

Morphology, anatomy, and ontogeny in the Asterothyriaceae (Ascomycota: Ostropales), a misunderstood group of lichenized fungi

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Received 21 February 2001, accepted 17 January 2002

Henssen, A. & Lücking, R. 2002: Morphology, anatomy, and ontogeny in the Asterothyriaceae (Ascomycota: Ostropales), a misunderstood group of lichenized fungi. — *Ann. Bot. Fennici* 39: 273–299.

Based on morphological, anatomical, and ontogenetical data, the systematics of *Asterothyrium*, *Psorotheciopsis*, and *Gyalidea* (including *Solorinella*) is revised. The three genera form a natural group for which the name Asterothyriaceae is retained; they share hemiangiocarpous apothecia, true paraphyses, non-amyloid, “annelascaceous” asci, euseptate ascospores, and a chlorococcoid phycobiont. Apothecial ontogeny is characterized by the formation of a covering layer which ruptures during development. Apothecia are sessile (most species of *Gyalidea*, *Psorotheciopsis*) or immersed-erumpent with overarching or recurved teeth formed by the covering layer (some species of *Gyalidea*, *Asterothyrium*). Flask-shaped, immersed pycnidia (type I) occur in all three genera. Squad-conical pycnidia adnate to the margin of the thallus (type II) were found in *Psorotheciopsis* and *Asterothyrium*, while applanate pycnidia immersed in the thallus centre (type III) are restricted to *Asterothyrium*. All pycnidial types produce conidia of variable size, shape and septation. Several characters shared by *Psorotheciopsis* and *Asterothyrium*, i.e. corticate, whitish thalli, pigmented and/or immersed-erumpent apothecia, large and thick-walled ascospores, and frequent formation of pycnidia, are possibly adaptations to their preferred habitat: canopy leaves in the tropical rain forests. The closest relative of the Asterothyriaceae is *Gyalideopsis* in the Gomphillaceae. It agrees in most aspects with *Gyalidea*, but differs by its anastomosing paraphysoids and hyphoporous conidiomata. Both families are placed in Ostropales, sharing hemiangiocarpous apothecia, non-amyloid asci, and “annelascaceous” ascus type, with the Stictidaceae, Odontotremataceae, Thelotremataceae, and Graphidaceae.

Key words: *Asterothyrium*, Gomphillaceae, *Gyalidea*, *Gyalideopsis*, lichen, *Psorotheciopsis*, *Solorinella*, taxonomy

Introduction

In his monograph of foliicolous lichens, Santesson (1952: p. 331) wrote about *Psorotheciopsis* Rehm: "The lichens of this genus have been stumbling-blocks for mycologists." Indeed, the three species recognized by him do have three generic synonyms and were referred to ten further

Table 1. Generic synonyms of *Asterothyrium* and *Psorotheciopsis*, and genera to which species of *Asterothyrium* and *Psorotheciopsis* were referred to by different authors (based on Santesson 1952, Lücking *et al.* 1998, 1999).

Asterothyrium (10 species):

Generic synonyms:

Asterothyrium Müll. Arg.
Psorotheciella Sacc. & Syd.
Stictoclypeolum Rehm
Lopadiopsis Zahlbr.
Diplopeltopsis P. Henn. ex von Höhnel
Actinoteichus Cavalc. & Poroca
Tegoa Bat. nom. inval.
Stictopela Bat. nom. inval.

Other genera to which species were referred:

Asterina Lév.
Diplopeltis P. Henn. nom. inval. (non *Diplopeltis* Endl.)
Myxodictyon A. Massal.
Linhartia Sacc. & Syd.
Psorotheciopsis Rehm
Gyalectidium Müll. Arg.
Platygrapha Berk. & Broome
Rotula (Müll. Arg.) Müll. Arg.
Mazosia A. Massal.
Microphiale (Stiz.) Zahlbr.
Ectolechia Trevis.
Sporopodium Mont.

Psorotheciopsis (3 species):

Generic synonyms:

Psorotheciopsis Rehm
Linhartia Sacc. & Syd.
Monospermella Speg.
Conicosolen F. Schill.

Other genera to which species were referred:

Calloria Fr.
Trichobelonium (Sacc.) Rehm
Johansonia Sacc.
Tapesia (Pers.) Fuckel
Actinoscypha P. Karst.
Megalospora Meyen
Microphiale (Stiz.) Zahlbr.
Patellaria Fr.
Catillaria A. Massal.
Bacidia DeNot.

genera of lichenized and non-lichenized fungi (Table 1). *Psorotheciopsis* itself was assigned to families such as the operculate Pezizaceae and Megalosporaceae in the Lecanorales (Table 2). A similar situation is found in *Asterothyrium* Müll. Arg.: the ten species listed in Santesson (including *A. rotuliforme* (Müll. Arg.) Sérus. and *A. umbilicatum* (Müll. Arg.) Müll. Arg.; see Sérusiaux & de Sloover 1986, Lücking *et al.* 1998) have seven generic synonyms (two of them invalid) and were partly referred to further 12 genera of lichenized and non-lichenized fungi (Table 1). *Asterothyrium* itself was included in the Patellariaceae and Thelotremaaceae, among other families (Table 2).

The Asterothyriaceae are based on Vainio's (1896) and Zahlbruckner's (1905) Ectolechiaceae, which included *Asterothyrium*, *Tricharia* Fée, *Echinoplaca* Fée, *Actinoplaca* Müll. Arg.,

Table 2. Families to which the generic names *Asterothyrium*, *Psorotheciopsis*, *Linhartia* (= *Psorotheciopsis*), *Solorinella*, and *Gyalidea*, were referred by different authors, before their rearrangement in Asterothyriaceae (Lücking 1999).

Asterothyrium

Patellariaceae (Müll. Arg. 1890)
 Ectolechiaceae (Zahlbruckner 1905)
 Asterothyriaceae (Watson 1929)
 Asterothyriaceae *s.lato* (Santesson 1952)
 Asterothyriaceae *s.stricto* (Vezda & Poelt 1987)
 Thelotremaaceae (Aptroot in Aptroot *et al.* 1994)

Psorotheciopsis

Mollisiaceae (Rehm 1900)
 Pezizaceae (Saccardo 1902)
 Asterothyriaceae *s.lato* (Santesson 1952)
 Megalosporaceae (Vezda 1973)
 Asterothyriaceae *s.stricto* (Lücking 1992)
 Gomphillaceae (Eriksson & Hawksworth 1987)

Linhartia

Mollisiaceae (Saccardo 1902)
 Asterothyriaceae *s.lato* (Santesson 1952)
 Asterothyriaceae *s.stricto* (Vezda & Poelt 1987)
 Solorinellaceae (Vezda & Poelt 1990)

Solorinella

Peltigeraceae Dumort
 Gyalectaceae (Vezda & Poelt 1969)
 Asterothyriaceae (Vezda 1979)
 Solorinellaceae (Vezda & Poelt 1990)

Gyalidea

Asterothyriaceae *s.lato* (Vezda 1966)
 Asterothyriaceae *s.stricto* (Vezda & Poelt 1987)
 Solorinellaceae (Vezda & Poelt 1990)

Sporopodium Mont., and *Byssolecania* Vain., among others. When first introducing the name Asterothyriaceae, Watson (1929) retained *Asterothyrium*, *Byssolecania*, and *Actinoplaca*, still a highly heterogeneous assemblage. Santesson (1952) recognized six genera as being related: *Asterothyrium*, *Psorotheciopsis*, *Calenia* Müll. Arg., *Gyalectidium* Müll. Arg., *Echinoplaca* (including *Actinoplaca*), and *Tricharia*. This group largely corresponds to Ectolechiaceae *sensu* Vainio and Zahlbruckner, but since the type genus, *Sporopodium*, had to be referred to the Lecanorales, Santesson adopted the name Asterothyriaceae.

Ve zda (1979) presented the first modern treatment of the family, adding *Gyalidea* Lett. (Ve zda 1966, Lumbsch *et al.* 1991), *Solorinella* Anzi (Poelt & Ve zda 1969), *Gyalideopsis* Ve zda (Ve zda 1972, Lumbsch & Hawksworth 1987), *Gomphillus* Nyl., and *Aulaxina* Fée. *Linhartia* was segregated from *Psorotheciopsis*, and the latter, on account of its large, thick-walled ascospores, was referred to the Megalosporaceae (Ve zda 1973) and, more recently, to the Gomphillaceae (Eriksson & Hawksworth 1987, 1993). Ve zda (1979) recognized two entities within the Asterothyriaceae: one with branched and anastomosing paraphysoids and hyphophorous conidiomata (Ve zda 1973), and a one with unbranched paraphyses and pycnidial conidiomata, including *Asterothyrium*, *Gyalidea*, *Linhartia*, and *Solorinella*. After segregating the taxa producing hyphophores in a separate family Gomphillaceae (Ve zda & Poelt 1987), the remaining four genera were retained as Asterothyriaceae *s. stricto* (Eriksson & Hawksworth (1987).

However, Ve zda and Poelt (1987) considered *Asterothyrium* to take an isolated position, although they gave no reasons for their view, and later assigned *Gyalidea*, *Linhartia*, and *Solorinella* to a new family Solorinellaceae (Ve zda & Poelt 1990). *Asterothyrium*, the only genus left in the Asterothyriaceae, was then compared to *Chroodiscus* (Müll. Arg.) Müll. Arg. and eventually referred to the Thelotremataceae (Ve zda 1979, Ve zda & Poelt 1987, Eriksson & Hawksworth 1993, Hawksworth & Eriksson 1994, Aptroot in Aptroot *et al.* 1994), and the Asterothyriaceae temporarily “disappeared” into oblivion.

This view was partly confirmed by a preliminary phylogenetic study of the group performed

by Denetière and Péroni (1998), analyzing 15 characters in 15 taxa. *Psorotheciopsis premmella* fell in a clade with *Linhartia*, while *Asterothyrium* merged with Graphidaceae and Thelotremataceae. However, performing a more detailed analysis of 31 characters in 24 taxa, Lücking (1999) found that Asterothyriaceae *sensu* Eriksson and Hawksworth (1987) and Gomphillaceae *sensu* Ve zda and Poelt (1987) form coherent groups related to Thelotremataceae and Graphidaceae in the Ostropales. He therefore reinstated Asterothyriaceae *sensu* Eriksson and Hawksworth (1987), placing Solorinellaceae in synonymy. Based on another analysis, using 125 phenotype characters in 24 species, and following earlier observations made by Aptroot and Sipman (1991), Aptroot and Lücking (2002) merged *Solorinella* with *Gyalidea*, leaving the Asterothyriaceae with three genera.

In this paper, we present data on the apothecial morphology, anatomy and ontogeny of *Gyalidea* (including *Solorinella*), *Psorotheciopsis*, and *Asterothyrium*, in order to test our view of this group as a natural entity and to study the relationships between the different genera and species.

Material and methods

The following taxa were used for morphological, anatomical, and ontogenetic studies:

Asterothyrium anomalum Kalb & Ve zda var. *anomalum*: **Brazil**, Kalb *s.n.* (hb. Ve zda, isotype). **Argentina**, Vanni *et al.* 3654 (CTES, hb. Lücking).

Asterothyrium anomalum var. *pallidum* Lücking & Henssen: **Costa Rica**, Lücking 92-51 (hb. Lücking).

Asterothyrium argenteum Müll. Arg. (type species of *Asterothyrium*): **Costa Rica**, Lücking 91-44 (hb. Henssen, hb. Lücking), 91-131 (hb. Lücking), 91-857, 92-4184 (both hb. Lücking). **Ecuador**, Lücking 96-241 (hb. Lücking). **Brazil**, Puiggari 1748 (G, holotype).

Asterothyrium aspidospermatis (Peres) Lücking & Sérus.: **Brazil**, Heringer *s.n.* (URM 72025).

Asterothyrium atomarginatum Herrera-Campos & Lücking: **Mexico**, Herrera-Campos *et al.* *s.n.* (MEXU, holotype).

Asterothyrium aulaxinoides Lücking: **Costa Rica**, Lücking 92-1913 (ULM, holotype), 91-3469 (hb. Lücking). **Ecuador**, Lücking 96-242, 96-301 (hb. Lücking).

Asterothyrium chroodisciforme Lücking: **Costa Rica**, Lücking 91-4014, 91-6000 (both hb. Lücking). **Peru**, Santesson & Santesson *s.n.* (UPS).

Asterothyrium decipiens (Rehm) R.Sant. (type species of *Stictoclypeolum*): **Brazil**, *Ule* 1238 (UPS, isoelectotype of *Stictoclypeolum decipiens* Rehm). **Philippines**, *Elmer* 14473c (B).

Asterothyrium gyalideoides Henssen & Lücking: **Costa Rica**, *Lücking* 91-361 (hb. Henssen, hb. Lücking, Lich. Fol. Exs. 78), 91-1519 (hb. Lücking).

Asterothyrium hedbergii Kalb & Vezda: **Brazil**, *Kalb* s.n. (hb. Kalb, holotype).

Asterothyrium leptosporum Müll.Arg.: **Costa Rica**, *Pittier* 5111 (G, holotype). **Brazil**, *Theissen* s.n. (S).

Asterothyrium leucophthalmum (Müll.Arg.) R.Sant.: **Costa Rica**, *Lücking* 92-47 (hb. Lücking). **Ecuador**, *Lücking* 96-241 (hb. Lücking). **Brazil**, *Malme* 414:2 (S), 414:3 (UPS), *comm. Rick* s.n. (S). **Argentina**, *Henssen* 24112b & *Vobis* (hb. Henssen).

Asterothyrium longisporum Lücking: **Ecuador**, *Lücking* 96-266 (hb. Lücking).

Asterothyrium microsporum R.Sant. (type species of *Tegoa* nom. inval.): **Costa Rica**, *Lücking* 88-120, 91-3864, 91-3460 (all hb. Lücking). **Ghana**, *Hughes* 1226 (UPS). **Philippines**, *Robinson* (BM, filed under type of *A. robinsonii* = *A. pittieri*).

Asterothyrium monosporum Müll.Arg. (type species of *Psorotheciella*): **Costa Rica**, *Lücking* 92-1914, 91-861 (both hb. Lücking). **Ecuador**, *Lücking* 96-112 (QCA). **Peru**, *R. & B. Santesson* s.n. (UPS). **Brazil**, *Puiggari* 2805 (G, holotype).

Asterothyrium octomerum R.Sant. (type species of *Stictopela* nom. inval.): **Guinea**, *Lisowski* 1157 (hb. Vezda). **IVORY COAST**, *Santesson* 10740 (UPS). **DR Congo**, *Vanderyst* 38505 (UPS, holotype).

Asterothyrium pittieri Müll.Arg. (type species of *Diplopeltopsis*): **Costa Rica**, *Pittier & Tonduz* 6025 (BM), *Pittier* 5110 (G, holotype), *Lücking* 91-52 (hb. Henssen, hb. Lücking). **Ecuador**, *Lücking* 96-216 (hb. Lücking). **Ivory Coast**, *Santesson* 10479 (UPS). **Angola**, *Welwitsch* 288 (UPS, isotype of *A. welwitschii* Vain.). **Indonesia**, *Zimmermann* s.n. (S, isotype of *Diplopeltopsis zimmermanniana* P. Henn.). **Philippines**, *Robinson* 9688 (TUR, holotype of *A. robinsonii* Vain.), *Elmer* 14449 (TUR, holotype of *A. elmeri* Vain.).

Asterothyrium rondoniense Bat. & H.Maia ex Henssen & Lücking: **Costa Rica**, *Pittier & Tonduz* 6025 (BM). **Ecuador**, *Lücking* 96-302 (QCA, holotype, hb. Lücking). **Brazil**, *Baker* s.n. (S).

Asterothyrium rotuliforme (Müll.Arg.) Sérus. (type species of *Lopadiopsis*): **Costa Rica**, *Lücking* 92-2 (hb. Henssen, hb. Lücking), 92-48 (hb. Lücking). **Ecuador**, *Lücking* 96-240 (QCA). **Peru**, *Santesson & Thor* (UPS). **Brazil**, *Lücking* s.n. (hb. Henssen, hb. Lücking), *Theissen* s.n. (S); *ibid.*, *comm. Rick* s.n. (S). **Paraguay**, *Balansa* 4013 (G, holotype). **Argentina**, *Henssen* 24112c & *Vobis* (hb. Henssen). **Ivory Coast**, *Santesson* 10434 (UPS).

Asterothyrium septemseptatum Lücking: **Costa Rica**, *Lücking* 88-580 (hb. Lücking).

Asterothyrium tetrasporum Lücking: **Costa Rica**, *Lücking* 88-39 (ULM, holotype).

Asterothyrium umbilicatum (Müll.Arg.) Müll.Arg. (type

species of *Actinoteichus*): **Costa Rica**, *Lücking* 91-23 (hb. Lücking). **Ecuador**, *Lücking* 96-338 (hb. Lücking). **Brazil**, *da Silva* s.n. (URM 46652, holotype of *Actinoteichus maranhensis* Cavalc. & Poroca). **Paraguay**, *Balansa* 4013 (G, holotype).

Asterothyrium uniseptatum Lücking: **Honduras**, *Standley* 7703 (UPS). **Costa Rica**, *Lücking* 91-54 (hb. Lücking). **Paraguay**, *Schinini & Bordas* 20792 (CTES).

Asterothyrium sp. (pyncnidia): **Brazil**, *Malme* 414:3 (S, filed as *A. leucophthalmum*).

Gyalidea astericus (Anzi) Aptroot & Lücking (type species of *Solorinella*): **U.S.A.**, *Thor* 8888 (S). **Switzerland**, *Theobald* s.n. (UPS). **Czech Republic**, *Suza* s.n. (UPS).

Gyalidea epiphylla Vezda: **Costa Rica**, *Lücking* 91-1844, 91-5664 (both hb. Lücking). **Guinea**, *Lisowski* s.n. (hb. Vezda, holotype).

Gyalidea fritzei (Stein) Vezda: **Slovakia**, *Vezda* s.n. (hb. Henssen; Vezda: *Lich. Sel. Exs.* 533).

Gyalidea hyalinescens (Nyl.) Vezda [incl. var. *mexicana* (B.deLesd.) Vezda]: **Costa Rica**, *Sipman* 12387 (B). **Ecuador**, *Culberson* 20555 (B; Vezda: *Lich. Sel. Exs.* 3506). **Canada** (hb. Henssen, Vezda: *Lich. Sel. Exs.* 1427). **Portugal**, *Henssen* 25545a (hb. Henssen).

Gyalidea lecanorina (Knight) P.James & Galloway: **New Zealand**, *Henssen* 30360a (hb. Henssen).

Gyalidea lecideopsis (A.Massal.) Lett. ex Vezda var. *lecideopsis* (type species of *Gyalidea*): **Slovakia**, *Vezda* 26342 (hb. Vezda). **Germany**, *Arnold* s.n. (MB, Rabenhorst: *Lich. Eur. Exs.* 340).

Gyalidea lecideopsis var. *eucarpa* (Servít) Vezda [= *G. lecideopsis* var. *convarians* (Nyl.) Vezda]: **Austria**, *Arnold* s.n. (M).

Gyalidea multispora Lumbsch & Vezda: **Papua New Guinea**, *Aptroot* 17819b (B).

Gyalidea phyllophila Vezda: **Georgia**, *Vezda* (hb. Henssen, Vezda: *Lich. Sel. Exs.* 1569). **Guinea**, *Lisowski* s.n. (hb. Vezda, holotype). **Ivory Coast**, *Santesson* 10741: 4 (UPS).

Gyalidea praetermissa Foucard & Thor: **Sweden**, *Foucard & Thor* s.n. (UPS, holotype).

Psorotheciopsis albomaculans (Rehm) Vezda: **Costa Rica**, *Lücking* 92-4705 (hb. Lücking).

Psorotheciopsis guajalilensis Lücking: **Ecuador**, *Lücking* 96-181 (hb. Lücking).

Psorotheciopsis gyalideoides (Vezda) Henssen & Lücking: **Guinea**, *Lisowski* 1118 (hb. Vezda).

Psorotheciopsis patellarioides (Rehm) R.Sant. (type species of *Linhartia*): **Costa Rica**, *Lücking* 92-1811 (hb. Lücking). **Guinea**, *Lisowski* (hb. Henssen, hb. Vezda, *Lich. Sel. Exs.* 1158). **Ivory Coast**, *Santesson* 10481b (UPS).

Psorotheciopsis premneella (Müll.Arg.) R.Sant. (type species of *Psorotheciopsis*): **Costa Rica**, *Lücking* 88-593 (hb. Lücking). **Brazil**, *Puiggari* 2803 (G, holotype). **Ivory Coast**, *Santesson* 10614 (UPS). **Togo**, *Hughes* 968 (UPS).

Psorotheciopsis varieseptata (Vezda) Henssen & Lücking: **Guinea**, *Lisowski* 1175 (hb. Vezda, holotype).

Psorotheciopsis philippinensis (Rehm) Lücking: **Costa Rica**, *Lücking* 92-5736 (ULM, holotype of *Linhartia vezdana*). **Ecuador**, *Lücking* 96-340 (hb. Lücking).

Specimens were studied under a Wild M7 dissecting microscope and a Zeiss dissecting microscope (8–50×). Thin sections of thallus, apothecia and pycnidia of different developmental stages were made with a freezing microtome. Sections were stained in Lacto-Glycerine/Cotton-Blue (LB) and studied under a Wild M20 compound microscope and a ZEISS microscope (32–1000×). Hand sections and squeeze mounts were further used to study paraphyses, asci and ascospores. I_{Lugol} (I) and KOH (K) were applied for microchemical tests (I+/-: Lugol only; KI+/-: Lugol after pretreatment with KOH). Anatomical photographs were made with a Wild M20 compound microscope, using Kodak professional film 5-TMX 120 in 6 × 6 cm format. Habit photographs were made with a Wild M7 dissecting microscope and a Nikon F301 camera with 4:1/90 mm macro combination, using Kodak professional film 5-TMX 120 in 6 × 6 cm format and Fuji Sensia II 100 colour slide in 36 × 24 mm format.

Terminology follows Henssen and Jahns (1973) and Henssen (1981). Hypothecium refers to the layer below the hymenium including ascogoneous hyphae (sometimes called subhymenium by other workers). True paraphyses grow vertically with free tips, while paraphysoids are branched and anastomosing and frequently develop first from the generative tissue and are later replaced by true paraphyses. Periphysoids develop as lateral paraphyses from the proper excipulum into the cavity between excipulum and hymenium. Plasma-rich generative tissue is identified by its strong stain in LB. In hemiangiocarpous apothecia, the generative tissue develops a roof that encloses the hymenium and is separated from the latter by a split. The roof, together with adjacent thallus tissue, form the covering layer.

Results

Thallus morphology and anatomy

Gyalidea (including *Solorinella*) forms diffuse, hardly delimited thalli on soil and rock surfaces. Some species grow on bryophytes, dead plants

and bark, while *Gyalidea epiphylla* and *G. phyllophila* are foliicolous (Figs. 1, 6A and 7A). In foliicolous species, the thallus is small and thin and partly dispersed into rounded patches, while in saxicolous and terricolous taxa it can cover large areas of the substrate and, if well-developed, be up to 500 μm thick and fissurate-areolate. Otherwise, the thallus is typically smooth to minutely farinose.

In cross sections of *Gyalidea* species, three layers are usually visible: a more or less indistinct, cartilaginous cortex (absent in species with thin thallus), a single- to multilayered algal layer with dense arrangement of chlorococcoid algal cells, and an indistinct to well-developed medulla composed of interwoven hyphae which, in saxicolous and terricolous taxa, encloses substrate particles.

The thallus in *Psorotheciopsis* and *Asterothyrium* consists of dispersed, eventually confluent patches 1–3 mm across, which are connected by an invisible prothallus formed by hyaline hyphae. Depending on the species, the patches exhibit a characteristic, greyish to silvery white colour (Figs. 2–3, 8A, 9A–B and 14A). In *Psorotheciopsis patellarioides* and *Asterothyrium atromarginatum*, the margin of the thallus patches is bordered by a thin, blackish line, caused by dark pigmented cortical cells at the periphery of the thallus (Figs. 2B and 8A). Most species have a thin, translucent prothallus free of algal cells.

A section through the thallus of *Psorotheciopsis* and *Asterothyrium* reveals up to four strata: (1) a cellular cortex, (2) an uni- to multistratose algal layer, (3) a more or less well developed medulla, and (4) a thin submedullary layer (Fig. 4). The cortex is one of the most distinctive features in the two genera, consisting of dead, rectangular cells which, when seen from above, form a unistratose layer of branched, radiate cell rows, similar to the thallus of a free-living *Phycopeltis* alga (Fig. 5). This cortex is responsible for the whitish thallus colour, since the dead, rectangular cells are physically light-reflective.

Depending on the thickness of the thallus, the algal layer consists of 1–3 irregular strata of rounded, 4–8 μm large cells. The phycobiont seems to be *Trebouxia* in all studied cases. Below

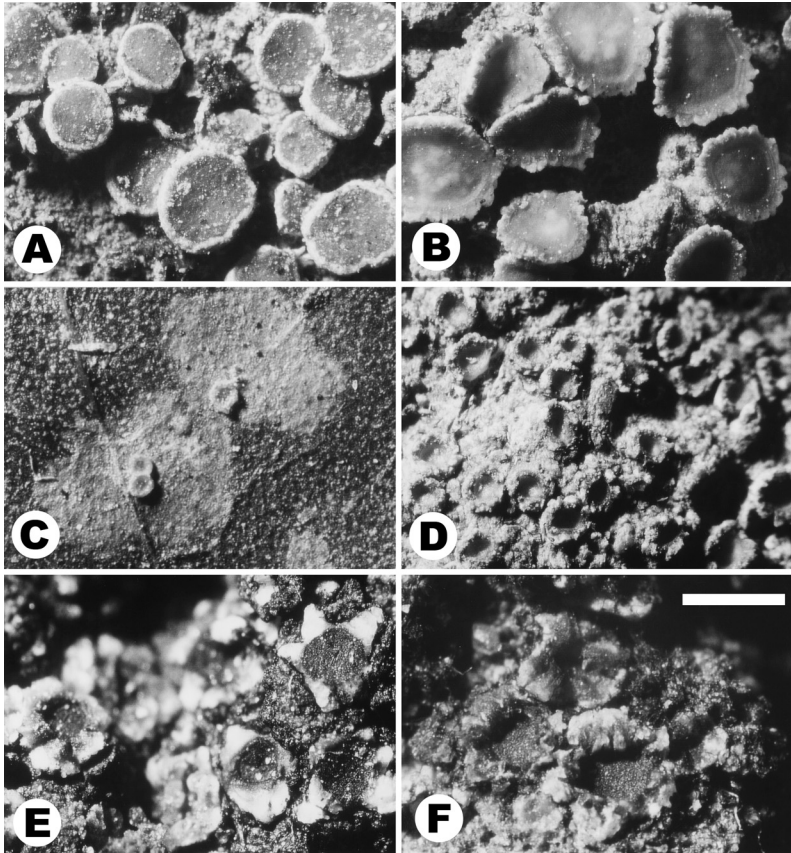


Fig. 1. General habit of *Gyalidea* species. — **A–B:** *Gyalidea hyalinescens* (**A:** Costa Rica, *Sipman 12387*; **B:** Ecuador, *Culbertson 20555*); note the small teeth on the apothecial margin in **B**. — **C:** *G. phyllophila* (holotype); thallus with three apothecia. — **D:** *G. multispora* (Papua New Guinea, *Aptroot 17819b*); note the distinct marginal teeth of the apothecia. — **E–F:** *G. asteriscus* (**E:** Switzerland, *Theobald s.n.*; **F:** Czech Republic, *Suza s.n.*); note the well-developed, triangular marginal lobes. Scale for **A–B** = 2 mm, **C** = 0.7 mm, **D–F** = 1.2 mm.

the algal layer, a medullary tissue may be developed, which consists of rather loosely packed hyphae with inflated, 4–6 μm broad cells which do not stain in LB. It is particularly conspicuous in thick thalli of *Asterothyrium leucophthalmum*, *A. rotuliforme* (Fig. 4B), and *A. umbilicatum* (Fig. 14E), but inconspicuous or absent in other species, e.g. *Psorotheciopsis patellarioides* (Fig. 4A). Below the medullary tissue, a thin, irregular tissue of small (ca. 2 μm in diam.), plasma-rich cells is found (Fig. 4A–B).

Apothecial morphology, anatomy and ontogeny in *Gyalidea*

Apothecia are typically sessile and basally constricted (*Gyalidea hyalinescens*), but may remain semi-immersed or immersed-erumpent in *G. lecanorina*, *G. praetermissa*, *G. multispora*, and *G. asteriscus* (Figs. 1A–F, 6A–B and 7A). The lateral excipulum is hyaline or

partly pigmented (e.g. in *G. lecideopsis* and *G. fritzei*), giving the apothecia a biatorine or lecideine appearance (Figs. 1A, 6A–B and 7G–H). The basal part is continuous (cupular excipulum; Fig. 7B and F), or sometimes thin and interrupted (annular excipulum; Fig. 6B and F). The apothecial margin can form small to rather large teeth and be covered with remnants of thallus tissue (Figs. 1B–F and 7B). In sections of mature apothecia, the lateral excipulum is conspicuously enlarged and in most species composed of branched and partly anastomosing hyphae embedded in a gelatinous matrix (Fig. 7B, E and G–H). In a few species, these hyphae are compacted to form a paraplectenchymatous tissue, as in *Gyalidea epiphylla*, *G. phyllophila*, and *G. lecanorina* (Figs. 6G and 7F).

In *Gyalidea lecanorina*, the primordium differentiates into a globose structure with paraplectenchymatous roof and a nucleus with paraphysoids and basal ascogoneous hyphae being surrounded by a cupular excipulum

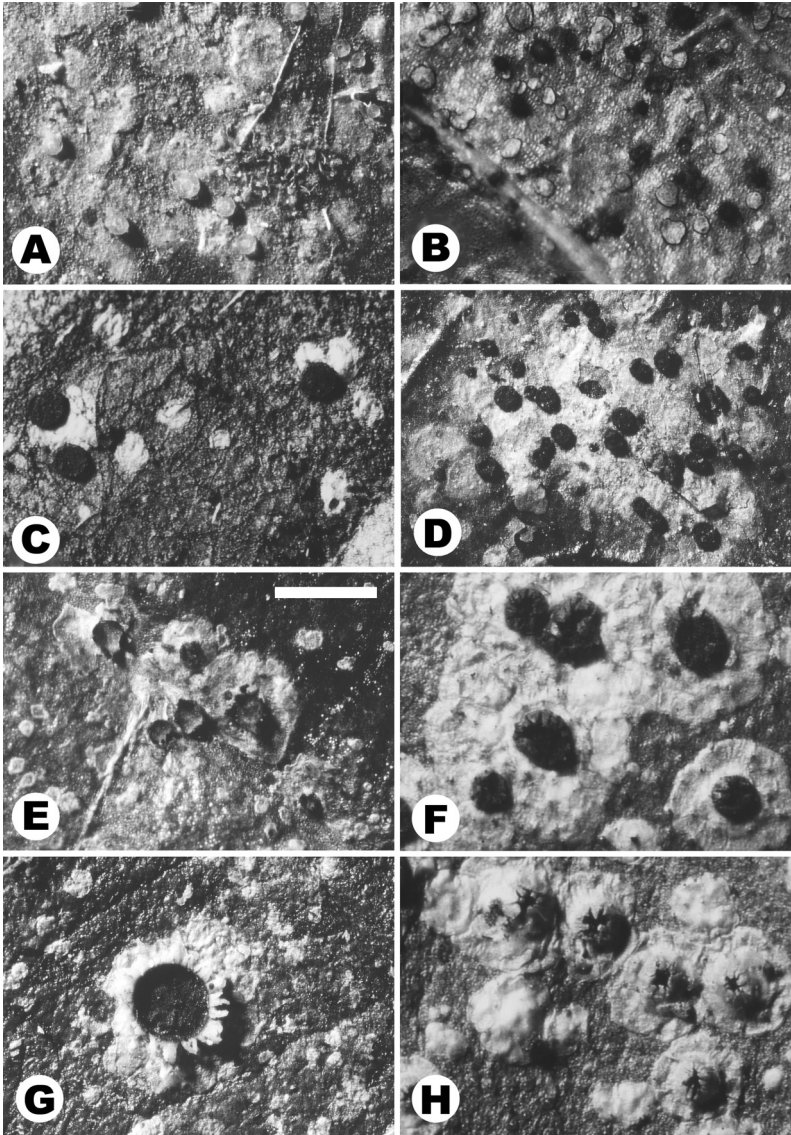


Fig. 2. General habit of *Psorotheciopsis* and *Asterothyrium* species. — **A:** *Psorotheciopsis gyalideoides* (holotype); thallus with unpigmented apothecia. — **B:** *P. patellarioides* (Costa Rica, *Lücking 92-1811*); with marginally black apothecia; note the thin black line around the thallus patches. — **C:** *P. albomaculans* (Costa Rica, *Lücking 92-4705*); the black apothecia that are formed at the margin of the algeriferous thallus patches. — **D:** *P. premneella* (Costa Rica, *Lücking 88-593*); thallus with numerous black apothecia. — **E:** *Asterothyrium aulaxinoides* (Costa Rica, *Lücking 96-301*); note the unpigmented, translucent apothecial discs and thin black teeth. — **F:** *A. pittieri* (Costa Rica, *Lücking 91-52*); thallus with brownish black apothecial discs that are covered by heavily pigmented teeth. — **G:** *A. chroodisciforme* (Costa Rica, *Lücking 91-6000*); note the large, brownish black apothecial disc and recurved, unpigmented teeth. — **H:** *A. uniseptatum* (Costa Rica, *Lücking 91-54*); the apothecial disc is covered by unpigmented teeth. Scale = 1 mm, for **F–H** = 0.7 mm.

(Fig. 6C). Along with the rupture of the paraphysoids and vertical growth of true paraphyses, the roof ruptures in upper part to expose the hymenium (Fig. 6D–F). The uppermost parts,

which later form the edges of the excipulum, thereby retain short periphysoids (Fig. 6F). In the mature apothecium, the lateral parts of the excipulum are \pm paraplectenchymatous in upper

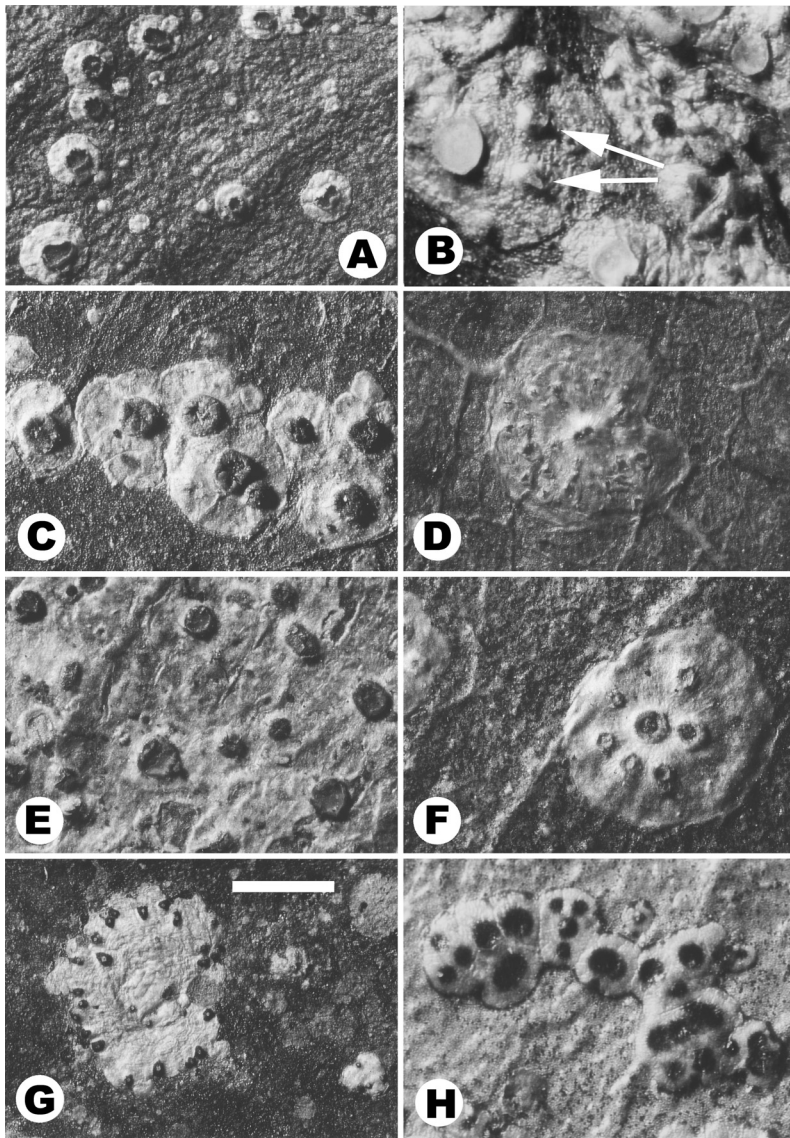


Fig. 3. General habit of *Asterothyrium* species. — **A:** *A. argenteum* (Costa Rica, Lücking 91-131); the pale apothecial disc is partly covered by unpigmented teeth. — **B:** *A. gyalideoides* (an isotype); note the sessile apothecia and pycnidia with extruded conidial mass (arrow); no thallus margin is apparent around the apothecia. — **C:** *A. octomerum* (Guinea, Lisowski 1157); dispersed thallus with several apothecia. — **D:** *A. septemseptatum* (Costa Rica, Lücking 92-48a); the oldest apothecia in the centre surrounded by a whitish area, while the apothecial teeth are reduced and very thin. — **E:** *A. anomalum* var. *anomalum* (Argentina, Vanni *et al.* 3654); the apothecial discs partly covered by blackish marginal teeth. — **F:** *A. rotuliforme* (Brazil, Lücking *s.n.*); the oldest apothecia in the centre surrounded by a whitish area, and the apothecial teeth completely reduced. Note the external similarity between *A. octomerum* (ascospores 7-septate) and *A. anomalum* (ascospores muriform) on one hand and between *A. septemseptatum* (ascospores 7-septate) and *A. rotuliforme* (ascospores muriform) on the other. — **G:** *Asterothyrium microsporum* (Costa Rica, Lücking 91-3460); sterile specimens with marginal, squad-conoid pycnidia (type II). — **H:** *A. umbilicatum* (Costa Rica, Lücking 91-23), sterile specimens with centrally immersed, applanate pycnidia (type III). Scale = 1 mm, for **B** and **H** = 0.7 mm.

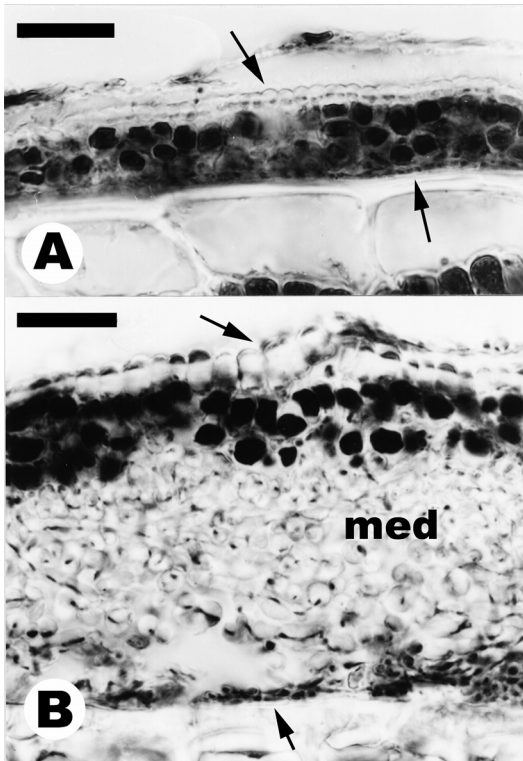


Fig. 4. Thallus anatomy in *Asterothyrium* and *Psorotheciopsis* (microtome sections in LB). — **A:** *Psorotheciopsis patellarioides* (Guinea, Lisowski s.n.; Vezda: *Lich. Sel. Exs. 1158*); a medulla is not developed but note the basal layer of small, strongly staining cells in LB and the unistratose cortex (arrows). — **B:** *Asterothyrium rotuliforme* (Costa Rica, Lücking 92-2); note the basal layer of small, strongly staining cells in LB (arrow), the well developed medulla (med), the multistratose algal layer, and the unistratose cortex composed of rectangular cells in cross section (arrow). Scale = 20 μ m.

and outer parts but composed of parallel, radiating hyphae in inner parts close to the hymenium; its uppermost parts are pigmented, while its lateral parts are covered with algeriferous thallus tissue where the apothecia are semi-immersed in the thallus (Fig. 6G).

Apothecial primordia in *Gyalidea hyalinescens* appear as globose structures composed of short cells strongly staining in LB (Fig. 7C). In later stages, the roof and lateral excipulum are comparatively thin and composed of densely packed, interwoven hyphae; asci develop rather soon (Fig. 7D). Mature apothecia feature a mostly hyaline excipulum composed of densely packed,

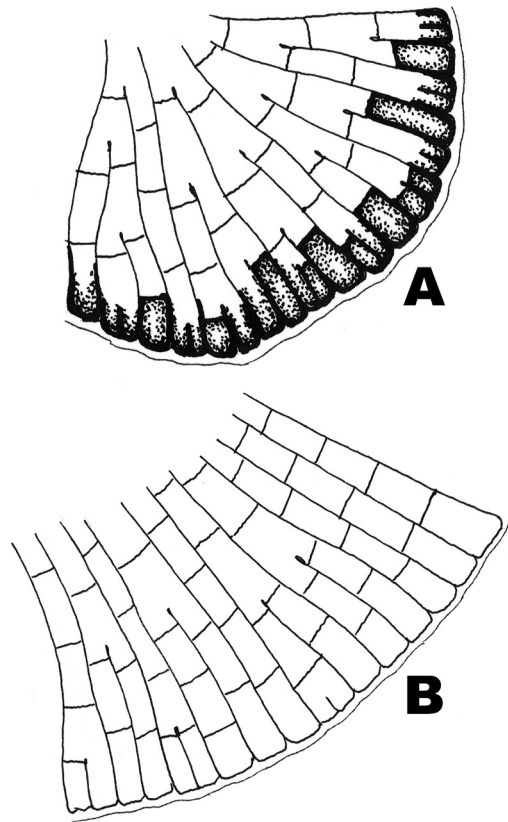


Fig. 5. Thallus anatomy in *Asterothyrium* and *Psorotheciopsis*. — **A:** *Psorotheciopsis patellarioides* (Guinea, Lisowski s.n.; Vezda: *Lich. Sel. Exs. 1158*); thallus cortex seen from above. — **B:** *Asterothyrium argenteum* (Costa Rica, Lücking 91-131); thallus cortex seen from above. Scale = 10 μ m.

parallel and radiating hyphae, pigmented in upper part and laterally covered by a thin, amorphous thallus tissue containing algal cells (Fig. 7E). In *G. lecideopsis* var. *lecideopsis*, the rupturing roof forms rather thick edges (Fig. 7G), as is also seen in *Psorotheciopsis* (see below).

Gyalidea asteriscus is characterized by its comparatively large, immersed-erumpent apothecia that feature distinct, more or less triangular lobes (Fig. 1E–F). In section, these lobes are composed of branched and partly anastomosing, parallel and more or less radiate hyphae with thin lumina and thick, strongly gelatinizing walls. In the lower, outermost parts, a more or less well-developed thallus tissue covers the excipulum. We were unable to study young stages of apothecia, but from the structure of the apoth-

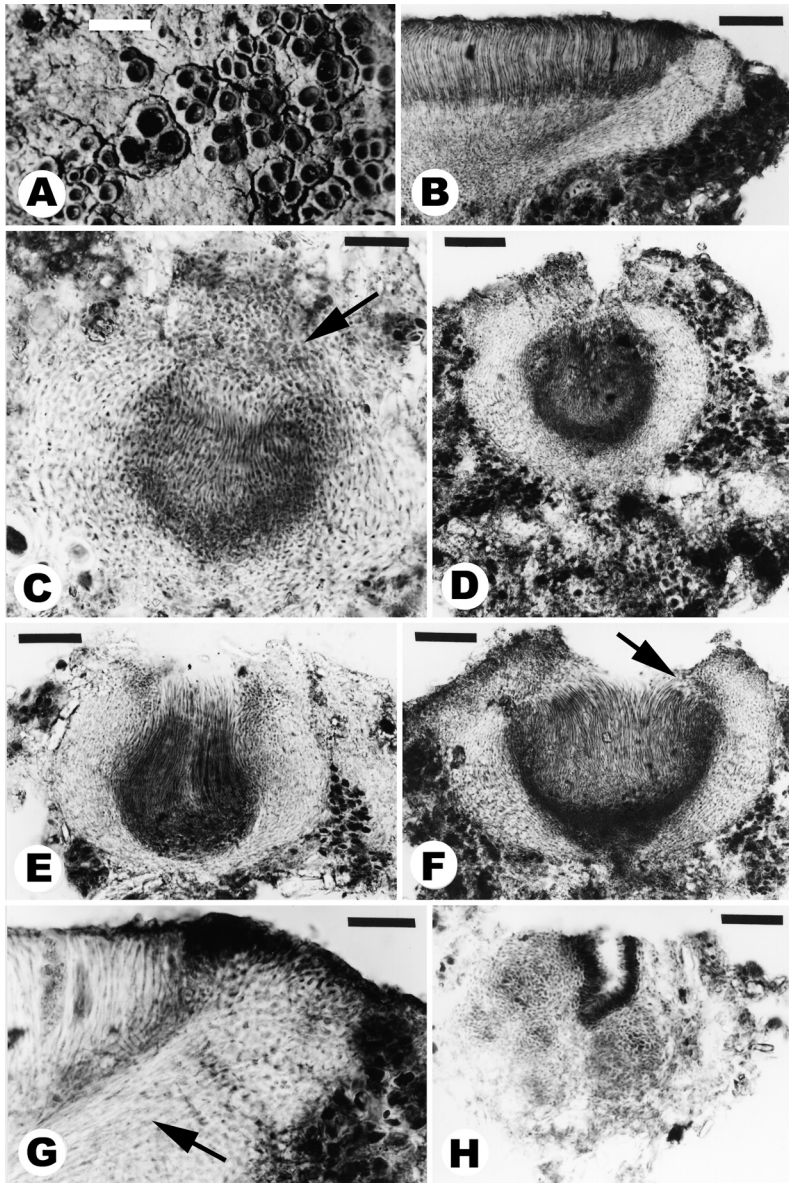


Fig. 6. Apothecial anatomy and ontogeny in *Gyalidea lecanorina* (New Zealand, *Henssen 30360a*; **B–H** microtome sections in LB). — **A**: General habit; note the semi-immersed apothecia surrounded by a whitish thallus rim. — **B**: Section through mature apothecium; note the well-developed, annular excipulum basally and laterally surrounded by algiferous thallus tissue. — **C**: Primordium with nucleus of strongly staining hyphae (paraphyses and subhymenium) and paraplectenchymatous roof (arrow). — **D**: Young apothecium opening by an apical fissure in the roof; note the external thalline tissue on the roof. — **E–F**: Young apothecium with open roof; the lateral hyphae of the hamathecium are connected to the roof, and their upper parts resemble periphysoids (arrow); note the annular excipulum in **F**. — **G**: Margin of mature apothecium; note the apically paraplectenchymatous excipulum which is connected to parallel-radiate hyphae near the hymenium. — **H**: Section through pycnidium. Scale for **A** = 1 mm, for **B, D–F** = 50 μ m, for **C, G–H** = 20 μ m.

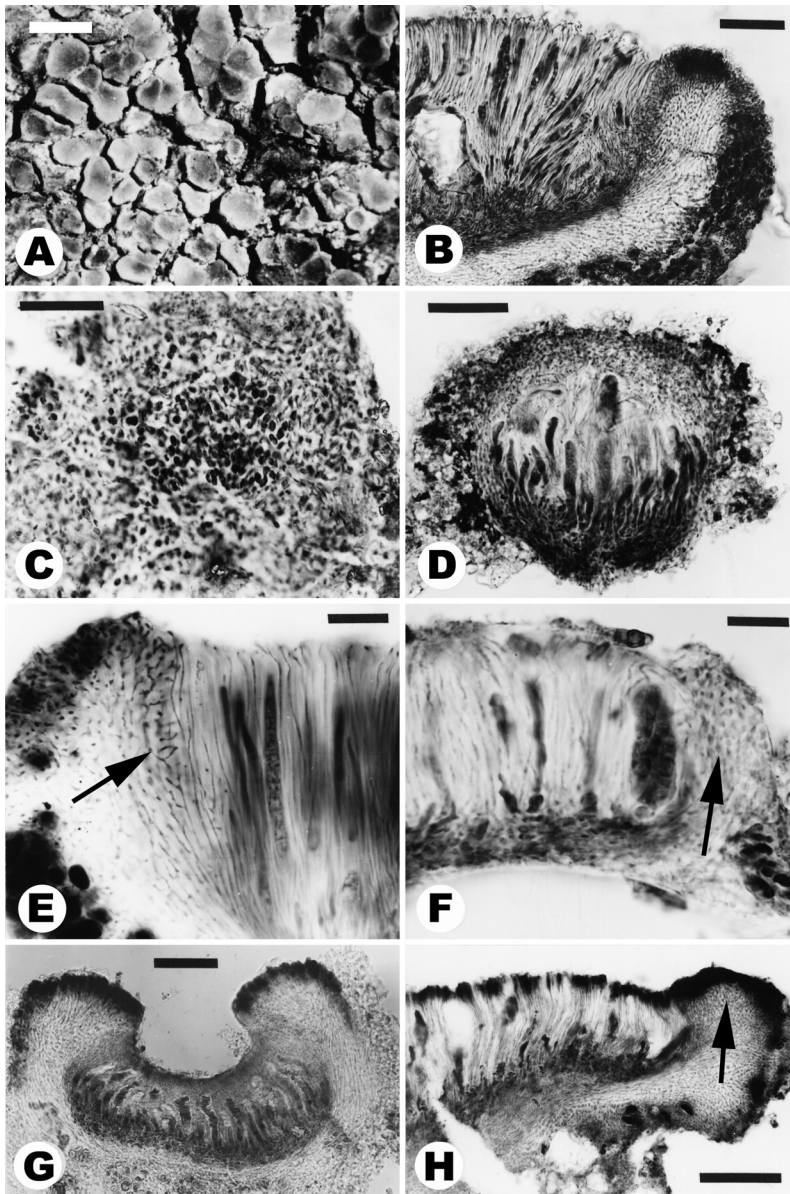


Fig. 7. Apothecial anatomy and ontogeny in *Gyalidea* (B–H microtome sections in LB). — A–E: *Gyalidea hyalinescens*. — A: General habit (Canada, Vezda: *Lich. Sel. Exs.* 1427); note the finely dentate apothecial margins. — B: Section through mature apothecium (Portugal, *Henssen* 25545a); note the external algaliferous thallus tissue covering the lateral excipulum. — C: Primordium of strongly staining cells (Canada, Vezda: *Lich. Sel. Exs.* 1427). — D: Young apothecium with developing asci (Portugal, *Henssen* 25545a); note the closed roof and excipulum. — E: Margin of mature apothecium (Portugal, *Henssen* 25545a); border between hymenium and excipulum of mature apothecium showing periphysoids (arrow). — F: *G. phyllophila* (Georgia; Vezda *s.n.*; Vezda: *Lich. Sel. Exs.* 1569), section through mature apothecium with paraplectenchymatous excipulum (arrow). — G: *G. lecideopsis* (Slovakia, Vezda 26342); section through young apothecium showing large edges formed by the roof. — H: *G. fritzei* (Slovakia, Vezda *s.n.*, Vezda: *Lich. Sel. Exs.* 533); section through mature apothecium showing apically pigmented excipulum (arrow). Scale for A = 1 mm, for B, D, G–H = 50 μ m, for C, E–F = 20 μ m.

ecial margin we assume that the young apothecia have a well-developed covering layer composed of roof and thallus tissue, which is turned upside-down after rupturing and exposure of the hymenium. Since the lateral lobes are much larger than the young primordia, we suspect that roof and lateral excipulum enlarge secondarily after rupturing, a phenomenon which is also found in *Asterothyrium rondoniense* (see below).

Apothecial morphology, anatomy and ontogeny in *Psorotheciopsis*

Apothecia in *Psorotheciopsis* are sessile and not covered by thallus tissue laterally (Figs. 2A–D and 8A). Most species have lecideine, pure black apothecia, such as *P. albomaculans* or *P. premneella* (Fig. 2C–D), or a black margin combined with a pale disc, like *P. patellarioides* (Figs. 2B and 8A), while *P. gyalideoides* features translucent apothecia (Fig. 2A). The apothecial margin is usually smooth and not prominent, but might produce small, teeth-like protuberances in *P. patellarioides* and *P. varieseptata*. The lateral excipulum is composed of slightly branched hyphae embedded in a gelatinous matrix. External parts of the excipulum are hyaline, while internal and basal parts are mostly black pigmented (Fig. 8B–I).

Apothecia are either formed on the algiferous thallus patches, as in *Psorotheciopsis guajalitenensis*, or marginally on the hyaline prothallus, as in *P. patellarioides* and *P. albomaculans* (Figs. 2B–C and 8A). In *P. patellarioides*, the primordium is seen as applanate generative tissue which differentiates a heavily pigmented roof (Fig. 8C). The primordium is covered by thallus tissue, which in early stages is difficult to tell apart from the generative tissue but soon ruptures and separates from the proper roof. Soon after, a cavity between hymenium and roof is formed, and the proper roof ruptures in the centre (Fig. 8C–D). In that stage, the roof typically appears as \pm black, triangular structure in section, which its thickest parts oriented towards the centre and its tapering sides lateral of the hymenium.

With the growth of the hymenium and maturation of asci, the roof is further torn aside by prolongation of the paraphyses and finally inte-

grated into the apothecial margin, where it forms the innermost, pigmented part of the proper excipulum (Fig. 8B). In mature apothecia, the roof is not or only slightly elevated above the hymenium surface and sometimes forms short, irregular teeth. A particular feature is the secondary growth of slightly branched hyphae from the lateral and basal part of the roof (Fig. 8E–G); these hyphae are embedded in a gelatinous matrix and, in mature apothecia, form the major part of the proper excipulum (Fig. 8B). Since these hyphae originate from the roof, i.e. the generative tissue, they are part of a true excipulum and are not to be confused with a zeorine thallus margin. Due to the growth of these secondary excipular hyphae, the thallus tissue which originally covered the primordium is bent down towards the leaf surface and finally hidden below the mature apothecium, where it is visible as a strongly recurved black line (Fig. 8B).

Apothecial development in *Psorotheciopsis premneella* resembles that of *P. patellarioides*. Young stages exhibit a black roof which, in sections, ruptures into \pm triangular halves (Fig. 8H). Again, the thin thallus tissue originally covering the primordium is pushed away by the growth of secondary hyphae from the lateral and basal part of the roof, and the excipulum of mature apothecia is composed of slightly branched hyphae embedded in a gelatinous matrix, very much like in *Gyalidea*, while the original roof is \pm reduced (Fig. 8I). As in *P. patellarioides*, the thallus tissue originally covering the primordium remains as a straight to strongly recurved black line near the apothecial base, while the basal part of the excipulum remains small and hyaline.

Apothecial morphology, anatomy and ontogeny in *Asterothyrium*

The apothecia of *Asterothyrium* are typically immersed in the thallus but erumpent and eventually prominent when mature. Mature apothecia feature a thallus margin composed of obliquely oriented, triangular lobes or teeth covering the apothecial disc (Figs. 2E–H, 3A, C, E and 9A–B). In *A. chroodisciforme* and *A. rondoniense*, the thallus teeth are recurved and give the apothecia a characteristic, star-like appearance

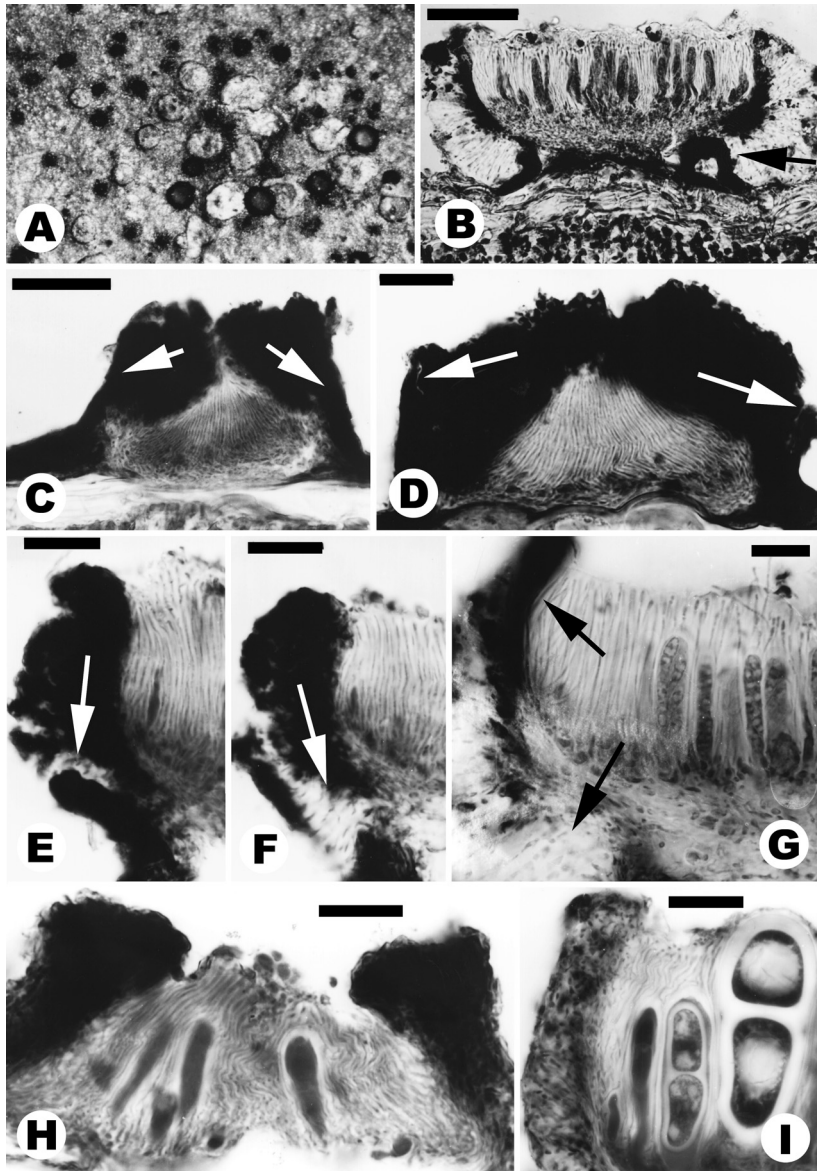


Fig. 8. Apothecial anatomy and ontogeny in *Psorotheciopsis* (**B–I** microtome sections in LB). — **A–G:** *P. patellarioides* (Guinea, *Lisowski s.n.*; *Ve zda: Lich. Sel. Exs. 1158*). — **A:** General habit; note the thin black lines around the thallus patches and the formation of the apothecia between the thallus patches on an algal-free prothallus. — **B:** Mature apothecium; the roof is visible as black inner part of the excipulum, while the black thallus tissue remains as a strongly bent line at the lateral apothecial base (arrow). — **C:** Young apothecium, with the roof centrally ruptured; note the cavity between the upper part of the hymenium and the roof; the thallus tissue begins to separate laterally from the roof (arrows). — **D:** Subsequent stage, with paraphyses and black roof; the thallus tissue has ruptured and covers the lateral parts of the roof (arrows). — **E–G:** Development of excipulum; the black inner part of the proper excipulum represents the original roof from which, secondarily, branched hyphae embedded in a gelatinous matrix are growing out; the black thallus tissue which originally covers the primordium is bent down towards the leaf surface by the growth of the proper excipulum while the original roof remains in the upper part of the excipulum (arrows). — **H–I:** *P. premneella* (holotype). — **H:** Young apothecium with immature asci and thick black apical roof that ruptured in the centre. — **I:** Marginal part of mature apothecium with asci and ascospores; the original black roof has almost completely disappeared and is replaced by the secondary excipulum composed of short hyphae embedded in a gelatinous matrix. Scale for **A** = 1 mm, for **B–C** and **E–I** = 20 μm , for **D** = 50 μm .

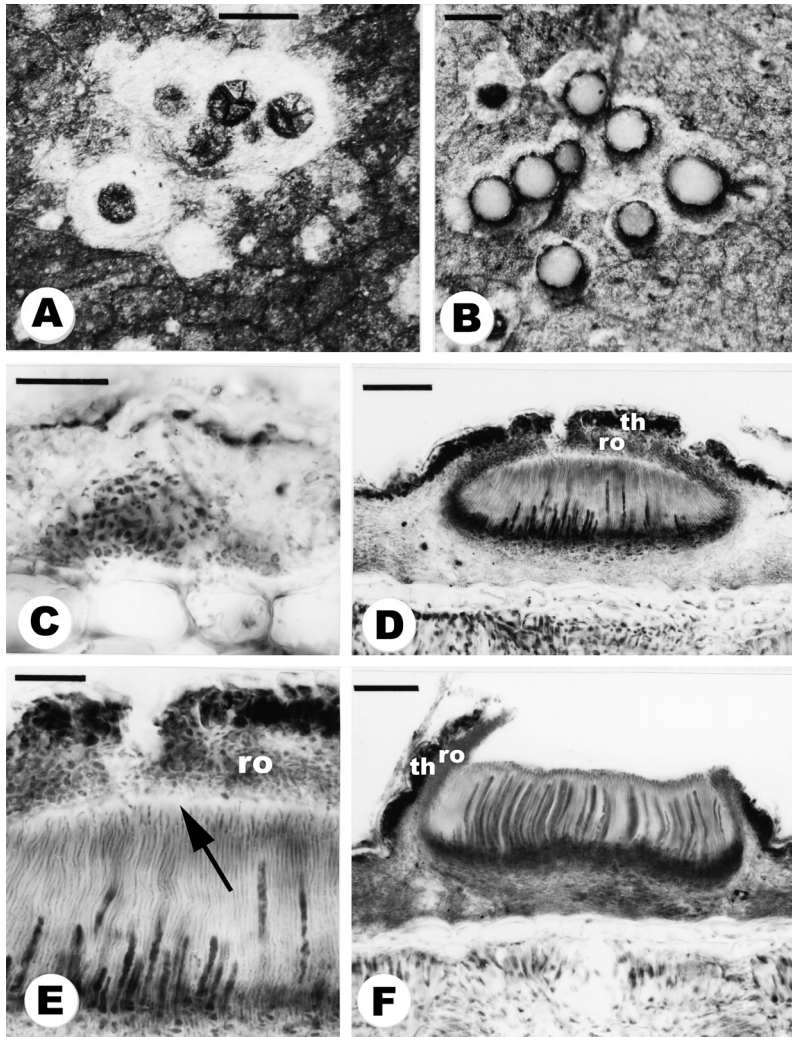


Fig. 9. Apothecial anatomy and ontogeny in *Asterothyrium leucophthalmum* (C–F: microtome sections in LB; A–B and D–F: Brazil, *Malme 414:2*; C: Argentina, *Henssen 24112b*). — **A**: General habit in dry condition; note the pigmented teeth which are formed by thallus and excipular tissue and cover the disc in mature apothecia. — **B**: General habit in moist condition, teeth bent upwards to expose the unpigmented disc. — **C**: Initial stage of generative tissue. — **D**: Young apothecium, with the covering layer formed by the roof (ro) and the pigmented, corticate thallus tissue (th); the covering layer partly rupturing. — **E**: Same stage as in D but with higher magnification, showing details of the young hymenium and the covering layer; note the cavity between the hymenium and the covering layer (arrow), and the paraplectenchymatous roof (ro) which originates from the generative tissue. — **F**: Mature apothecium, the lateral tooth composed of the internal paraplectenchymatous roof or proper excipulum (ro) and the closely adnate, pigmented and corticate thallus tissue (th). Scale for **A–B** = 0.7 mm, for **C** and **E** = 20 μm , for **D** and **F** = 50 μm .

(Fig. 2G). In *A. rotuliforme*, and partly also in *A. leptosporum*, the thallus margin is entire, with no teeth visible (Fig. 3F). Reduced, very small or short teeth are found in *A. anomalum* var. *pallidum* and *A. septemseptatum* (Fig. 3D–E). In *A. gyalideoides*, the mature apothecia are sessile,

and the excipulum is not covered by adjacent thallus tissue (Fig. 3B).

Interspecific variation is mainly found in apothecial size and the colour of disc and margin. In *Asterothyrium anomalum* var. *pallidum*, *A. argenteum*, *A. monosporum*, and *A. uniseptatum*,

the marginal teeth are pale (Figs. 2H and 3A), while *A. anomalum* var. *anomalum*, *A. aulaxinoides*, *A. leucophthalmum*, *A. octomerum*, *A. pittieri* and *A. tetrasporum* have grey to brownish black teeth (Figs. 2E–F, 3C, E and 9A–B). The disc might be pale and translucent in *A. argenteum*, *A. aulaxinoides*, and *A. microsporum* (Figs. 2E and 3A), yellowish to reddish brown in *A. monosporum*, *A. rondoniense*, and *A. uniseptatum*, or brownish black in *A. chroodisciforme*, *A. pittieri* and *A. tetrasporum* (Fig. 2F–G). In most species, the small thallus patches produce a single, central apothecium (Figs. 2H and 3A), but eventually become confluent to form a polycarpous thallus (Figs. 2F, 3C and 9A). In *A. septemseptatum* and *A. rotuliforme*, the single thallus patches are polycarpous from the beginning, with 1–2 central apothecia surrounded by a concentric ring of 5–15 apothecia. The central apothecia are usually older and larger and surrounded by a whitish area (Fig. 3D and F).

The apothecia of *Asterothyrium* have a very characteristic anatomy. The proper excipulum is paraplectenchymatous and distinctly cupular, visible as a thin layer below the hypothecium (Figs. 9F and 10D), and reacts I+ red. *Asterothyrium chroodisciforme* and *A. rondoniense* differ from the general pattern in having the excipulum composed of branched, net-like hyphae embedded in a gelatinous matrix, with a large extension of the lateral part (Fig. 11A–D). In all species, the basal part of the apothecium is formed by a thin layer of small, shortly anticlinal cells (Fig. 10D). The excipulum is laterally covered by thallus tissue which may contain dark pigments in the cell walls and is covered by the cellular thallus cortex (Figs. 9F, 10C and F–G). In *A. gyalideoides*, the paraplectenchymatous excipulum is laterally free and not covered by thallus tissue (Fig. 10L). *Asterothyrium rotuliforme* is the only species which retains epithelial algae (Fig. 12).

The typical apothecial ontogeny is found in *Asterothyrium leucophthalmum*, *A. argenteum* (the type species), *A. pittieri*, and *A. monosporum*. In *A. leucophthalmum*, the disc of mature apothecia is covered by teeth-like remnants of the covering layer in the dry condition but exposed in the wet condition (Fig. 9A–B). The lens-shaped to globose generative tissue is formed at the thallus base by irregularly arranged, short-

celled hyphae strongly staining in LB (Fig. 9C). In young apothecia, mainly true paraphyses are formed by vertical growth of hyphae within the generative tissue. The basal part of the primordium develops into a thin hypothecium, while its periphery differentiates into a paraplectenchymatous cortical layer, which later forms the basal and lateral excipulum, and the paraplectenchymatous roof being separated from the hymenium by a narrow cavity (Fig. 9D–E). The roof is covered by a dark pigmented thallus tissue, the pigments being deposited in the walls of the vegetative thallus hyphae below the cortex, which itself remains unpigmented. The lateral parts of the excipulum are rather thin and not well separated from the thick, dark hypothecium and the lateral parts of the hymenium. In the mature apothecium, the hymenium is still surrounded by a cup-shaped excipulum and a pigmented thallus tissue, both being closely adnate and surpassing into the overarching teeth (Fig. 9F).

Developmental morphology in *Asterothyrium argenteum* corresponds closely to that found in *A. leucophthalmum*. The covering layer above the cavity of young apothecia is composed of the paraplectenchymatous roof and a thick layer of dark pigmented thallus tissue including the hyaline cortex (Fig. 10A–B). In mature apothecia, the thallus tissue might apically separate from the paraplectenchymatous excipulum which itself arises from periclinally arranged hyphae (Fig. 10C). In *A. pittieri*, ascus initials might be visible in the primordium (Fig. 10E). In most species, a split is formed between the hymenium and the lateral excipulum (Figs. 9F, 10F–G and 10I).

A particular feature of most *Asterothyrium* species is the intimate connection between the paraplectenchymatous roof and the adjacent thallus tissue to form a multistratose covering layer, composed of the thallus cortex, the often pigmented subcortical thallus tissue lacking algal cells, and the paraplectenchymatous roof. In young apothecia, e.g. of *A. leucophthalmum* and *A. argenteum*, this covering layer ruptures in the centre (Figs. 9D–E and 10A–B). Along with the growth of the hymenium and maturation of asci and ascospores, the ruptured covering layer is pushed away laterally, but remains lateral of the hymenium in mature apothecia, its remnants being visible as triangular teeth partly covering

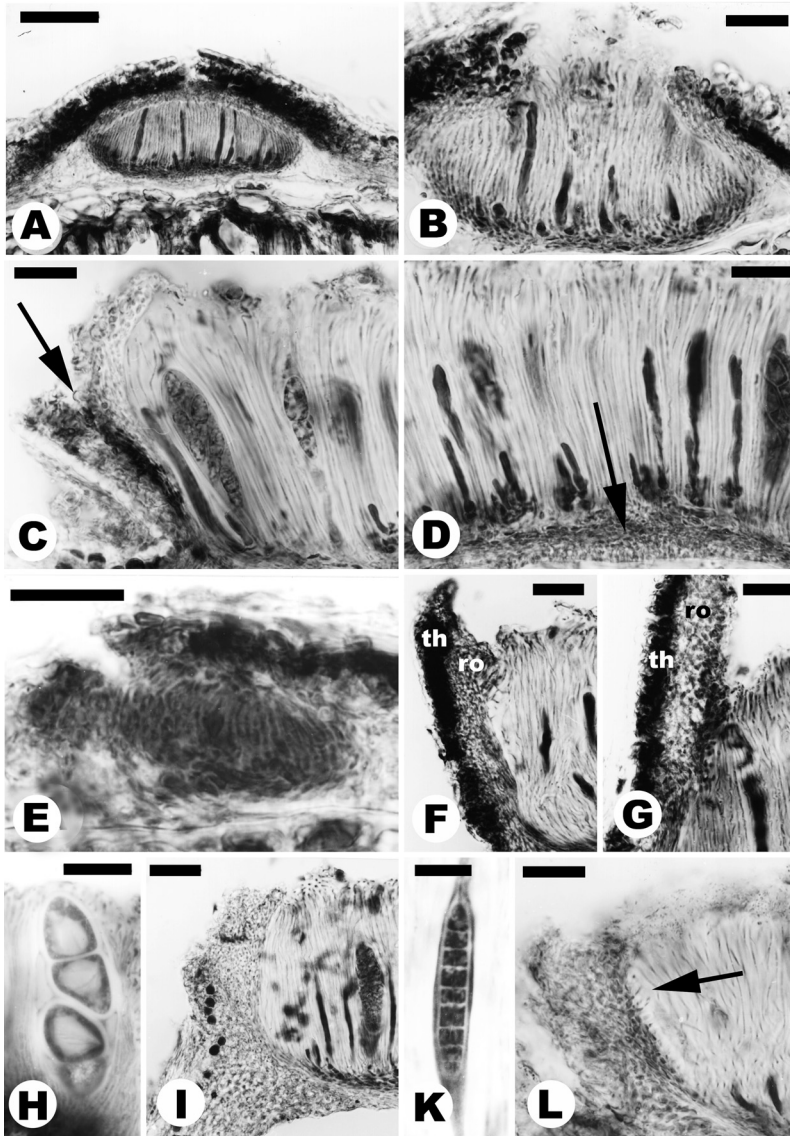


Fig. 10. Apothecial anatomy and ontogeny in *Asterothyrium* (microtome sections in LB). — **A–D:** *A. argenteum* (Costa Rica, Lücking 91-44). — **A:** Young apothecium, same stage as in Fig. 9D, the covering layer rupturing in the centre. — **B:** Subsequent stage, the covering layer largely ruptured; note the connection between the paraplectenchymatous lateral part of the proper excipulum and roof and the basal part of the excipulum, composed of parallel hyphae. — **C:** Marginal part of mature apothecium; the corticate thallus tissue partly separated from the lateral excipulum (arrow). — **D:** Central part of mature apothecium; note the paraplectenchymatous excipulum basally composed of small, shortly anticlinal cells (arrow). — **E–G:** *A. pittieri* (**E:** Costa Rica, Lücking 91-52; **G:** Costa Rica, Pittier & Tonduz 6025). — **E:** Primordium with ascus initials, covered by a pigmented, corticate thallus tissue; the roof is not yet apparent. — **F–G:** Marginal parts of mature apothecia, same stage as in Fig. 9F and 10C; the lateral tooth composed of the internal paraplectenchymatous roof or proper excipulum (ro) and the closely adnate, pigmented and corticate thallus tissue (th). — **H:** Central part of mature apothecium with hymenium, showing mature ascus with ascospores. — **I–K:** *A. anomalum* var. *pallidum* (Costa Rica, Lücking 92-51). — **I:** Marginal part of mature apothecium of a specimen with reduced teeth; note that the thallus tissue covering the paraplectenchymatous proper excipulum carries algal cells in its lower part; excipulum and thallus tissue are largely confluent and not well separated. — **K:** Young ascus; the immature ascospore which later becomes muriform closely resembles the mature ascospores in *A. octomerum*. — **L:** *A. gyalideoides* (an isotype); marginal part of mature apothecium, the lateral excipulum not covered by thallus tissue; note the short periphysoids (arrow). Scale for **A, F, H** = 50 μm , for **B–D, G, I–K** = 20 μm , for **E** = 10 μm .

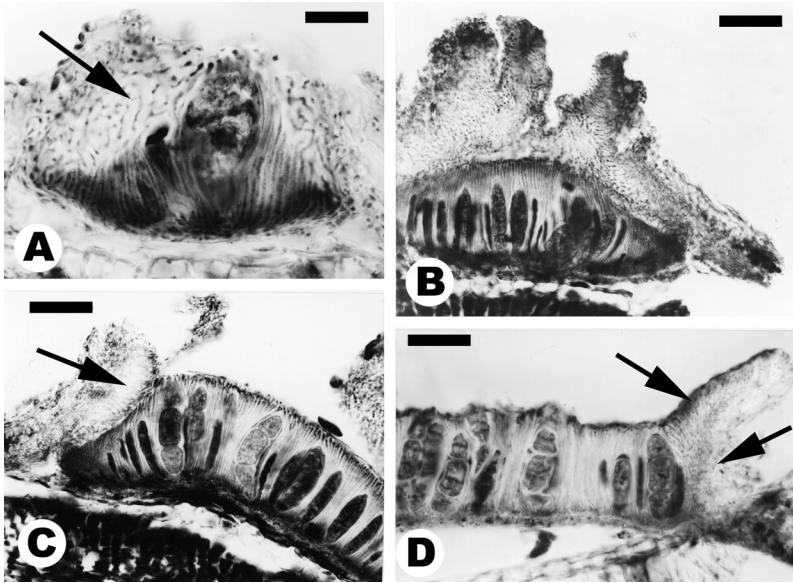


Fig. 11. Apothecial anatomy and ontogeny in *Asterothyrium rondoniense* (microtome sections in LB; **A, D**: Costa Rica, *Pittier & Tonduz 6025*; **B–C**: Brazil, *Baker s.n.*). — **A**: Young apothecium, roof composed of branched, net-like hyphae partly connected to the upper part of the paraphyses as paraphysoids (arrow). — **B**: Subsequent stage, the covering layer partly rupturing. — **C**: Mature apothecium, the internal part (roof and excipulum) of the lateral tooth composed of branched hyphae embedded in a gelatinous matrix (arrow). — **D**: Same stage but other side of apothecium, again with excipulum composed of branched hyphae in a gelatinous matrix (arrow); note that the proper excipulum is not well separated from the covering, unimpigmented thallus tissue (arrow). Scale for **A** = 20 μm , for **B–D** = 50 μm .

the apothecial disc (Fig. 2F and H). In that way, the lateral parts of the original roof are integrated into the cup-shaped excipulum of mature apothecia, while the central parts remain in the over-arching teeth. The internal structure of the teeth is the same as in the original covering layer, with the thallus cortex, the pigmented subcortical thallus tissue, and the paraplectenchymatous excipulum or roof (Figs. 9A, F and 10F–G).

A slightly deviating pattern is found in *Asterothyrium gyalideoides*. The apothecial ontogeny chiefly follows that of *A. argenteum*, but the covering thallus tissue is unpigmented from the beginning and already in young apothecia separates from the paraplectenchymatous roof. The roof itself ruptures earlier than in other species and is soon pushed away laterally. In mature apothecia, the margin is thus only formed by the proper excipulum that is not covered by thallus tissue (Fig. 10L), and projecting teeth are not apparent (Fig. 3B). The apothecia of *A. gyalideoides* are therefore not erumpent but sessile in mature condition and externally resemble those

of *Psorotheciopsis* and *Gyalidea* (Fig. 3B). Their internal anatomy, however, is identical with that of other *Asterothyrium* species, in having a paraplectenchymatous excipulum and basal layer. In certain stages of *A. gyalideoides*, the inner part of the excipulum forms short hyphal threads resembling periphysoids (Fig. 10L).

Asterothyrium chroodisciforme and *A. rondoniense* exhibit a third pattern of apothecial development, which differs in that the roof and excipulum are not paraplectenchymatous but composed of branched, net-like hyphae embedded in a gelatinous matrix, very much like the excipular structure in *Gyalidea* (Fig. 11A–B). In the lateral parts of the apothecia, the paraphysoids are more distinctly seen than in other species (compare Figs. 10B and 11A), while the remaining interscal hyphae are true paraphyses. A strand of densely interwoven hyphae arises in the upper part of the gelatinous roof underneath the unpigmented thallus tissue, and the roof breaks up by several splits (Fig. 11B). In mature apothecia, the thick lateral teeth are recurved

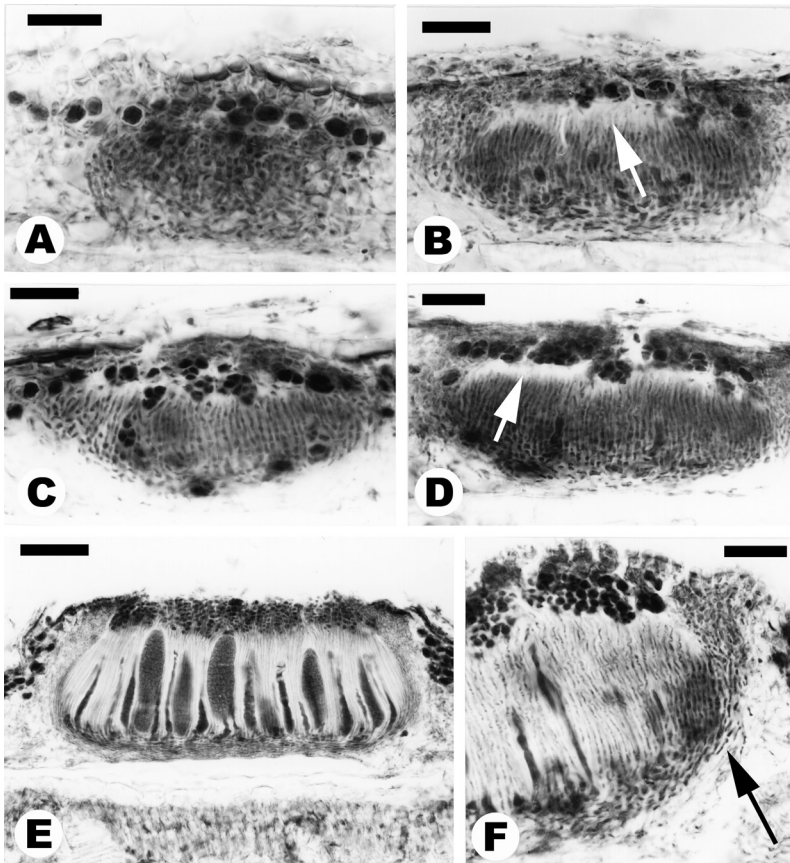


Fig. 12. Apothecial anatomy and ontogeny in *Asterothyrium rotuliforme* (microtome sections in LB; **A–D**: Costa Rica, *Lücking 92-2*; **E–F**: Brazil, *Rick s.n.*). — **A**: Generative tissue covered by unpigmented, corticate thallus tissue; note the algal cells enclosed in the upper part. — **B**: Primordium with ascus initials; note the cavity (arrow) between the upper part of the hymenium and the roof, which itself is not well developed and laterally connected to the excipulum. — **C**: Lateral section of young apothecium with covering, corticate thallus tissue; note the algal cells above the hymenium in state of division. — **D**: Central section of same young apothecium with two ascus initials; note again the distinct cavity (arrow) between the upper part of the hymenium and the roof containing the algal cells. — **E**: Mature apothecium with ascospores and abundant epithelial algae. — **F**: Marginal part of apothecium; note the connection between the paraplectenchymatous lateral part of the proper excipulum and the basal part of the excipulum, composed of parallel hyphae (arrow). Scale for **A–D**, **F** = 20 μm , for **E** = 50 μm .

and expose the inner surface of the original roof, retaining their gelatinous structure with radiating hyphae and being separated from the hymenium by a split (Fig. 11C–D).

Asterothyrium rotuliforme differs from all other species of the genus by the presence of epithelial algae. The primordium arises at the base of the often thick thallus and is covered by a corticate thallus tissue in which the pigmentation is much reduced and which includes algal cells (Fig. 12A). The generative tissue is composed of densely aggregate, short-celled hyphae and in

upper part encloses cells of the phycobiont. The roof of the primordium is rather thin and more or less directly formed beneath the thallus cortex; it incorporates the algal cells above the generative tissue which immediately begin cell division (Fig. 12B–C). The algal cells multiply in the cavity, the roof, the marginal parts of the young apothecium, and partly between the paraphyses. With the formation of the roof, the cavity which separates roof and hymenium becomes visible (Fig. 12B and D). Contrary to other species of *Asterothyrium*, the covering layer, mainly formed by

the thin roof and the thallus cortex and including the algal cells, does not rupture, but disintegrates completely to liberate the algal cells which then become epithelial algae (Fig. 12E–F). Therefore, in mature apothecia the lateral margin is formed by the proper excipulum and a thallus tissue that basally includes algal cells, while teeth are not apparent. The structure of the excipulum is the same as in other species, however, and like in *A. argenteum*, the transition between the basal vertical hyphae and the lateral paraplectenchymatous excipulum is visible (Fig. 12F).

Hymenium, ascus structure and ascospores

The hamathecium in *Gyalidea*, *Psorotheciopsis* and *Asterothyrium* consists of true, unbranched paraphyses which are not distinctly thickened at their apices (Figs. 7B, E–F, 8B, G, I, 9E–F, 10C, G–I, 11D and 12E). The paraphyses are only weakly gelatinized and easily separable in squash mounts. The asci are more or less clavate, and immature asci exhibit a more or less distinct apical tholus. All parts of the ascus wall are I– and KI–, while the ascus lumen usually becomes I+ yellowish red to reddish brown (mostly the colour of the I-solution itself). In immature asci, a ring-like structure can be observed that projects downwards from the lower part of the tholus into the lumen. In broken asci, the tholus is seen as a more or less globose structure, and the ring-like structure as a reversed V-shaped ocular chamber extending basally into the ascus lumen. This ascus type is here called *Gyalidea* type, since it was first described for the genus *Gyalidea* (Vezda 1966). It is the same type as described by Hafellner (1984) for *Psorotheciopsis premeella* and *Asterothyrium argenteum*.

Ascospores in *Gyalidea* are typically thin-walled and slightly constricted at the septa. Septation ranges from transversely septate to submuriform (Fig. 13), and the number of ascospores per ascus varies mostly from eight to one. *Gyalidea asteriscus* and *G. multispora* have polysporous asci (30–60 ascospores per ascus), and 10–14 ascospores per ascus are found in *G. polyspora*. Most species of *Psorotheciopsis* have thin-walled, 1-septate ascospores,

such as *P. patellarioides* (Fig. 8G), *P. gyalideoides*, *P. guajalicensis*, and *P. philippinensis*. Three further types are found (Fig. 13). In *P. varieseptata*, ascospores are thin-walled and irregularly 1–11-septate, with no constrictions visible. *P. albomaculans* has rather characteristic ascospores: the central septum is very thick (up to 2.5 μm) and provided with a very thin channel which connects both cells. In *P. premeella*, the ascospores are 1-septate as in most other species but very large and thick-walled and occur single in the asci (Fig. 8I). In certain stages, a narrow channel can be observed in the thick septum connecting both cells.

Ascospores in *Asterothyrium* are principally thin-walled and 1-septate, as in *A. microsporium*, *A. decipiens*, *A. argenteum*, and *A. gyalideoides* (Fig. 10C–D). Three distinct lines of ascospore variation are present (Fig. 13). In *A. leucophthalmum*, *A. leptosporum*, and *A. longisporum*, the ascospores become elongate to acicular and often break into halves. The ascospores of *A. decipiens* and *A. longisporum* are rather large and often have gelatinous outer walls, representing a transition towards the second type, i.e. the large, thick-walled ascospores found in *A. hedbergi*, *A. tetrasporum*, *A. pittieri* (Fig. 10H), *A. monosporum*, *A. uniseptatum*, *A. aulaxinoides*, *A. chroodisciforme*, and *A. rondoniense* (Fig. 11D). In these species, the number of ascospores is continuously reduced, from six to finally one per ascus. In *A. rondoniense*, the large, 2-septate ascospores might appear secondarily divided to resemble muriform ascospores.

A third type is found in *Asterothyrium septemseptatum*, *A. octomerum*, *A. anomalum*, and *A. rotuliforme*, with multiseptate and muriform ascospores, respectively (Fig. 13). In these species, ascospores are basically thin-walled but exhibit a gelatinous outer wall in *A. octomerum*. The number of ascospores per ascus is variable but constant within a species: eight in *A. septemseptatum*, four in *A. octomerum*, and one in *A. anomalum* and *A. rotuliforme* (Fig. 12E). The young ascospores in *A. anomalum* and *A. rotuliforme* go through a 7-septate stage (Fig. 10K), very much resembling the mature ascospores of *A. octomerum* and thus demonstrating the close relationship between the transversely septate and muriform type.

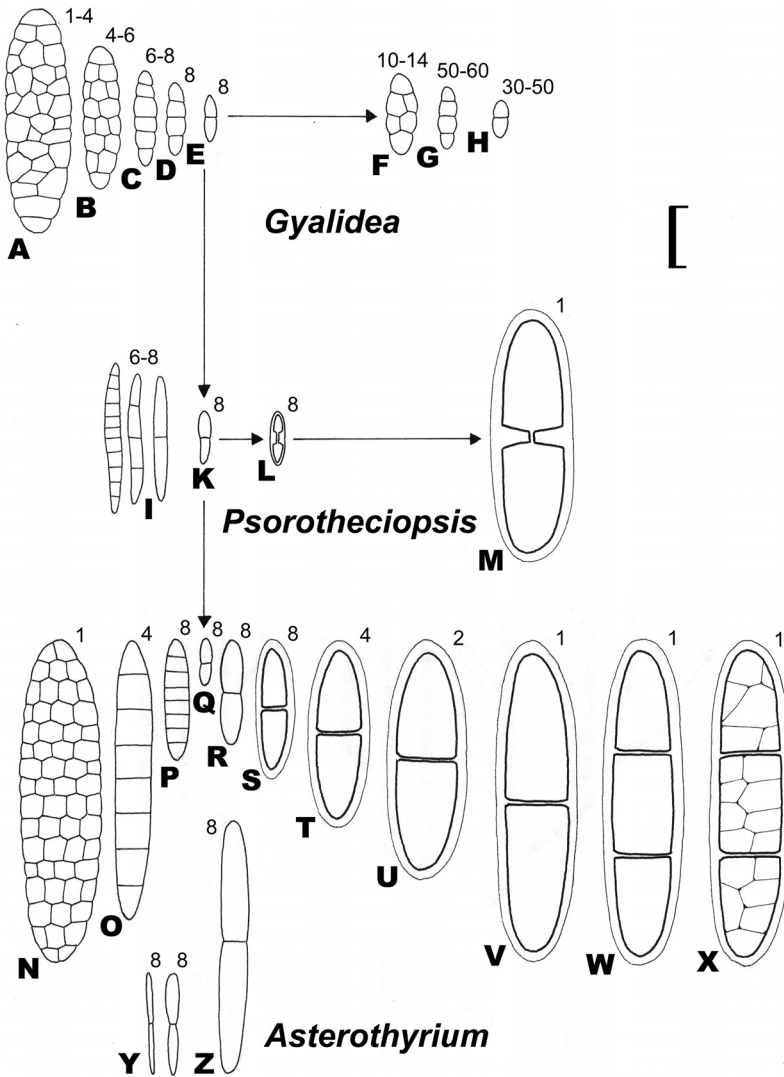


Fig. 13. Variation of ascospore size, septation, and number per ascus (indicated on top of each ascospore) in *Gyalidea*, *Psorotheciopsis*, and *Asterothyrium*. — **A:** *Gyalidea lecideopsis* var. *eucarpa*. — **B:** *G. lecideopsis* var. *lecideopsis*. — **C:** *G. phyllophila*. — **D:** *G. hyalinescens*. — **E:** *G. diaphana*. — **F:** *G. polyspora*. — **G:** *G. multispora*. — **H:** *G. asteriscus*. — **I:** *Psorotheciopsis varieioseptata*. — **K:** *P. patellarioides*. — **L:** *P. albomaculans*. — **M:** *P. premneella*. — **N:** *Asterothyrium rotuliforme*. — **O:** *A. octomerum*. — **P:** *A. septemseptatum*. — **Q:** *A. microsporum*. — **R:** *A. argenteum*. — **S:** *A. decipiens*. — **T:** *A. tetrasporum*. — **U:** *A. pittieri*. — **V:** *A. uniseptatum*. — **W:** *A. monosporum*. — **X:** *A. rondoniense*. — **Y:** *A. leptosporum* (left) and *A. leucophthalmum* (right). — **Z:** *A. longisporum*. Scale = 10 μ m.

Pycnidia and conidia

Pycnidia are rare in *Gyalidea*, but abundant and often found on otherwise sterile thalli of *Psorotheciopsis* and *Asterothyrium*. Since species often grow intermingled and the dispersed thallus patches are difficult to tell apart, one must be cautious when assigning pycnidia to a particular

species. Being aware of that problem, we have only accepted pycnidia as belonging to a given species when they were found on thalli carrying both apothecia and pycnidia.

While pycnidia are rather uniform in *Gyalidea*, usually being immersed and flask-shaped (Fig. 6H), *Psorotheciopsis* and *Asterothyrium* exhibit three different pycnidial types. Type I

consists of immersed, flask-shaped pycnidia scattered over the thallus surface, similar to those of *Gyalidea*, often appearing as narrow, tubular openings surrounded by a thin darker thallus zone. Such pycnidia were found in *Asterothyrium argenteum*, *A. pittieri*, *A. septemseptatum*, *A. rotuliforme* (Fig. 14D), and *Psorotheciopsis philippinensis*. The conidia produced in these pycnidia are mostly small ($5\text{--}7 \times 1\text{--}1.5 \mu\text{m}$), fusiform and non-septate, as in *Asterothyrium rotuliforme* and *Psorotheciopsis philippinensis* (Fig. 15A and K), but acicular ($25\text{--}30 \times 1\text{--}1.5 \mu\text{m}$) and 1-septate in *A. argenteum* (Fig. 15B).

Type II is rather abundant but mostly found on sterile thalli. The pycnidia are larger than in type I, squad-conoid in outline and formed superficially at incisions of the thallus margin (Figs. 3G and 14A–C). Their wall is heavily pigmented and appears black or greyish when seen from above. Pure black pycnidia producing small ($6\text{--}7 \times 2 \mu\text{m}$), ellipsoid, unseptate conidia are typical of *Asterothyrium microsporum* (Fig. 15C), *A. decipiens*, and *A. hedbergii*. In *A. leucophthalmum* (Fig. 14B) and *A. gyalideoides*, the pycnidia are covered by a thin thallus tissue and therefore greyish, and the conidia are narrower ($5\text{--}7 \times 1\text{--}1.5 \mu\text{m}$) and fusiform (Fig. 15D). A pycnidial type resembling that of *A. leucophthalmum* was found on a specimen from Brazil (Fig. 14C), but the conidia are much longer (up to $20 \mu\text{m}$) and almost acicular (Fig. 15E). In most species, the conidia are often extruded through the pycnidial opening and appear as a translucent, yellowish brown mass resembling a beak. A true beak formed by the same tissue as the pycnidial wall is found in pycnidia of *Psorotheciopsis*, e.g. *P. patellarioides*, but these pycnidia are otherwise very similar to those of *Asterothyrium*.

The third pycnidial type (type III), consists of applanate, disc-like pycnidia immersed in the centre of the thallus patches or arranged in a concentric manner (Figs. 3H and 14E–F). This type is known from several sterile species of *Asterothyrium*, namely *A. umbilicatum*, *A. aspidospermatis*, and *A. pernambucense*, whose relationships to fertile taxa cannot be established at present. Their generic identity is proved, however, by the thallus structure, which closely resembles that of *A. rotuliforme*, particularly

through the well developed medulla (Fig. 14E). In specimens of *A. umbilicatum*, rudimentary apothecial primordia were found which resemble those of other *Asterothyrium* species. The pycnidia remain closed for a long time but finally open by narrow slits. The internal anatomy is similar to that of the other two types and resembles that of young apothecia, with a \pm paraplectenchymatous proper wall covered by a corticate, pigmented thallus tissue. The conidia found in these pycnidia belong to four types: (1) small ($3\text{--}4 \times 1 \mu\text{m}$), fusiform and unseptate in *A. pernambucense* (Fig. 15F), (2) intermediate ($8\text{--}12 \times 1\text{--}1.5 \mu\text{m}$), narrowly fusiform and unseptate in *A. aspidospermatis* (Fig. 15G), (3) long ($15\text{--}25 \times 1\text{--}1.5 \mu\text{m}$), acicular and unseptate or rarely 1-septate in *A. umbilicatum* (Fig. 15H), and (4) very long ($35\text{--}50 \times 1\text{--}1.5 \mu\text{m}$), acicular to filiform and 1–3-septate in an undescribed species (Santesson 1952: p. 318; Fig. 15I). The pycnidia of type III were discussed by Santesson (1952) and described as a separate anamorph genus *Actinoteichus* (Cavalcante *et al.* 1971, Lücking *et al.* 1998).

Discussion

Apothecial ontogeny and intergeneric relationships

Apothecial ontogeny in the Asterothyriaceae is hemiangiocarpous (*see also* Henssen 1976, 1981). The generative tissue differentiates into an upper roof and lateral excipulum, and a lower part which develops into hymenium, hypothecium and basal excipulum. During the ontogeny, the roof ruptures and is pushed away in lateral direction by the growing hymenium. In mature apothecia, parts of the original roof remain as parts of the proper excipulum. The roof may be covered by a more or less distinct thallus tissue, to form a covering layer which, in immature apothecia, might be separated from the hymenium by a cavity. In species where the hymenium is exposed only late during the ontogeny, e.g. *Asterothyrium*, both the covering layer and the cave are well-developed, while in *Gyalidea* and *Psorotheciopsis*, they are much less distinct.

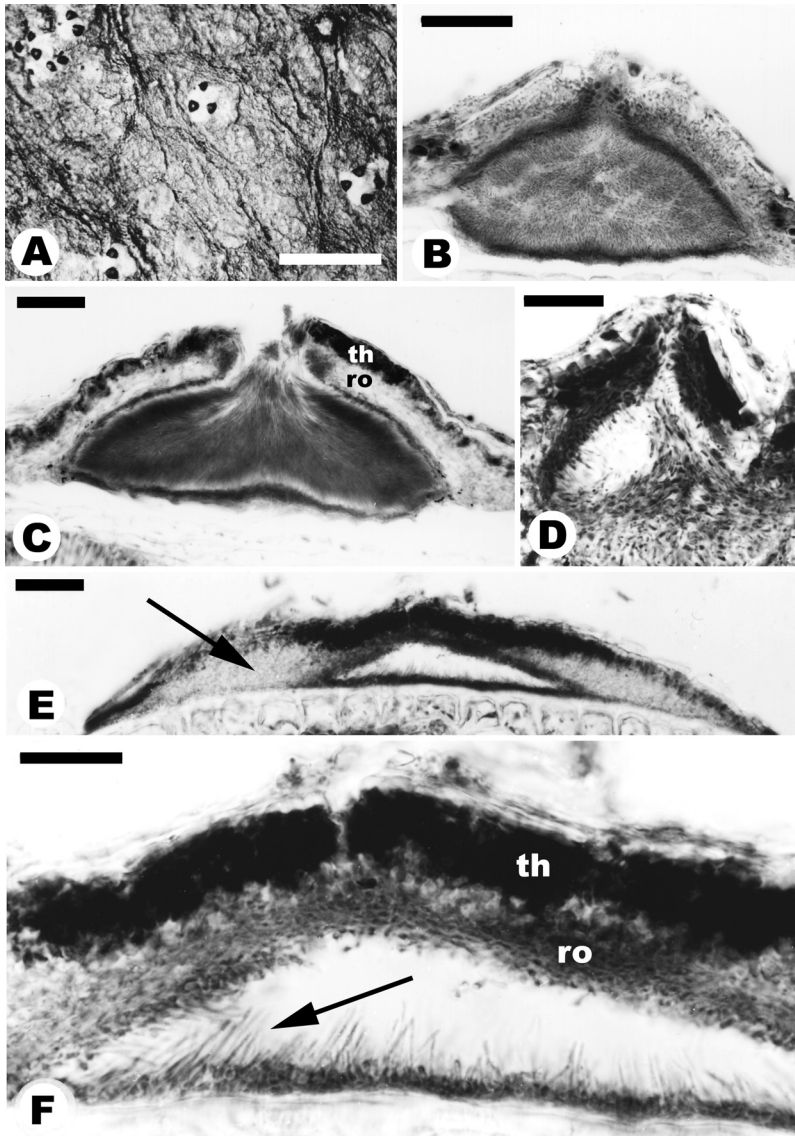


Fig. 14. Pycnidia in *Asterothyrium* (B–F microtome sections in LB). — **A:** *A. microsporum* (Philippines, *Robinson s.n.*); superficial, squad-conoid pycnidia formed at the margins of the thallus patches (type II). — **B:** *A. leucophthalmum* (Brazil, *Rick s.n.*); section through marginal pycnidium (type II) with fusiform conidia. — **C:** *Asterothyrium* sp. (Brazil, *Malme 414:3*); section through marginal pycnidium (type II) with acicular conidia; note the multistratose covering layer, with an inner roof (ro) and a pigmented, corticate thallus tissue (th). — **D:** *A. rotuliforme* (Costa Rica, *Lücking 92-2*); section through laminal, flask-shaped pycnidium (type I) with fusiform conidia. — **E–F:** *A. umbilicatum* (Costa Rica, *Lücking 91-23*). — **E:** Section through thallus with centrally immersed, applanate pycnidium (type III); note the well-developed thallus medulla (arrow). — **F:** Same stage but with higher magnification, showing the acicular conidia; note that the anatomy of the covering layer (ro, th) is the same as in type I (Fig. 14D) and in type II (Fig. 14B), and closely resembles that of the apothecia. Scale for **A** = 1 mm, for **B–C, E** = 50 μm , for **D** and **F** = 20 μm .

Although the three studied genera are more or less well distinguished, which was also confirmed by recent phylogenetic studies (Aptroot & Lücking 2002), transitional forms concern-

ing the morphology, anatomy, and ontogeny, do occur. *Psorotheciopsis* differs from *Gyalidea* in its corticate thallus and black apothecia, but *Psorotheciopsis gyalideoides* has hyaline apoth-

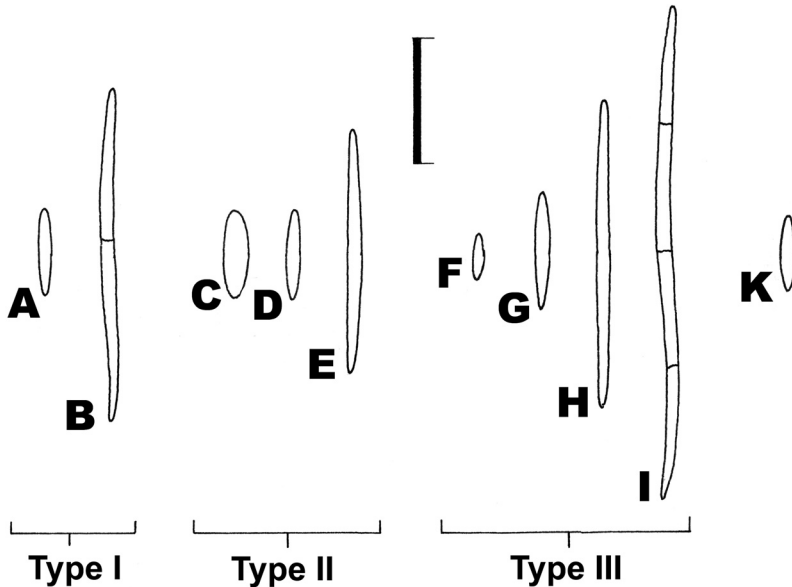


Fig. 15. Variation of conidial shape and septation in *Asterothyrium* and *Psorotheciopsis* (type of pycnidia indicated). — **A:** *Asterothyrium rotuliforme*, fusiform conidia in pycnidia of type I: — **B:** *A. argenteum*, acicular conidia in pycnidia of type I: — **C:** *A. microsporum*, ellipsoid conidia in pycnidia of type II. — **D:** *A. leucophthalmum*, fusiform conidia in pycnidia of type II. — **E:** *Asterothyrium* sp., acicular conidia in pycnidia of type II. — **F:** *A. pernambucense*, fusiform conidia in pycnidia of type III. — **G:** *A. aspidospermatis*, bacillar conidia in pycnidia of type III. — **H:** *A. umbilicatum*, acicular conidia in pycnidia of type III. — **I:** *Asterothyrium* sp., filiform conidia in pycnidia of type III. — **K:** *Psorotheciopsis philippinensis*, fusiform conidia in pycnidia of type I. Scale = 10 μm .

ecia with the same structure as most *Gyalidea* species, and *G. lecideopsis* features marginally black apothecia. The black roof in *Psorotheciopsis* might therefore be homologous to the hyaline roof found in *Gyalidea*. Ascospores in *Gyalidea* and *Psorotheciopsis* are basically of the same type, but while polyspered asci are not found in *Psorotheciopsis*, the latter features large, thick-walled ascospores in *P. premneella* similar to those present in several *Asterothyrium* species. In the latter, a continuous transitional series exists between different extremes, while in *Psorotheciopsis*, the ascospores types are more distinct between the species. Still, the large ascospores of *P. premneella* are connected to the small, thin-walled type via *P. albomaculans*, whose small ascospores having a very thick septum. Generic separation on account of the ascospore type into *Psorotheciopsis* s.str. and *Linhartia* is thus not justified, as already stated by Lücking (1999).

Psorotheciopsis and *Asterothyrium* share the corticate thallus but differ in the sessile vs. immersed-erumpent apothecia with overarching

marginal teeth, and in the hyphal vs. paraplectenchymatous excipulum. Again, transitional species do occur: *Asterothyrium gyalideoides* has sessile apothecia without marginal teeth, resembling *Psorotheciopsis gyalideoides* but differing in its paraplectenchymatous excipulum, while *Asterothyrium chroodisciforme* and *A. rondoniense* feature a hyphal excipulum similar to that found in *Gyalidea*. They also correspond to *Gyalidea astericus* in exhibiting secondary growth of the marginal teeth. A paraplectenchymatous excipulum is found in some *Gyalidea* species as well. Ascospore variation in *Asterothyrium* is greater than in the other genera but basically the same (Lücking 1999): the thick-walled ascospores of *Asterothyrium pittieri* and related species correspond to those of *Psorotheciopsis premneella*, while multiseptate and muriform ascospores are also found in *Gyalidea*. All genera share a simple pycnidial type (I), while *Psorotheciopsis* and *Asterothyrium* feature a second, derived type (II), and *Asterothyrium* a third, very particular type (III). Thus far, no significant correlation has been found between the

type of apothecia, pycnidia, and conidia produced by different species of *Asterothyrium*, but more material with conidiomata is required to study the possible taxonomic importance of pycnidial and conidial variation in this genus.

Perhaps the most particular species in *Asterothyrium* is *A. rotuliforme*, only recently included in the genus (Sérusiaux & de Sloover 1986). It is characterized by polycarpous thalli, a thick medulla, unpigmented apothecia without marginal teeth, disintegration of the roof during apothecial ontogeny, epithelial algae, and single, muriform ascospores. None of these characters are unique to this species, however, and hence separation into a monotypic genus would not be justified. *A. septemseptatum*, too, has polycarpous thalli, while a thick medulla is found in *A. leucophthalmum* and *A. umbilicatum*. The disintegration of the roof during apothecial development and the lack of apothecial pigments and marginal teeth is correlated with the presence of epithelial algae, since these features are preconditions necessary to integrate the algal cells from the covering thallus tissue into the hymenium. The occurrence of epithelial algae itself is widespread among non-related lichens and often correlates with single, muriform ascospores, as for example in *Gyalideopsis vulgaris* (Müll.Arg.) Lücking, *Calenia monospora* Vezda, *Calenia aspidota* (Vain.) Vezda, and *Gyalectidium filicinum* Müll.Arg. in the Gomphillaceae, and *Sporopodium* in the Ectolechiaceae (Santesson 1952, Lücking 1997a).

Several features characteristic of *Psorotheciopsis* and *Asterothyrium* correspond to the particular ecology of these species, which are typically found on leaves in exposed microsites, such as the outer canopy of tropical rain forests (Lücking 1995, 1997b, 1999). The whitish thalli with a dead, cellular cortex that reflects light might be an adaptation to high light intensities. The same is true for the black pigmentation of the apothecia in *Psorotheciopsis* and the overarching teeth in *Asterothyrium*, possibly protecting the developing asci from excessive UV-radiation. The high variation of ascospore types in both genera is striking and might be explained by accelerated evolution caused by UV exposition, while the thick-walled ascospores could represent protection after dispersal. Hymenia in species of *Asterothyrium* and *Psorotheciopsis* are indeed frequently damaged

(Santesson 1952, Lücking, pers. obs.).

The results presented here correspond well to the systematic redistribution of Asterothyriaceae by Lücking (1999) and Aptroot and Lücking (2002), who merged *Linhartia* with *Psorotheciopsis* and *Solorinella* with *Gyalidea*, and reinstated Asterothyriaceae sensu Eriksson and Hawksworth (1987) including the genera *Gyalidea*, *Psorotheciopsis*, and *Asterothyrium*. In this circumscription, the family is characterized by the following features: (1) hemiangiocarpous apothecial ontogeny, (2) true paraphyses, (3) I-negative hymenium, (4) “annelascaceous” asci (sensu Chadefaud 1973) of the *Gyalidea* type, and (5) chlorococcoid phycobiont.

Systematic relationships of Asterothyriaceae

The combination of features outlined above, especially apothecial ontogeny and ascus type, clearly place Asterothyriaceae within the Ostropales, together with the chiefly non-lichenized Stictidaceae and Odontotremataceae and the lichenized Gomphillaceae, Thelotremataceae, and Graphidaceae (Gilenstam 1969, Sherwood 1977, Sherwood-Pike 1987, Lücking 1997a, Lumbsch *et al.* 1997). Indeed, parallelisms to the developmental morphology in Asterothyriaceae are met with in other families of the order (Henssen & Jahns 1973, Henssen 1976, Sherwood 1977, Lücking 1997a). The formation of a roof and cavity in *Asterothyrium* corresponds to *Gyalectidium* (Gomphillaceae) and *Chroodiscus* (Müll. Arg.) Müll. Arg. (Thelotremataceae), while a gelatinous roof with netlike structure is found in *Graphina mendax* (Nyl.) Müll. Arg. (Graphidaceae). Similar trends are seen in *Absconditella* Vezda, *Cryptodiscus* Corda, and *Schizoxylon* Pers. (Stictidaceae). The lateral paraphysoids in *Gyalidea* and *Asterothyrium* are comparable to the paraphysoids in Gomphillaceae, while paraphyses similar to those of *Asterothyrium gyalideoides* and *Gyalidea* are known from Thelotremataceae. Also in some species of *Schizoxylon*, the paraphyses are apically branched and resemble paraphysoids. Internal carbonisation of the proper margin is found in *Gyalideopsis* (Gomphillaceae), *Conotrema* Tuck. (Stictidaceae), and *Gyrostomum* Fr. (Graph-

idaceae). *Schizoxylon* shows a tendency towards polyspory, as in *Gyalidea*, but the mechanism is different (partition in the former, multiplication in the latter). Large, thick-walled ascospores are otherwise rare in the Ostropales but found, for example, in the non-lichenized *Propolidium* Sacc. (Stictidaceae). In *Stictis* and *Biostrictis* Petr. (Stictidaceae), the host tissue covering the apothecia splits up into triangular lobes, very much like the overarching teeth in *Gyalidea asteriscus* and *Asterothyrium*, and species of *Calenia* and *Aulaxina* in the Gomphillaceae.

According to phylogenetic analyses (Denetière & Péroni 1998, Lücking 1999, Aptroot & Lücking 2002), the following character states appear to be plesiomorphic/apomorphic in the Asterothyriaceae: (1) sessile/immersed-erumpent apothecia, (2) ecorticate/corticate thallus, (3) hyphal/paraplectenchymatous excipulum, (4) 8-spored/less than 8-spored or polyspored asci, (5) transversely septate/muriform ascospores, (6) thin-walled/thick-walled ascospores, (7) flask-shaped/squad-conoid/applanate pycnidia, and (8) non-foliicolous/foliicolous growth habit. The distribution of plesiomorphic features clearly identifies certain *Gyalidea* species as the basal group within the family. From there, different evolutionary trends are observed: (1) immersed-erumpent apothecia being laterally covered by overarching teeth (homoplastic in *Gyalidea* and *Asterothyrium*), (2) cellular thallus cortex (synapomorphic in *Psorotheciopsis* and *Asterothyrium*), (3) paraplectenchymatous excipulum (homoplastic in *Gyalidea* and *Asterothyrium*), (4) polysporous asci (possibly synapomorphic in *Gyalidea*), (5) large, thick-walled ascospores (homoplastic in *Psorotheciopsis* and *Asterothyrium*), and (6) specialized pycnidia (synapomorphic in *Psorotheciopsis* and *Asterothyrium*).

Since *Gyalidea* conforms a plesiomorphic and *Asterothyrium* an apomorphic element, the closest relative of the Asterothyriaceae must be searched for near the former and not the latter, as often erroneously done (Vezda & Poelt 1990, Denetière & Péroni 1998, Lücking 1999). When introducing *Gyalideopsis*, Vezda (1972) compared it with *Gyalidea*, from which it was distinguished by branched and anastomosing paraphyses and hyphophores, but the obvious relationship between *Gyalidea* and *Gyalideop-*

sis was eventually obscured by the disintegration of the Asterothyriaceae (Vezda & Poelt 1987, 1990). For example, in the description of *Gyalideopsis*, the ascus type was given as "... von gleichem Bau wie bei *Gyalidea* ..." (Vezda 1972: p. 205), but later described as fissitunicate by Vezda & Poelt (1987). This was based on observations made by Hafellner (1984) on *Gomphillus* "..., probably due to the long and thin asci with very thin, needle-shaped ascospores". In certain Ostropales, the ascus apparatus might appear bitunicate but is not functionally so: "... bitunicate asci are difficult to demonstrate in specimens of filiform-spored fungi ..." (Sherwood 1977: 27).

Thus, the differences between *Gyalidea* and *Gyalideopsis* are exactly as outlined by Vezda (1972). Both genera share the same ascus type and are identical in other features (Table 3). Differences are only seen in the branched and anastomosing paraphysoids and the formation of hyphophores in *Gyalideopsis*. However, paraphysoids occur in the lateral parts of the hymenium in some *Gyalidea* species, and species of *Gyalideopsis* may have almost unbranched paraphyses and lack hyphophores. Therefore, *Gyalidea* and *Gyalideopsis* may share a common ancestor, indicating that Asterothyriaceae and Gomphillaceae are closely related families with

Table 3. Comparison of morphological, anatomical, and ontogenetical features in *Gyalidea* and *Gyalideopsis* (based on Vezda 1966).

Features shared between the genera:

gyalectoid (often slightly translucent) apothecia
 hemiangiocarpous apothecial ontogeny
 excipulum of branched hyphae embedded in
 gelatinous matrix, rarely
 paraplectenchymatous
 non-amyloid (I-negative) hymenium
 "annelascaceous" asci with apical ring
 (*Gyalidea*-type)
 transversely septate to muriform, thin-walled
 ascospores, constricted at septa
 chlorococcoid phycobiont

Features separating the genera:

<i>Gyalidea</i>	<i>Gyalideopsis</i>
true paraphyses (unbranched)	paraphysoids (branched and anastomosing)
pycnidia (rare)	hyphophores (common)

parallel evolutionary trends, such as the foliicolous growth and the evolution of immersed-erumpent (paedomorphic?) apothecia.

Members of the Ostropales were excluded from most large-scale phylogenetic studies of the Ascomycota (Gargas *et al.* 1995, Stenroos & DePriest 1998). Only recently, the monophyly of the order, including representatives of Stictidaceae (*Stictis radiata* (L.) Pers., *Conotrema populorum* Gilenstam), Thelotremataceae (*Diploschistes ocellatus* (Vill.) Norman), and Graphidaceae (*Graphis scripta* (L.) Ach.), was established by Winka *et al.* (1998) based on SSU rDNA sequences. This was confirmed by LSU rDNA data, and it was even found that this group should include the Gyalectales (Lutzoni *et al.* 2001, Lumbsch *et al.* 2001, Kauff & Lutzoni 2002; and R. Lücking *et al.* unpubl.). Judging from phenotype data, besides the Gyalectaceae/Coenogoniaceae, there appear to be three lineages within the order in its present circumscription: the largely non-lichenized Stictidaceae/Odontotremataceae, the lichenized Asterothyriaceae/Gomphillaceae, and the lichenized Thelotremataceae/Graphidaceae. Whether all these are natural entities, and whether lichenized clades evolved from non-lichenized ones or viceversa (or both?), remains to be studied and requires more detailed approaches including molecular methods.

Acknowledgements

This study was supported by travel grants of the Deutsche Forschungsgemeinschaft (DFG) to AH and by a research and a habilitation grant of the Deutsche Forschungsgemeinschaft (DFG) to RL (Lu 597/1-1 to 4-1). The authors would like to thank A. Vezda and the curators of the herbaria mentioned for placing valuable collections at our disposal.

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