criticae de Lichenibus Suecanis, Part II, p. 9 (UPS), thallus in the middle of the specimen, indicated 1.)	Kalb & Elix (1998)
<i>B. dispersa</i> A. Massal.	France, Pyrénées-Orientales: Chaîne des Albères W of Port-Vendres, valley to Ermit. N. D. de Consolation, vineyard at the E-slope, big siliceous boulder, 60 msm, 19 vii 1985, C. Scheidegger & K. Jaggi (Sch-7547)	Scheidegger (1993)
<i>B. leptoclina</i> (Flot.) A. Massal.	Norway, Sør Trøndelag: Oppedahl hd. In the vicinity of Kongsvald, 1 km W of the highest point of Mt Knutshö, on siliceous boulders, 1964, <i>Tibell</i> 2239a (Tibell)	Scheidegger (1993)
<i>B. ocellata</i> (Flot.) Körb.	France, Pyrénées-Orientales: Chaîne des Albères. Banyuls, between Pic Joan and Tour Carroig near Font Fresque, 320 msm, 1 viii 1985, C. Scheidegger & K. Jaggi (Sch-8486)	Scheidegger (1993)
<i>B. spuria</i> (Schaer.) Anzi	Italy, Trieste: 'Litorale austriacum: ad saxa arenaria in agro tergestino.' 1899 <i>Schuler</i> . <i>Kryptogamae exsicc.</i> 59 (W)	Scheidegger (1993)
<i>B. triphragmia</i> (Nyl.) Arnold	Austria, Tirol: Allgäuer Alpen, Vorarlberg, Kleines Walsertal, Bärgeuntbach S von Baad, subalpine forest. 1300–1400 msm, on <i>Alnus incana</i> , 1979, J. Hafelner. Pl. Graec. Lich. 187 (UPS 75718)	Kalb & Elix (1998)

TABLE 1. *Continued*

Taxon	Specimen	Chemistry
<i>Dermatisicum thumbergii</i> (Ach.) Nyl.	South Africa , Cape Prov: Montagu Div., Kogmans Kloof near Montagu, on perpendicular rock faces, exposed, c. 300 m, 1949, <i>R. A. Maas Geesteranus</i> 6731. Almborn, Lich. Afric. 56 (GZU)	Culberson (1970), Harper & Letcher (1966)
<i>Dermisicellum catanzensis</i> (Willey) Hafellner & Poelt	USA , South Carolina: Chester Co. Landsford, on rocks in Catawba River, 27 xii 1886, <i>W. A. Green</i> (H-Nyl. 29092)	Hafellner <i>et al.</i> (1979)
<i>Dimelaena oreina</i> (Ach.) Norman	Austria , Steiermark: Eastern slope of Seetaler Alps, Zirbitzkogel, 10 km SW of Judenburg, 200 m N of Winterleitenhütte, about 1800 m, vii 1987, <i>W. Obermayer & J. Hafellner</i> (GZU)	Leuckert <i>et al.</i> (1981), Leuckert <i>et al.</i> (1975)
<i>Diploicia africana</i> (Tuck.) Matzer, H. Mayrhofer & Rambold	South Africa , Cape Province: Wynberg, E slopes of Table Mt., along Skeleton Stream, 1953, <i>O. Almborn</i> 11388	Matzer <i>et al.</i> (1997b)
<i>D. canescens</i> (Dicks.) A. Massal.	France , Bretagne: Ploescat, Réserve de Kéremma. <i>P. Clere & C. Scheidegger</i> (Scheidegger)	Elix <i>et al.</i> (1988)
<i>Dirinaria confluens</i> (Fr.) D. D. Awasthi	Kenya , Central Prov: 1972, <i>Nannfeldt</i> 22092 (UPS)	Awasthi (1975)
<i>Hafellia leptoclinoides</i> (Nyl.) Scheideg. & H. Mayrhofer	France , Pyrénées-Orientales: Chaîne des Albères S of Argelès-sur-Mer, between Pic Saillfort and Tour de la Massane, SW exp. 810 msm, 18 vii 1985, <i>C. Scheidegger</i> (Sch) Kalb. Lichenes Neotropici Nr. 372	Scheidegger (1993)
<i>H. parastata</i> (Nyl.) Kalb	USA , Florida: Sanford, on trees. Mai 1928, <i>S. Rapp</i> (UPS-158435), rev. A. Nordin (1996)	Birbeck <i>et al.</i> (1990)
<i>Heterodermia erinacea</i> (Ach.) W. A. Weber	Mexico , Baja California: 1989, <i>R. Moberg</i> 8909 (UPS)	Moberg & Nash III (1999)
<i>H. hypoleuca</i> (Ach.) Trevis.	Russia , Vladivostok: Lazo, 1991, <i>Moberg</i> 9858 (UPS)	Moberg & Nash III (1999)
<i>Hyperphyscia syncolla</i> (Nyl.) Kalb	USA , Wisconsin: Lich. Wisc. exs. no 88 (UPS)	Moberg (1987)
<i>Lecanora argentata</i> (Ach.) Malme	Sweden , Uppland: Almunge parish, 'Harpbol lund' (= on the southern shore of Långsjön, W of Uvberget). On <i>Alnus glutinosa</i> , 4 vi 1961, <i>R. Santesson</i> (UPS 14089)	Brodo (1984)
<i>Mobergia calcitiformis</i> (W. A. Weber)	Mexico , Baja California: Guadalupe Island, Melpomene Cove, southern tip of the island; abundant on cobbles, level summit of first plateau just above the weather station, near the rim of the cliffs on the southeast coast, 200–500 ft. alt., 21 iv 1963, <i>W. A. Weber</i>	Mayrhofer <i>et al.</i> (1992), Weber (1964)
H. Mayrhofer & Sheard		
<i>Phaeophyscia ciliata</i> (Hoffm.) Moberg	Norway , Oppland: 1969, <i>Moberg</i> 1313a (UPS)	Moberg (1977)
<i>Phaeorrhiza umbrosa</i> (Fr.) H. Mayrhofer & Poelt	Austria , Salzburg: Hohe Tauern, east slope of Edelweisspitze near road Grossglockner, 2500–2600 m <i>R. Türk & H. Wittmann</i> (GZU)	Huneck <i>et al.</i> (1989)
<i>Physcia stellaris</i> (L.) Nyl.	Sweden , Angermanland: 1973, <i>Moberg</i> 2009 (UPS)	Moberg (1977)
<i>Physconia distorta</i> (With.) J. R. Laundon	Sweden , Uppland: 1974, <i>Moberg</i> 2314 (UPS)	Moberg (1977)

TABLE 1. *Continued*

Taxon	Specimen	Chemistry
<i>Pyxine berteroniana</i> (Fée) Imshaug	Tanzania , Tanga Prov.: 1971, <i>Moberg</i> 1494b (UPS)	Hunekl <i>et al.</i> (1987)
<i>Rinodina atrocinerea</i> (Hook.) Körb.	Norway , Hordaland: Lindås-Halvøya, near Nesbø, 20–100 m, 8 ix 1976, <i>A. Buschard, P. M. Jørgensen & J. Poelt</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>R. bischoffii</i> (Hepp) A. Massal.	Austria , Steiermark: Grazer Bergland, southern slope of Gamskogel, W of Kleinsüßing, 450–650 m, 7 v 1977, <i>J. Poelt</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>R. confragosa</i> (Ach.) Körb.	Austria , Steiermark: Koralpe, Kumpfkogel N of Glashütten, 23 v 1976, <i>J. Poelt</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>R. conradii</i> Körb.	Austria , Tirol: Ötztal Alps, along path Tasachtal to Taschachferner, 2050 m, 17 viii 1986, <i>E. Hinteregger</i> (GZU)	Wirth (1995)
<i>R. gemmani</i> Bagl.	Greece , Attika: Rocks W of Lavrion, close to Kap Sunion, 7 iv 1971, <i>J. Poelt</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>R. sophodes</i> (Ach.) A. Massal.	France , Corse, Haute-Corse: Col Prato, E of Morosaglia, slopes of Monte San Petrone, S of Col de Prato, 1200 m, 10 v 1990, <i>H. Mayrhofer & K. Ropin</i> (GZU)	Ropin & Mayrhofer (1993)
<i>R. thiomela</i> (Nyl.) Müll. Arg.	New Zealand , South Island: Canterbury, Banks Peninsula E of Christchurch, summit Road 7 km S of Okains Bay, 18 km N of Akaroa, c. 550 m, 1981, <i>H. Mayrhofer</i> 2383 (GZU)	Elix & Porrelli (1990), Leuckert & Mayrhofer (1984)
<i>R. trachytica</i> (A. Massal.) Bagl. & Carestia	Italy , Parma: S-W exposed slopes of Monte Prinzerza at northern border of Boschi di Bardone, 600–800 m, 29 x 1978, <i>J. Poelt</i> (GZU)	Mayrhofer & Leuckert (1985)
<i>R. turfacea</i> (Wahlenb.) Körb.	Austria , Steiermark: Schladminger Tauern, Kleinsöllktal, W exposed slopes of Schaufelspitze, 2350 m, 1985, <i>M. & H. Mayrhofer</i> 4943 (Mayrhofer)	Wirth (1995)
<i>R. szuwachhiana</i> (Kremp.) Körb.	Austria , Kärnten: Kanzianiberg near Finkenstein SE of Villach, 650–700 m, 10 ii 1974, <i>J. Poelt</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>Rinodina controversa</i> (A. Massal.) H. Mayrhofer & Poelt	Greece , Fthiotis: Kallidromo-mountains, along the road between Rengino and Modi, 600–640 m, 14 ix 1989, <i>Mayrhofer & Scheidegger</i> (GZU)	Hecklau <i>et al.</i> (1981)
<i>Santessonia namibensis</i> Hale & Vobis	Namibia , Outjo district: Skeleton Coast Park (grid 2313 BA), marble ridge N of the entrance gate at Ugabmond, on exposed marble and on pebbles on the ground. 9 i 1986, <i>I. Kärnejelt</i> (8609-23; Almborn, Lich. Afric. Nr. 144)	Hale & Vobis (1978), Sérusiaux & Wessels (1984)
<i>Tornabea scutellifera</i> (With.) J. R. Laundon	Somalia , Bari Prov.: 1986, <i>Thulin & Warfa</i> 5878 (UPS)	Galun (1970)

75 informative characters (Table 2) used for the cladistic analyses. The characters were divided into five groups describing the morphology and anatomy of the vegetative thallus (10), the conidiomata and conidia (4), the morphology and anatomy of the apothecia (8), the ontogeny of the ascospores (10) and secondary metabolites of the thallus and pigments (43). Logically dependent absent characters were marked with '?'.

Morphology and anatomy

The methods are explained in detail in recent taxonomic revisions published by the authors (Moberg 1977; Mayrhofer 1984; Scheidegger 1993).

Spore ontogeny

Sections cut by hand through well-developed apothecia of herbarium specimens were slightly squashed and examined in water under a microscope (Aristoplan, Leica) at $\times 1000$ magnification (aperture 1.32) with a drawing tube. Drawings were made at $\times 3000$ magnification. The gradually intensifying pigmentation of the spore wall during the spore ontogeny was used to arrange the series of developmental stages (Scheidegger 1993). The terminology of the spore wall layers follows Scheidegger (1993). Only sections where the complete spore ontogeny, from non-septate to mature spores, was well developed were considered. All developmental stages were drawn from one section and the developmental stages specified below were further used for the description of the spore ontogeny: (i) spore non-septate, hyaline, (ii) spore 1-septate, hyaline, thin walled, (iii) thickenings beginning at septum and/or apices (sometimes subapically), wall unpigmented or faintly pigmented, (iv) fully developed thickenings at apices and septum, wall faintly pigmented, (v) wall fully pigmented. Overmature spores and untypical forms were not considered.

Although the data presented in this paper originate from one specific specimen only, we generally checked much more material and found no significant deviations from the ontogeny presented in this paper.

Chemistry

Information concerning the secondary metabolites was either taken from literature recorded in Table 1, or obtained by thin layer chromatography (TLC) carried out during these studies following Culbertson & Ammann (1979). The presence of chemical substances and the corresponding biosequential patterns (Huovinen & Ahti 1982) was denoted by '1' and the absence of '0'. The logically dependent absent characters are marked with '?'.

Cladistic analyses

The cladistic analyses were carried out with PAUP (3.1.1) (Swofford 1993); trees were analysed with MacClade (3.07) (Maddison & Maddison 1992). *Lecanora argentata* was used as outgroup and all characters were

unordered. Three analyses were run with different character weighting. In the first analysis, characters remained unweighted. A general heuristic search where only the shortest trees were kept was run. In a second analysis characters were weighted in order that the five character groups (1–5: vegetative thallus morphology, apothecial anatomy, conidial characters, spore anatomy and ontogeny, and secondary products) had an equal importance in the analysis. Therefore the weight of each character was calculated as the reciprocal value of the number of characters belonging to the respective group. In order to compensate for the number of character states, the character of weight was further multiplied by the reciprocal value of the number of character states. The weight of each character is given in Table 2. In the third analysis, the weights of the following characters were additionally increased: 'conidial shape' (120 instead of 40), 'presence of apical thickenings' (48 instead of 16) and 'septation delayed' (60 instead of 24).

Results

The characters investigated are summarized in Table 3. The chemical, general morphological and anatomical characters need no further explanation.

Spore ontogeny

In the post-meiotic ascus the first stages of the ascospore development were always non-septate, thin-walled and hyaline (Figs 1–4). In the majority of the species investigated a septum was formed very early in the spore development, when the spore wall was still completely unpigmented and considerably thinner than in the mature spores (Figs 1–3). In Fig. 1 the spore ontogeny was simple and after septum formation the pigmentation of the perispore layer slowly intensified until it was dark brown at the mature stage. The thickness of the endospore layer gradually increased during spore development and reached the maximum thickness at the mature stage or shortly before. In Fig. 2 the pigmentation of the perispore was the same as the spores described in Fig. 1. However, the thickness of the endospore increased much more in the medium part of the ascospore and formed more or less thick cushions on both sides of the septum. In *Rinodina lecanorina* these median thickenings were relatively small and later disappeared completely during

TABLE 2. Description of the characters, the character states and the character weights used in the cladistic analyses

Character	Character states	Character group			Weight in analyses
		2	3	3	
1 Growth form	(1) crustose (effuse), (2) foliose, (3) fruticose dorsiventral, (4) fruticose erect, (5) umbilicate, (6) placodioid	1	7	7	7
2 Upper cortex	(1) absent, (2) prosoplectenchymatous, (3) sclerenchymatous, (4) paraplectenchymatous	1	12	12	12
3 Pruina consists of dead cells (dark in polarized light)	(0) absent, (1) present	1	24	24	24
4 Pruina consists of calcium oxalate (bright in polarized light)	(0) absent, (1) present	1	24	24	24
5 Cortical hyphae with pigment	(0) hyaline, (1) brown	1	24	24	24
6 Lower cortex	(1) absent, (2) paraplectenchymatous, (3) prosoplectenchymatous	1	16	16	16
7 Pigmentation of lower cortex	(1) hyaline, (2) brownish, (3) black	1	16	16	16
8 Rhizinae	(0) absent, (1) simple, (2) brush-like, (3) squarrose	1	16	16	16
9 Cilia	(1) present, (0) absent	1	24	24	24
10 Soredia	(1) present, (0) absent	1	24	24	24
11 Presence of pycnidia	(1) present, (0) absent	2	60	60	60
12 Conical shape	(0) filiform, (1) bacillar, (2) ovoid	2	40	40	120
13 Conidiogenous cells	(0) intercalary, (1) terminal	2	60	60	60
14 Conidiogenesis pleurogen	(1) present, (0) absent	2	60	60	60
15 Position of apothecium	(1) sessile, (2) innate	3	30	30	30
16 Presence of thalline margin	(0) absent, (1) present	3	30	30	30
17 Presence of algae in thalline margin	(1) present, (0) absent	3	30	30	30
18 Proper exciple	(0) absent, (1) parathecial, (2) lecidine	3	20	20	20
19 Disc pruina	(0) absent, (1) present	3	30	30	30
20 Oil droplets in hymenium	(0) absent, (1) present	3	30	30	30
21 Colour of hypothecium	(0) hyaline, (1) pale brown, (2) dark brown	3	20	20	20
22 Terminal cells of paraphyses	(1) incrassate, (0) not incrassate	3	30	30	20
23 Spore septation	(0) 0-septate, (1) 1-septate, (2) 3- or more septate, (3) muriform or submuriform	4	16	16	16

TABLE 2. *Continued*

Character	Character states	Character group			Weight in analyses	
		2	3	4		
24	Septation delayed			4	24	60
25	Presence of apical thickenings	(0) yes, (1) no, septation prior to complete spore wall development		4	16	48
26	Median thickenings	(0) absent, (1) indistinct, (2) distinct		4	24	24
27	Spore wall swelling in KOH	(0) absent, (1) present		4	24	24
28	Lateral thickenings	(1) swelling, (0) not swelling		4	24	24
29	Spore length (mean values)	(1) present, (0) absent		4	24	24
30	Spore surface ornamentation	(0) <10 µm, (1) 10–20 µm, (2) >20 µm		4	24	24
31	Spore colour	(0) smooth, (1) verrucose, (2) striate		4	24	24
32	Torus	(1) brown, (0) hyaline		4	24	24
33	Iodine reaction of medulla	(1) distinct, (0) diffuse		4	24	24
34	A acetate—polymalonate pathway	(1) amyloid, (0) not amyloid		5	5	5
35	Orcinol series	(1) present, (0) absent		5	5	5
36	Paradepsides and tridepsides	(1) present, (0) absent		5	5	5
37	Confluent acid	(1) present, (0) absent		5	5	5
38	2'-O-methylperlatolic acid	(1) present, (0) absent		5	5	5
39	Divaricatic acid	(1) present, (0) absent		5	5	5
40	Gyrophoric acid	(1) present, (0) absent		5	5	5
41	Lecanoric acid	(1) present, (0) absent		5	5	5
45	Lobaric acid	(1) present, (0) absent		5	5	5
46	Gangaleoidin	(1) present, (0) absent		5	5	5
47	Variolaric acid	(1) present, (0) absent		5	5	5
48	β -Orcinol series	(1) present, (0) absent		5	5	5
49	Paradepsides	(1) present, (0) absent		5	5	5
50	Brialmontin			5	5	5
51	Atranorin	(1) present, (0) absent		5	5	5
52	Chloratranorin	(1) present, (0) absent		5	5	5
53	Squamatic acid	(1) present, (0) absent		5	5	5

TABLE 2. *Continued*

Character	Character states	Character group		Weight in analyses	
		2	3	2	3
54	Depsidones	(1) present, (0) absent	5	5	5
55	Fulgidin (incl. fulgoicin, etc)	(1) present, (0) absent	5	5	5
56	Norstictic acid	(1) present, (0) absent	5	5	5
57	Stictic acid	(1) present, (0) absent	5	5	5
58	Fumarprotocetraric acid	(1) present, (0) absent	5	5	5
59	Usnic acid and related	(1) present, (0) absent	5	5	5
60	Usnic acid	(1) present, (0) absent	5	5	5
61	Placodiolic acid	(1) present, (0) absent	5	5	5
62	Xanthonones	(1) present, (0) absent	5	5	5
63	Norlichexanthonones	(1) present, (0) absent	5	5	5
64	Lichexanthonones	(1) present, (0) absent	5	5	5
65	Thiomelin	(1) present, (0) absent	5	5	5
66	B mevalonic acid pathway	(1) present, (0) absent	5	5	5
67	Triterpenes	(1) present, (0) absent	5	5	5
68	C shikimic acid pathway	(1) present, (0) absent	5	5	5
69	Rhizocarpic acid	(1) present, (0) absent	5	5	5
70	D apothecial pigments	(1) present, (0) absent	5	5	5
71	Green; K ⁻ , HNO ₃ + red	(1) present, (0) absent	5	5	5
72	Brown; K ⁻ , HNO ₃ -	(1) present, (0) absent	5	5	5
73	Dull brown, K+ brownish solution, HNO ₃ -	(1) present, (0) absent	5	5	5
74	Orange-red, K+ red solution, HNO ₃ -	(1) present, (0) absent	5	5	5
75	Medullary pigment; yellow, K -	(1) present, (0) absent	5	5	5

TABLE 3. *Continued*

TAXON	Character number and states*																																						
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75		
<i>Amalindica conopsea</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>A. insperata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>A. povernanii</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>A. punctata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Andrychella ciliaris</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Australoecia streuhamii</i>	0	1	1	2	1	0	1	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Bielchia aculeata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. disciformis</i>	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. dispersa</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. leporina</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. ocellata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. sporita</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>B. triplicapita</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Dermatocisma flandbergii</i>	0	0	1	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Dermatocisma catenabasis</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Diplazia areolaris</i>	0	1	0	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>D. canescens</i>	0	1	0	0	1	1	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Dermaria confinis</i>	1	0	0	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Haplidia lepiclinooides</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>H. parastata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Heterodermia ermauca</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>H. hypoleuca</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Hyperphyscia synwalla</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Lecanora argenteata</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Mobergia californiensis</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Phaeophyscia ciliana</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Phaeophyscia nitidifera</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Physcia sullaris</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Physconia distorta</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Pyrenia borearum</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Rimodina atrinacruca</i>	0	1	1	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>R. bisulphurea</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. confragosa</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. conradii</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. gemmarii</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. siphoides</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. thiomela</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>R. trachytica</i>	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>R. turfacca</i>	0	0	0	1	1	0	0	0	1	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>R. zweckbachiana</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Rimodina compta</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Santessonia namibensis</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Tornabuoa scutellifera</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	

*Character states according to Table 2. '?' = logically dependent absent characters.

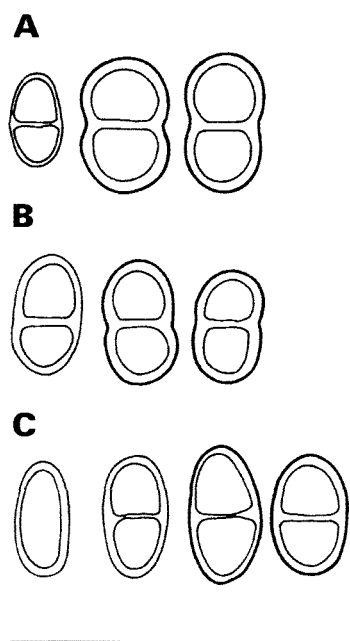


FIG. 1. Spore ontogeny with early septum formation; no internal wall thickenings are formed. A, *Dimelaena oreina*; B, *Dermatiscum thunbergii*; C, *Santessonia namibensis*. Scale = 10 μ m.

spore ontogeny. However, in *Physconia distorta* and *Tornabea scutellifera* the median thickenings were very prominent and persisted in the mature stage. In Fig. 3, in addition to the formation of median endospore thickenings, apical thickenings were also formed during the ascospore development. These apical thickenings may also later disappear during spore development. *Phaeophyscia ciliata* had much more prominent apical thickenings during early developmental stages than in mature ascospores.

Unlike the taxa described above, Fig. 4 shows species where the septum formation was delayed. The first, non-septate stage developed a rather thick endospore and a slight pigmentation of the perispore appeared before septation. In the genera *Australiaena*, *Diploicia*, *Dirinaria*, *Pyxine* and some *Rinodina* species, prominent apical thickenings of the endospore developed well before the septation. Median thickenings appeared later during the spore ontogeny and again disappeared in mature and

especially overmature spores. Generally, the perispore pigmentation was less intensive in this group than in the taxa described earlier. *Hafellia parastata* shared the delayed septation with the other taxa of this group but instead of an apical thickening of the endospore, it formed distinct lateral thickenings. The endospore was usually thinner at the apex of the spore and often also the perispore was less intensively pigmented at the apex than elsewhere.

Cladistic analyses

In the first analysis all characters received equal weight. A heuristic search found 182 shortest trees with a length of 244 steps. The strict consensus tree (Fig. 5) of *Rinodina* was poorly resolved with most of the species arising from polytomy at the base of the tree (A in Fig. 5). All foliose and subfruticose taxa were grouped in one clade (B in Fig. 5). However, the taxa, which were recorded in this clade included different conidial types, for example *Hyperphyscia* with filiform conidia, *Phaeophyscia* with ovoid conidia and *Anaptychia*, *Tornabea*, *Heterodermia*, *Dirinaria*, *Pyxine*, *Physconia* and *Physcia* with bacillar conidia. As well as in clade B, complex growth forms also appeared in clade E where crustose taxa of the genera *Buellia* and *Amandinea* were grouped with placodioid, umbilicate and bullate species. Except for *Diploicia* all genera that were represented with more than one species in our study appeared not to be monophyletic. *Buellia* (E in Fig. 5), and *Amandinea* (D and E in Fig. 5) were paraphyletic. In the latter genus three taxa were grouped in clade D (Fig. 5), whereas *A. petermannii* appeared as a sister group of *Dimelaena* in clade E. Crustose taxa with oil droplets in the hymenium i.e. *Buellia disciformis*, *B. triphragmia* and *Hafellia* spp. form a monophyletic group (F in Fig. 5).

Weighted characters

In the second analysis characters were weighted in an attempt to give each character group equal importance. With such weighted characters a heuristic search found 405 shortest trees with a length of

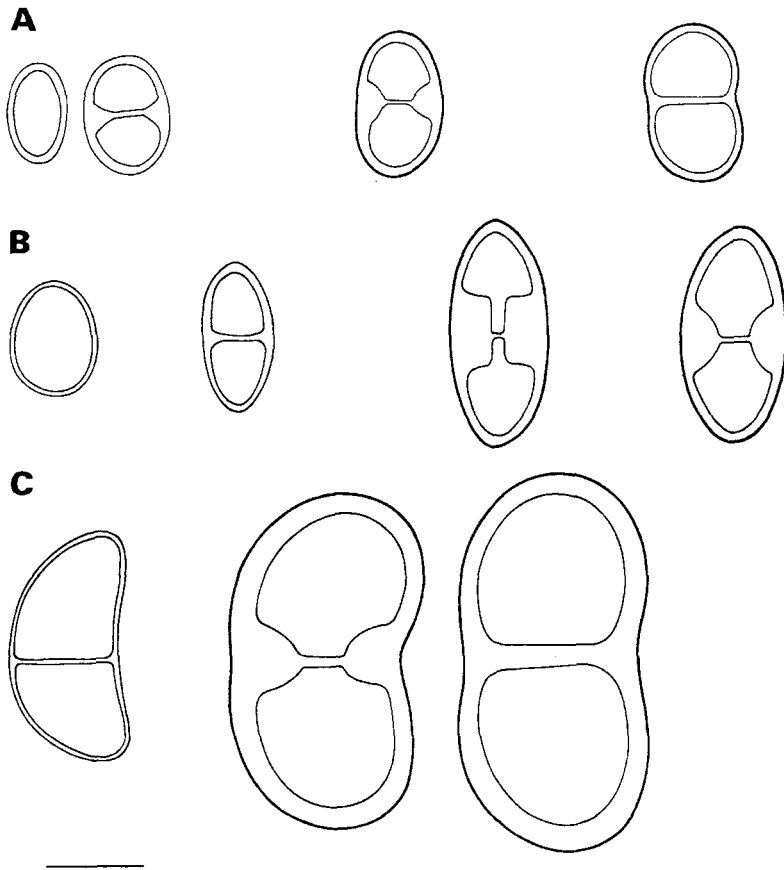


FIG. 2. Spore ontogeny with early septum formation; median but no apical thickenings are formed. A, *Rinodina lecanorina*; B, *Tornabea scutellifera*; C, *Anaptychia ciliaris*. Scale = 10 μm .

3320 steps. In the strict consensus tree (Fig. 6) the taxa with filiform conidia turned out to form a monophyletic group which included the crustose *Amandinea*, the placodioid *Australiaena* and the foliose *Hyperphyscia*. This clade formed the sister group of all other genera with bacillar or ovoid conidia (clade A in Fig. 6). However, the group with ovoid conidia, which included the genera, *Mobergia* and *Phaeophyscia*, was polyphyletic (clades C and E in Fig. 6). On the other hand, the genera with delayed spore septation with the genera *Hafellia*, *Diploicia* (clade G in Fig. 6), *Pyxine*, *Dirinaria* and *Rinodina gennarii* (clade B in Fig. 6), and *Rinodina conradii* (in clade D in Fig. 6), were paraphyletic. Unlike in the first analysis,

foliose and subfruticose taxa turned out to be polyphyletic in this analysis. Most foliose and subfruticose taxa remained grouped into one clade (C in Fig. 6), but *Hyperphyscia* appeared in clade A because of its filiform conidia and *Dirinaria* and *Pyxine* formed a distinct clade (B in Fig. 6). However, clade C with *Physcia*, *Anaptychia*, *Tornabea*, *Phaeophyscia*, *Physconia* and *Heterodermia*, still remained heterogeneous for bacillar and ovoid conidia.

In the third analysis, the weight of the two characters 'conidial shape' and 'septation delayed', which were considered of highest taxonomic importance by the authors, were further increased. With this addition, a heuristic search found 729 shortest trees with a

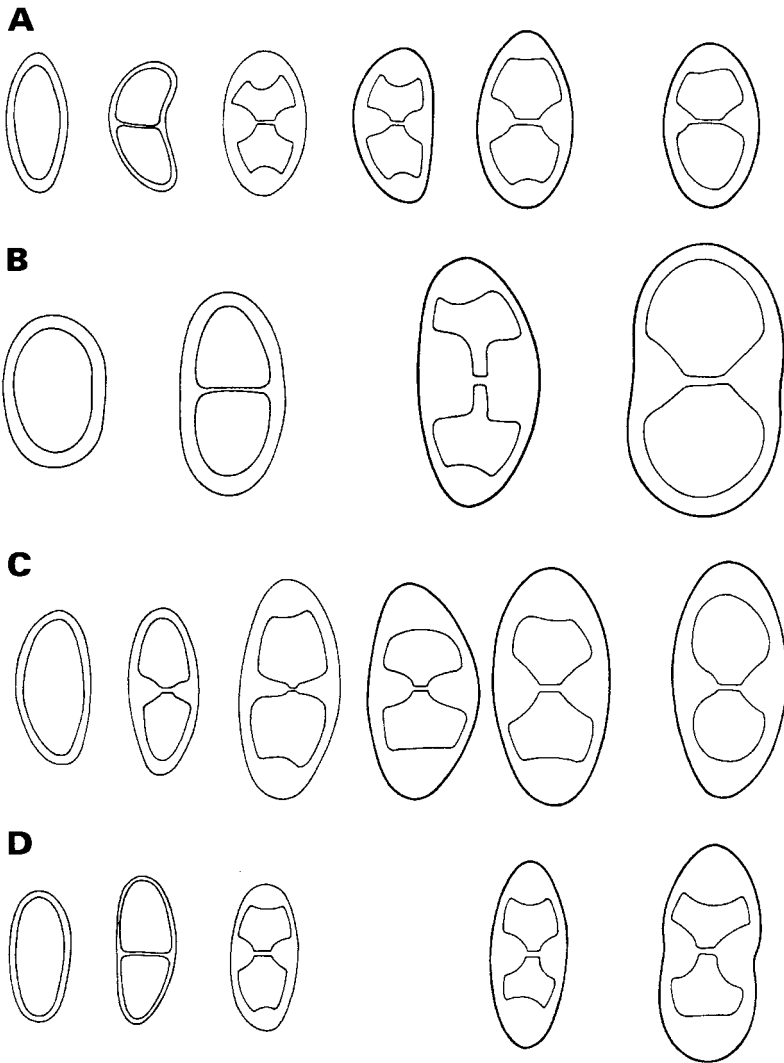


FIG. 3. Spore ontogeny with early septum formation; median and apical thickenings are formed. A, *Mobergia calculiformis*; B, *Physconia distorta*; C, *Phaeophyscia ciliata*; D, *Physcia aipolia* (Sweden). Scale = 10 μ m.

length of 3690 steps. In the strict consensus tree (Fig. 7) the two taxa with ovoid conidia, *Phaeophyscia ciliata* and *Mobergia calculiformis*, now formed a monophyletic group (clade B *pro parte*). Except for *Rinodina conradii* and *R. gennarii*, the taxa with delayed spore septation were now grouped in one distinct clade, D, with *Buellia disciformis*, *B. triphragmia*, *Hafellia*, *Diploicia*, *Dirinaria*

and *Pyxine*. Clade C linked members of the crustose genera *Rinodina*, *Buellia* and *Rinodina* with placodioid, umbilicate and fruticose taxa without internal wall thickenings. Apical and median thickenings which were found in *Rinodina trachytica* and *R. sophodes* are revealed as plesiomorphic character states in this clade. Apomorphic character states in clade C included the loss of apical

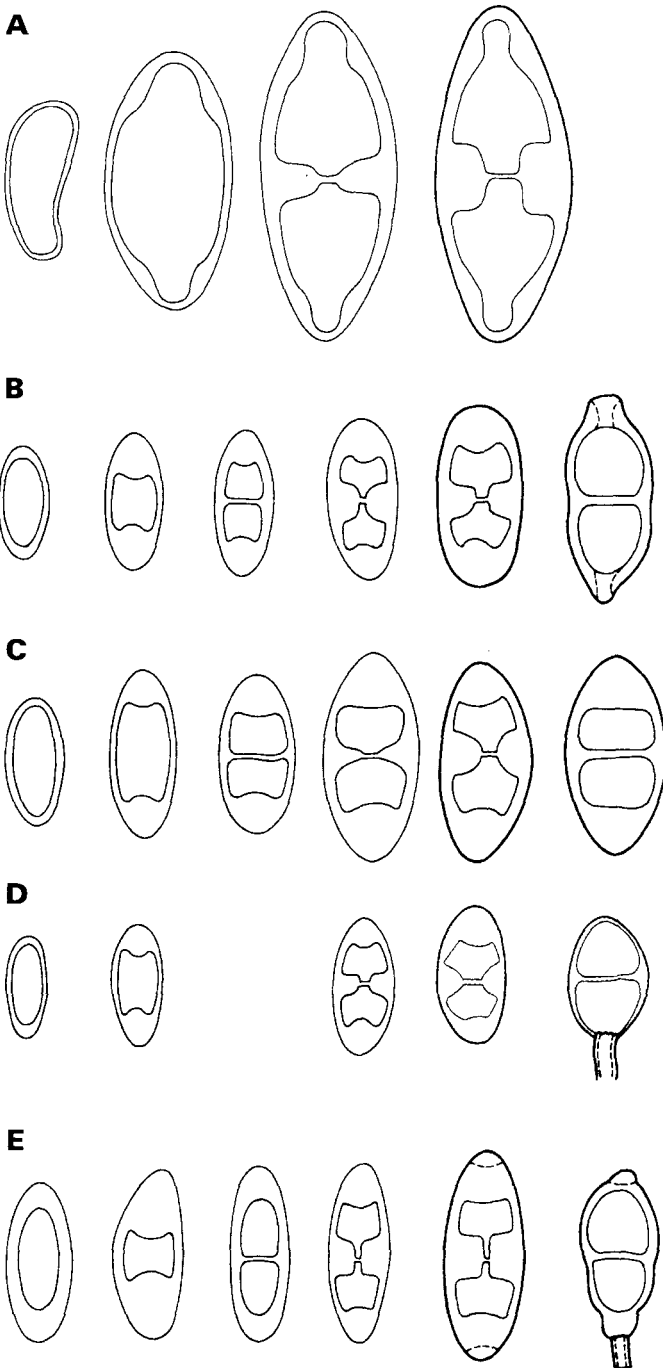


FIG. 4. Spore ontogeny with delayed septum formation. A with median and lateral internal wall thickenings, B–E with median and apical wall thickenings. A, *Hafellia dissa*; B, *Dirinaria confluens*; C, *Diploicia africana*; D, *Diploicia canescens*; E, *Pyxine berteriana*. Scale = 10 μ m.

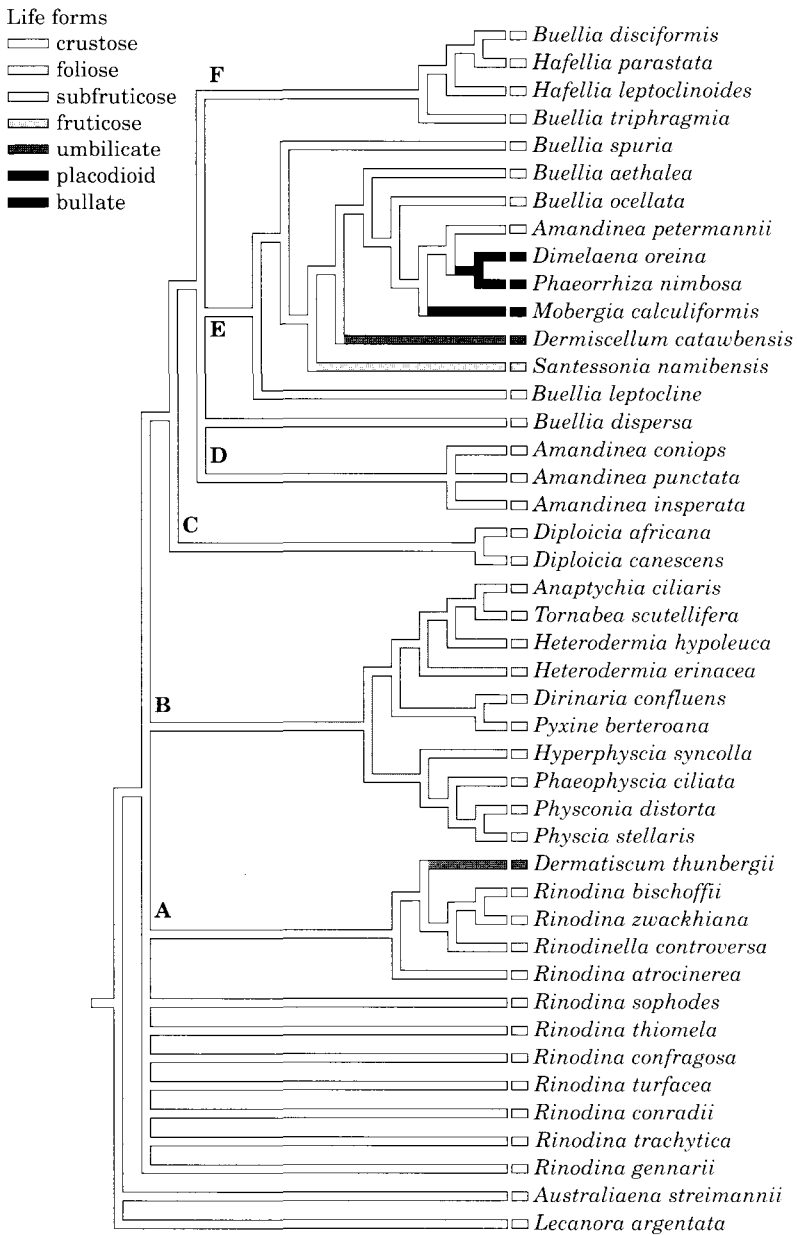


FIG. 5. Strict consensus tree of 182 shortest trees. Characters unweighted; tree length 244; consistency index 0.35. See text for discussion of clades A–F.

and median spore wall thickenings. Taxa without internal wall thickenings included the genera *Santessonia*, *Dermaticum*, *Dermiscellum*, *Dimelaena* and *Buellia pro parte*.

Discussion

Internal wall thickenings are often used as constant characters in the delimitation of

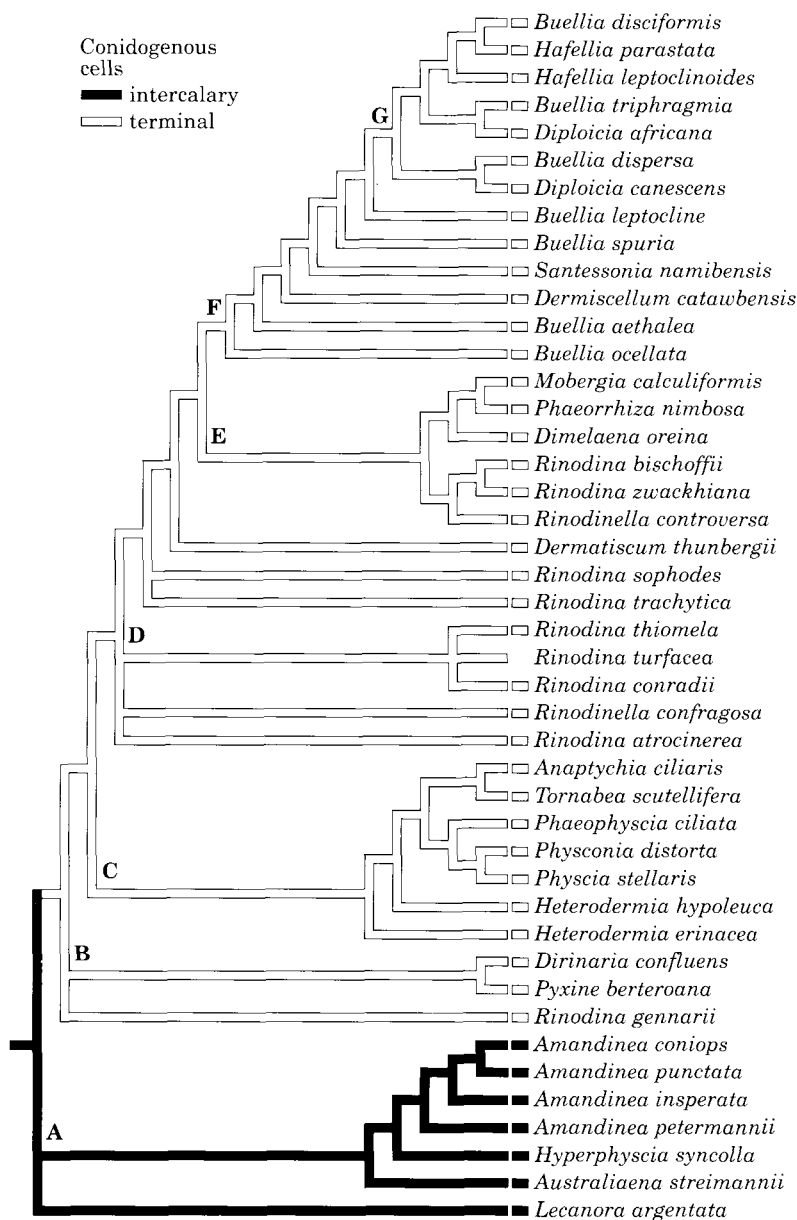


FIG. 6. Strict consensus tree of 405 shortest trees. Characters are weighted in order to give each character group equal importance; tree length 3320 consistency index 0.38. See text for discussion of clades A–G.

species of crustose genera, or even for entire foliose or fruticose genera. The study of the ascospore ontogeny of representative taxa over the entire family, however, revealed close relations among various spore types as

used so far in the taxonomic literature. For instance, a distinct developmental line with a delayed septum formation clearly shows transitions from spores with apical and median thickenings, such as *Dirinaria confluens*,

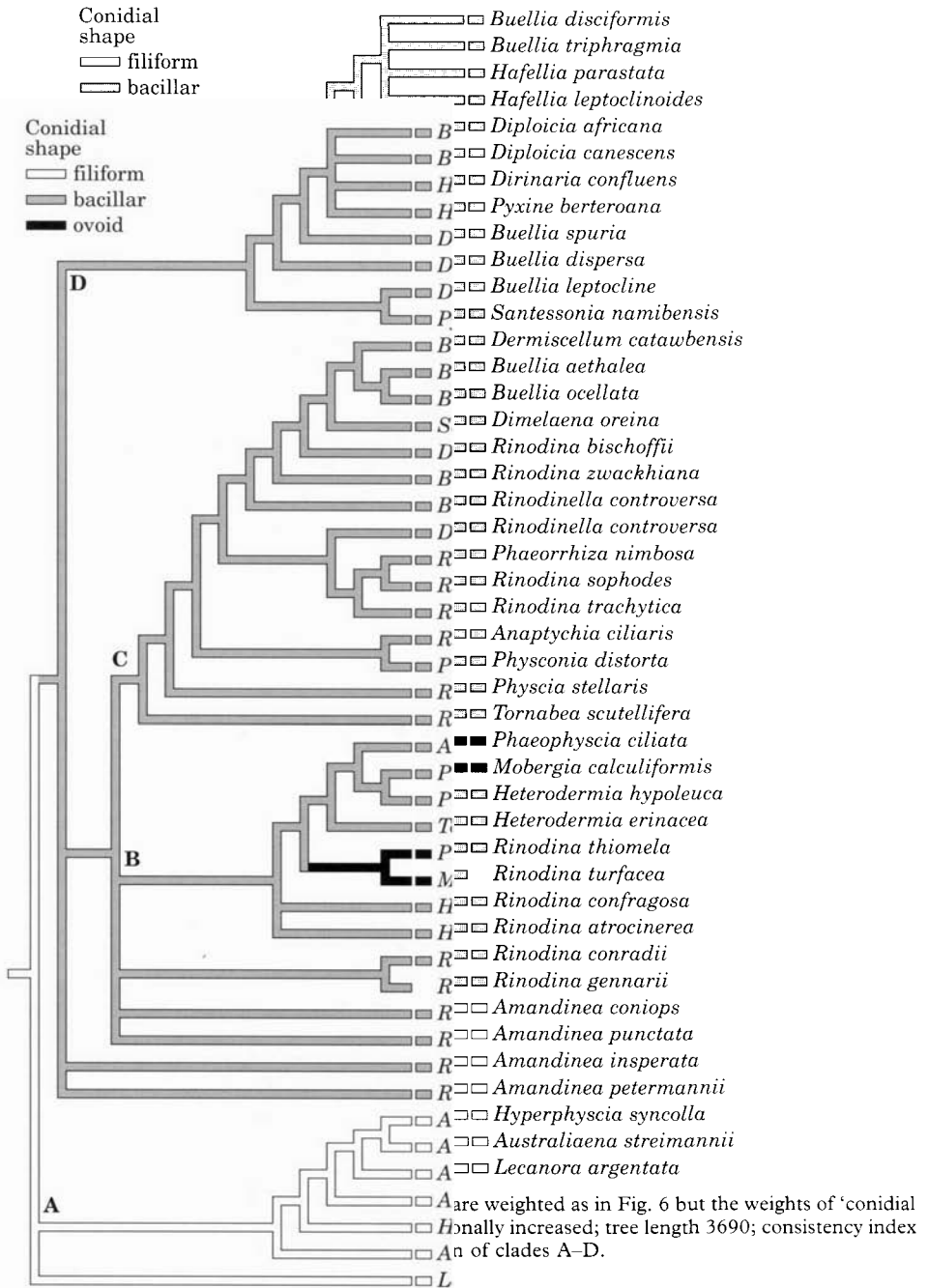


FIG. 6. Phylogenetic tree of Buellia and related genera. The tree is based on DNA sequence data. The weights of 'conidial shape' characters are increased; tree length 3690; consistency index 0.45. The tree is rooted with *Lecanora* as the outgroup. The clades A-D are defined as in the text.

to spores without apical, but still well-developed median thickenings, such as *Hafellia parastata*. Even the median thickenings may completely disappear in taxa so far

included in the genus *Buellia*, for example *B. disciformis* and *B. triphragmia*. In the second developmental line with an early septum formation, again taxa with no

thickenings, median thickenings only, and both median and apical thickenings were found. Although these characters are constant at a species level, median wall thickenings especially may vary among closely related taxa, for example in the genus *Amandinea*.

However, a heuristic search of unweighted morphological and chemical characters revealed a taxonomic structure which did not reflect ontogenetic characters of either conidia or ascospores. The strict consensus tree indicated a highly paraphyletic nature of the three conidial types as well as of the delayed septum formation during ascospore ontogeny (Fig. 5). Unlike recent morphology-based taxonomic concepts of the family (Hafellner *et al.* 1979) our unweighted tree suggests a monophyletic origin of all foliose and subfruticose taxa. Among the more complex growth forms, only bulate, placodioid, umbilicate and erect fruticose taxa were polyphyletic. In general, the consensus tree with unweighted characters had surprisingly close affinities with historic taxonomic structures discussed at the beginning of the twentieth century, for example by Zahlbruckner (1926).

We expect that the rather high number of characters, which described the upper and lower cortex led to an overweighting of the vegetative characters that were often directly dependent on growth form. Furthermore, homology was especially difficult to establish for the complex vegetative characters such as cortical plectenchyma.

After balancing the importance of the five character groups, the strict consensus tree supported the taxa with long filiform conidia as the sister group of the taxa having bacillar or ovoid conidia formed on intercalary conidiogenous cells. The delayed septum formation remained highly paraphyletic, and the group with ovoid conidia polyphyletic. Species with ovoid conidia became monophyletic in the last analysis only after the three characters 'conidial shape', 'delayed septum formation' and 'presence of apical thickenings' were given extra weighting. Most taxa with a delayed septum formation now appear in a clade with the

genera *Dirinaria*, *Diploicia*, *Hafellia*, *Pyxine*, *Buellia disciformis* and *B. triphragmia*, and the unresolved *Rinodina gennarii* and *R. conradii*. Outside this clade the character was shared with *Australiaena*. The close relationship between *B. disciformis* and *B. triphragmia* to the genus *Hafellia* was also supported in the consensus tree of the unweighted characters and support both the close relations between *Hafellia* and *B. disciformis*, and the paraphyly of the genus *Buellia*. Because *B. disciformis* is the type species of *Buellia*, nomenclatural relations between the two genera were recently discussed (Kalb & Elix 1998; Moberg *et al.* 1999). Also after the segregation of *Hafellia* and *Amandinea*, *Buellia* and *Rinodina* are still incompletely separated. The analyses of the five equally weighted character sets suggest that *Rinodina trachytica* and *R. sophodes* are sister species of the clade with *Buellia* s.str. Within this clade umbilicate and fruticose taxa of the genera *Dermaticum*, *Dermiscellum* and *Santessonia* are included. Further, *Rinodina thiomela* and *R. turfacea* form a sister group of the foliose and fruticose taxa with early spore septation and intercalary conidiogenous cells. The genus *Rinodina* shows therefore the most complex intergeneric relations within the *Physciaceae*, irrespective of the weighting scenarios, and needs substantial reconsideration in the future.

Our original understanding of the taxonomic structure of the *Physciaceae* shown in Fig. 7 was found only after the five character groups were given equal importance, and after further subjective *a priori* weighting increased the weight of three characters. This structure was not supported by the first cladistic analysis with equally weighted characters but reflects the biased character weighting of the present day *Physciaceae* taxonomy. The taxonomic importance of conidial characters and of anatomical and ontogenetical spore characteristics need therefore a careful reconsideration in future.

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