

Epibryon pedinophylli - a new leaf-perforating ascomycete on *Pedinophyllum interruptum* (Hepaticae)

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Abstract:

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The ascomycete *Epibryon pedinophylli* Döbbeler is described as a new species. The species obligately infects the hepatic *Pedinophyllum interruptum* (Plagiochilaceae, Jungermanniales) perforating the leaves from the ventral side by the apical papillae of its fruit-bodies. Screening of a large body of herbarium material reveals that the fungus occurs frequently and is widely distributed within the European host area. Its morphology is described and illustrated. The systematic position and several features are discussed. Bryophilous parasites may be excellent taxonomists: the *Pedinophyllum* fungus does not grow on the similar-looking *Plagiochila asplenioides* that is parasitized by the strictly specific *Epibryon plagiochilae*.

Zusammenfassung:

Die zu den Ascomyceten gehörende Art *Epibryon pedinophylli* Döbbeler wird neu beschrieben. Sie infiziert obligat das Lebermoos *Pedinophyllum interruptum* (Plagiochilaceae, Jungermanniales). Die Fruchtkörper bilden sich auf der ventralen Seite der Blätter, die sie mit einer apikalen Papille durchbohren. Die Durchsicht umfangreichen Herbarmaterials zeigt, daß der Pilz ziemlich häufig und im europäischen Wirtsareal weit verbreitet ist. Seine morphologischen Merkmale werden beschrieben und abgebildet. Die systematische Stellung und einige Besonderheiten werden diskutiert. Besondere Beachtung verdient die Tatsache, daß manche bryophile Parasiten ausgezeichnete Taxonomen sein können: Der *Pedinophyllum*-Pilz infiziert nicht die ähnlich aussehende *Plagiochila asplenioides*, während andererseits deren streng spezifisches *Epibryon plagiochilae* nicht auf *Pedinophyllum* wächst.

Introduction

The hepatic family Plagiochilaceae (Jungermanniales) contains only two genera in Europe: *Pedinophyllum* with the single European species *P. interruptum* (Nees) Kaal. and *Plagiochila* with eleven species (GROLLE 1983). Whereas the common *Plagiochila asplenioides* (L.) Dumort. s.l. is one of the most excellent hosts for hepaticolous fungi with ten species of ascomycetes known (DÖBBELER 1978, 1980; DÖBBELER & TRIEBEL 1985), no fungal parasite has yet been described for *Pedinophyllum interruptum* (RACOVITZA 1959, FELIX 1988). There is only one record in which *Pedinophyllum* was found as a host genus: DÖBBELER & TRIEBEL (1985) quote a Japanese collection of *P. truncatum* (Steph.) Inoue infected by the

discocarpous *Dactylospora heimerlii* (Zukal) Döbbeler & Triebel. This curious parasite is not specific to that host, but known from different hepatics belonging to various jungermannialian families. Screening for fungal infections on herbarium material of European *P. interruptum* frequently revealed an obligate ascomycete parasite that is described here as a new species.

***Epibryon pedinophylli* Döbbeler spec. nov.**

Holotypus: Germany, Bayern, Schwaben, Allgäu: Sauwald, bei Hinterstein, auf rotem Hornstein, 1006 m, 6.9.1882, Moosflora der Ostrachalpen 298, *Holler* (M).

Fig. 1, 2.

Ascomata 100–140 µm diametro, globosa, fusca ad nigra, subglabra vel hyphis brevibus plus minusve dense adhaerentibus; ascomata in parte ventrali evoluta (vel in parte interiore perianthiorum) et papilla folia hospitis perforantia; papilla dorsaliter vix protrudens. Ostiolum inconspicuum, plerumque cellulis elongatis et tenuitunicatis circumdatum. Excipulum superficie cellulis isodiametricis vel nonnihil irregularibus 3–6 µm diam. compositum. Parietes ascomatum in sectione 13–20 µm crassus, e seriebus nonnullis cellularum formatus; canalis ostioli periphysibus ornatus; tectum excipuli hyphis radiatim vestitum. Hyphae interascales deficientes. Asci 50–70 × 17–22 µm, late ellipsoideales usque ad subcylindrici, octospori, pauci. Sporae 21–28 × 6–8 µm, ellipsoideae, subfuscae, episporio laevi, plerumque 7 septis transversalibus et in nonnullis segmentis septo uno longitudinali divisae, cellulae terminales sporarum semper indivisae; interdum aliquae sporae solum transversaliter septatae. Hyphae inconspicuae, 1–2 µm latae, dilute coloratae, ramosae anastomosantesque, partim parietes anticlinales hospitis sequentes, partim irregulariter repentes; hyphae vel superficiales vel cuticula hospitis tectae vel intra parietes anticlinales crescentes. Neque appressoria neque haustoria praesentia. Cellulae conidiogenae non visae. Gelatina hymenii jodo (solutio Lugol) rubescens.

Habitat parasitice praecipue in foliis inferioribus veterioribusque hepaticae *Pedinophyllum interruptum*.

Ascomata (80–)100–140(–160) µm diam, globose, dark brown to black, nearly glabrous or with hyphal appendages; ascomata forming at the ventral leaf sides and perforating them with an irregular apical papilla, papilla ending at the dorsal leaf side or somewhat protruding; spores not discernible through the excipulum. Ostiolum inconspicuous, within the papillae, sometimes clearly surrounded by 2 µm thick, thin-walled, elongated cells. Excipulum seen from the outside with isodiametric or slightly and irregularly curved cells, cells (2)3–6(–8) µm; nearly always with some adjacent, short, hair-like hyphae, rarely excipulum tomentose (in which case it conceals the peridial cells) or even with bristle-like hyphae. In longitudinal sections lateral wall 13–20(–25 µm) thick, composed of 5 or 6 cell layers; outer part of excipulum wall obscure, inside colourless. Ostiolar canal lined with periphyses; in addition hyphae originating from the upper excipulum wall radiate into the centre. Interascal tissue absent. Asci 50–70(–75) × (15–)17–22(–25) µm, broadly ellipsoidal to nearly cylindrical, octosporous; only few mature asci per fruit-body. Spores (in lactic acid-cottonblue) (17–)21–28(–32) × (5.5–)6–8 µm, ellipsoidal, sometimes slightly curved, brown, episporium smooth; with (6–)7–8(–10) transverse septa and few perpendicular or oblique longitudinal septa, sometimes mature spores only transversely septate; young spores with cyanophilic cell walls; overmature spores slightly constricted at the septa. Vegetative hyphae on the host inconspicuous, 1–2(–2.5) µm wide, brownish, with delicate septa, branched and anastomosing, irregularly growing or following the anticlinal cell walls of the host, single or forming cords of two or more hyphae, near the ascocarps sometimes with few small hyphal plates; hyphae superficial, within the outermost host cell walls and growing from one side of the leaf to the

other through anticlinal cell walls; young hyphae with cyanophilic walls; appressoria, haustoria or conidiogenous cells absent. **Iodine reaction:** Hymenial jelly reddish with Lugol's solution, KOH pretreatment giving a blue colour. No reaction with Melzer's reagent.

Host: Known only on *Pedinophyllum interruptum* (Nees) Kaal.

Known distribution: Belgium, France, Germany, Switzerland, Austria, Italy, Poland, Hungary, Romania, Slovenia, Croatia, Greece.

Localization and biology

Epibryon pedinophylli undoubtedly grows parasitically. Fruit-bodies are found on green and healthy-looking leaves. No adverse effect on the host can be observed. However, for fruit-body formation the fungus clearly prefers older lower leaves, sometimes in early stages of decomposition. Algae and sterile hyphae belonging to unknown fungi are often present. Occasionally ascomata are formed on male shoots or on the inner side of perianthia, perforating them. Fruit-bodies can best be detected on the inner parts of a dense mat of the hepatic or its underside. The species is easily overlooked and confused with small, black and globular colonies of cyanobacteria. As with most of the bryophilous ascomycetes, it is impossible to detect the *Pedinophyllum* fungus under field conditions.

Ascomarps are usually scattered and sparse. A heavy infection may yield several fruit-bodies per leaf, but normally only one is formed. Sometimes individual shoots with five to ten fruit-bodies were observed amongst uninfected shoots suggesting a systemic infection.

Epibryon pedinophylli nearly always perforates the leaf blade with its apical papilla, so that the ostiolum is located on the dorsal leaf surface. Fruit-bodies are often found in the distal area of the leaves including the outermost parts. Primordia of ascomata conclusively demonstrate that perforation occurs **intercellularly**: Intercellular agglomerated hyphae press the adjacent cells apart. These collapse and make space for the apical papillae of mature fruit-bodies.

The *Pedinophyllum* fungus apparently tends to discharge its spores passively. Fruiting is mainly within the often dense mats of the host. This does not permit an effective spore discharge into the open air. Accordingly, overmature ascomata are not completely empty but still contain some ascospores. Different modes of spore discharge are an interesting aspect in the ecology of fungi on mosses and hepatics (DÖBBELER 1987, 1997).

Systematic position

Leaf perforation as demonstrated by *Epibryon pedinophylli* is a rather frequent strategy among hepaticolous pyrenomycetes. The 12 perforating species known presently represent about 15 percent of the more than 80 ascomycetes infecting foliose hepatics. In addition, there are four nectriaceous species which obligately colonize the developing sporophytes. Their perithecia perforate the perianthia so that the spores can be discharged into the open air (DÖBBELER, 1998). Leaf perforation *per se* is not an indication of generic relationship. Different perforation mechanisms occur, depending on the characters of the ascomata and hyphae.

The *Pedinophyllum* fungus is tentatively referred to *Epibryon*, extending once more the range of this artificial "genus". The alternative would have been to create a new genus. To define well-characterized genera for the various groups of the bryophilous ascomycetes is virtually impossible at present. Each new species could require essential modifications of the generic concept. The main differences between the generic type *E. plagiochilae* (Gonz. Frag.) Döbbeler and *E. pedinophylli* are shown in Table 1.

Table 1: Distinguishing characters between *E. plagiochilae* and *E. pedinophylli*

Characters	<i>E. plagiochilae</i>	<i>E. pedinophylli</i>
Ascomata	semiglobose; superficially at the dorsal leaf side	globose with an apical papilla; leaf-perforating
Primordia	on the anticlinal cell walls or the triangular cell junctions	within the anticlinal cell walls
Bristles	present, curved towards the leaf surface; ontogenetically formed very early	absent; adjacent hyphae present
Spores	2-celled, uncoloured, 10–14 × 3–4 µm	muriform, brown, 21–28 × 6–8 µm
Hyphae	superficial, rarely intracellular, not intercellular	within the outermost cell walls and intercellular
Host	<i>Plagiochila asplenoides</i> s.l.	<i>Pedinophyllum interruptum</i>

Epibryon pedinophylli belongs to a small group of non-nectriaceous, leaf-perforating, hepaticolous species with tiny, more or less glabrous fruit-bodies and a hemiamyloid reaction (BARAL 1987) of the hymenial jelly. These species belong to the genera *Epibryon*, *Hypobryon* and to the two monotypic *Philobryon* and *Punctillum*. *E. pedinophylli* appears most closely related to *E. perrumpens* Döbbeler which also perforates the leaves intercellularly (DÖBBELER 1982). A significant but not generic difference is the narrower and only longitudinally septate spore type of *E. perrumpens*. *E. hypophyllum* Döbbeler has very similar ascoma walls, and smaller and mostly triseptate spores. It is the only species that perforates the leaves intra-cellularly (DÖBBELER 1979). *Philobryon anuliferum* Döbbeler deviates with its bicellular spores and curious ringlike structures on the hyphae (DÖBBELER 1988). Rather thick and very regular hyphae within the host cell walls and bicellular hyphal conidia are typical of *Punctillum hepaticarum* (Cooke) Petr. & Syd. (DÖBBELER 1983). The combination of appressoria and haustoria clearly separate a well-defined group of six species referred to *Hypobryon* (DÖBBELER 1983; DÖBBELER & MENJÍVAR 1992). *E. pedinophylli* is the first leaf-perforating species with muriform ascospores.

The relations of the leaf-perforating species to those with superficial fruit-bodies formed on the dorsal surface of the substrate are generally not clear. Three bryophilous species with superficial fruit-bodies and muriform spores have been classified in *Epibryon* subgenus *Diaderma* Döbbeler (DÖBBELER 1979). Single spores of *E. diaphanum* Döbbeler and *E. pedinophylli* may be difficult to distinguish, but the ascomata are rather different.

Another problem concerns the systematic relations between *Epibryon pedinophylli* and several small biotrophic ascomycetes colonizing the leaf axils of different foliose hepatics including *Pedinophyllum* and *Plagiochila*. They are characterized by the same ascoma structure, ascus type, iodine reaction and muriform, coloured spores. The only important difference is that these fungi form their ascomata superficially. This group consists of *Pleospora hepaticola* Walt. Watson (WATSON 1914), *Pleosphaeria haploziae* Racov. (RACOVITZA 1959), *P. lophoziae* Racov. (RACOVITZA 1937, 1959) and *Teichospora jungermanniicola* (C.Massal.) Sacc. & P.Syd. (RACOVITZA 1959).

Frequency, geographical distribution

More than 120 herbarium collections of *Pedinophyllum interruptum* and several freshly collected mats were carefully investigated in order to determine the presence of the fungus. Thirty-six specimens were found to be infected. It is reasonable to assume that on an average *Epibryon pedinophylli* is present in one in every three to four collections deposited in a bryological herbarium.

Often only a very small portion of a host mat yields fruit-bodies, rendering their detection almost purely accidental. The random and patchy distribution of fruit-bodies was proved by studying freshly collected mats of *Pedinophyllum interruptum* in different parts of two valleys south of Munich (Isartal, Döbbeler 7052, and Kiental, Döbbeler 7016; see below). Only very few sporadically distributed fruit-bodies of *Epibryon pedinophylli* could be detected, though much material was screened (making it, unfortunately, inappropriate for type material). At the time of collection, fertile structures of the fungus were absent in most mats. The species is surely more frequent than the relation between infected and uninfected collections might suggest. It is likely that the fungus is virtually present in the whole European area of the host.

Pedinophyllum interruptum is of temperate-submediterranean distribution in Europe, reaching from the higher calcareous regions in the south to the northern border of the low mountain range in Central Europe. The hepatic is present in the British Isles and the Caucasus (see map in GROLLE 1969; MARSTALLER 1985). In North America it is an exceedingly rare species (SCHUSTER 1980). North American and British specimens were not available for investigation. From the Caucasian region 13 specimens, from which six were duplicates, were studied without result. This is, however, no proof of absence of *Epibryon pedinophylli* from that isolated host area, particularly since several mats were small.

Host specificity and associated fungi

Pedinophyllum interruptum (syn. *Plagiochila interrupta* Dumort.) is closely related to *Plagiochila asplenioides* s.l. (including the smaller *P. porelloides* (Torr.) Lindenb.). Both species are easily confused with each other (GROLLE 1969), especially if the plants are sterile (BISANG 1992, SCHUSTER 1980). But their most common parasites distinguish these similar hepatics very well: *Epibryon plagiochilae* is specific for and nearly always present on *Plagiochila asplenioides* s.l. An infection of *Pedinophyllum interruptum* by this species has never been observed. On the other hand, the *Pedinophyllum* fungus *E. pedinophylli* is restricted to *Pedinophyllum* and does not occur on *Plagiochila*, even in mixed populations of both bryophytes. These two parasites are excellent hepaticologists!

Many times black fruit-bodies were observed that occurred individually in the leaf axils of *Pedinophyllum* (and *Plagiochila*). In most cases the infections were so sparse and sporadic that only very few fruit-bodies in a mat could be detected. These fungi pertain to *Teichospora jungermannicola* and the related above-mentioned species which should be studied comparatively.

Interestingly, two relatively conspicuous but rather rare parasites on *Plagiochila asplenioides* s.l. have never been encountered on *Pedinophyllum interruptum*: *Dactylospora heimerlii* and *Octosporella jungermanniarum* (Crouan) Döbbeler, though the host spectrum of both fungi contains members of different jungermannialian families.

Endomycorrhiza-like fungal hyphae were repeatedly observed in rhizoids, in the peripheral ventral cells of the stem and even in leaf cells of *Pedinophyllum interruptum* and *Plagiochila asplenioides* s.l. SCHUSTER (1980) and BISANG (1992) used the presence or absence, respectively, as a key character to distinguish *Pedinophyllum interruptum* (with fungal infections) and *Plagiochila asplenioides* (without hyphae). Fungal infected cells were not recorded by POCOCK & DUCKETT (1985) in British material of both species.

Specimens examined (all deposited in the corresponding fungal collections):

Belgium. Namur: Rochers calcaires à Anseremme, 25.11.1888, *Zouglet* (B).

France. Dep. Meurthe et Moselle: Leverdun, 3.4.1927, *Gardet* (JE).

Germany. Niedersachsen. Hannover, Flora des Süntel, Amelungsberg, 28.5.1950, *Grützmann* (M). – Ith [Hils] bei Dielmissen, IV.1862 (M). – **Bayern.** Oberfranken: Quakenschloß bei Muggendorf, 2.6.1855 (M). – Kühfelsen im Veldensteiner Forst, 2–3 km westlich von Mosenberg, 440 m, 10.9.1990, *Mues* (M). – Schwaben: Memmingen, Felsenberg bei Großmannshofen, 700 m, 7.6.1890, *Holler* (M, 2 collections) – Ostrachalpen, am Eckbach bei Hinterstein, 876 m, 30.8.1887, *Holler* (M). – Oberpfalz: Regensburg, im Penker-Thale bei Etterzhausen, 400 m, 7.5.1902, *Familler* (GZU, Fl. exs. bav., Bryoph. 133, sub *Plagiochila interrupta*) – zwischen Maria Ort und Etterzhausen bei Regensburg, ca. 360 m, V.1905, *Familler* (M, Schiffner, Hep. eur. exs. 239). – Oberbayern: Zwischen Eichstätt und Landershofen, 1887 (M) – Isartal südlich München, bei Buchenhain zwischen Höllriegelskreuth und Baierbrunn, 570 m, 9.11.1997, *Döbbeler 7052* (M) – Waldweg von Baierbrunn nach Schäftlarn, 600 m, 12.10.1950, *Freiberg* (M) – Kiental zwischen Herrsching am Ammersee und Andechs, 600–700 m, 10.8.1997, *Döbbeler 7016* (M) – Arzbachtal nordöstlich der Benediktenwand u. südwestlich Tölz, 780 m, 28.9.1947, *Freiberg* (M) – Nordfuß der Glaswand bei Kochel, 1250 m, 7.7.1944, *Thyssen* (M) – Garmisch-Partenkirchen, Umgebung des Eibsees, ca. 900 m, 1.6.1979, *Düll & Lotto* (M) – Bernau am Chiemsee, Gerlachwand, 1200 m, 11.6.1916, *Paul & Ruoff* (M) – Inzell, Falkensee, 700 m, 7.7.1953, *Grützmann* (M) – Waging bei Traunstein, Bieberschwell bei Tengling, III.1873 (M).

Switzerland. Kanton Zürich: Thalwil, 17.6.1895, *Forster* (M).

Austria. Steiermark: Buchkogel bei Gösting, 350–450 m, VIII.1935 (GZU) – Poniglgraben bei Weiz, 550 m, 19.5.1962, *Maurer* (GZU).

Italy. Lombardia. Prov. Como: Oberhalb des Nino zwischen Como und Blevio, ca. 300 m, 22.10.1899, *Artaria* (W, Schiffner, Hep. eur. exs. 240). – Toscana. Prov. Massa e Carrara: Apuanischer Apennin, oberhalb des Dorfes Bergiola Maggiore, 300–350 m, 26.3.1965, *Düll* (JE).

Poland. Sudeti, iugum Góry Kaczawskie, supra vicum Podgórk, 500 m, 4.1.1956, *Szweykowski* (M, Hepaticotheca pol. 161) – Sudeti, iugum Góry Kaczawskie, prope vicum Myslibórz, 330 m, 10.9.1957, *Szweykowski* (M, Hepaticotheca pol. 162).

Hungary. Comit. Fejér: vallis Fáni-völgy prope pag. Verteskozma, 250–300 m, 10.4.1938, *Boros* (JE).

Romania. Jalomita beim Felsenkloster, 1500 m, 20.7.1897, *Loitlesberger* (W, Hep. alp. transylv. roman. 78, sub *Plagiochila interrupta*). – Dimbovitiora, 700 m, 2.8.1897, *Loitlesberger* (B, W; Hep. alp. transylv. roman. 101, sub *Plagiochila interrupta*).

Slovenia. Moschwald nahe Gottschee/Kocevje, 18.7.1910, *Glowacki* (GZU).

Croatia. Nordost-Istrien bei Rijeka, Adriaküste zwischen Medweja und Kraj, 20–30 m, 25.8.1977, *Düll* (W). – Dalmatien, Mosor Plan, über Kotlenice, ca. 850 m, 1.7.1911, *Baumgartner* (W).

Greece. Region Thessalia. Prov. Larisa: In monte Olympo Thessaliae, in fageto vallis Malta, 1450 m, 27.7.1927, *Handel-Mazzetti* (W).

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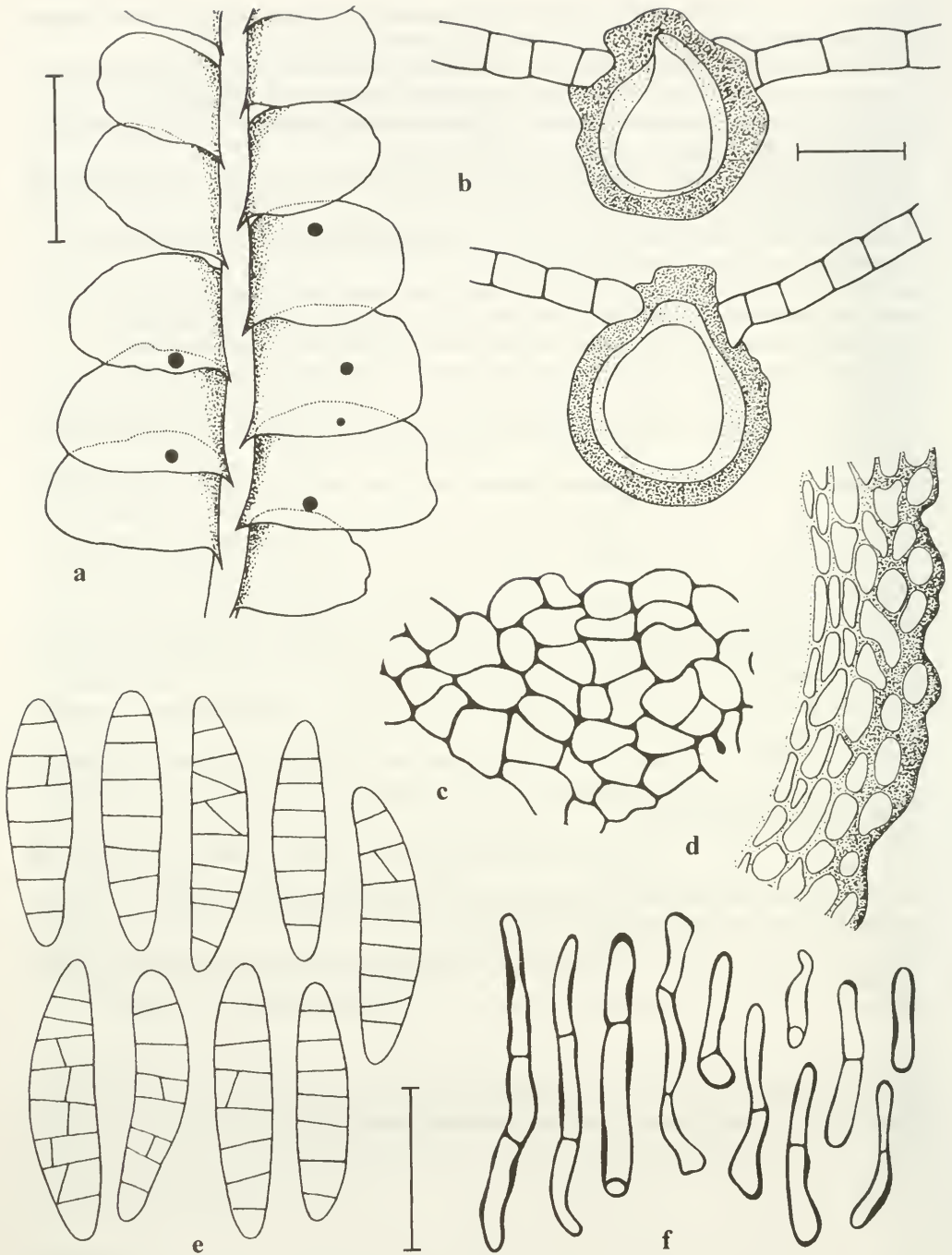


Fig. 1: *Epibryon pedinophylli*. a: Dorsal view of infected shoot of *Pedinophyllum interruptum* with six fruit-bodies; b: Leaf-perforating ascocarps in longitudinal section; c: Lower excipulum in surface view; d: Lateral excipulum in section; e: Spores; f: Hyphal appendages of the excipulum. Fig. a: Maria Ort, (M); Figs. b, c, d, f: holotype; Fig. e: lth bei Dielmussen (M). Scale bars: a: 1 µm; b: 50 µm; c–f: 15 µm.

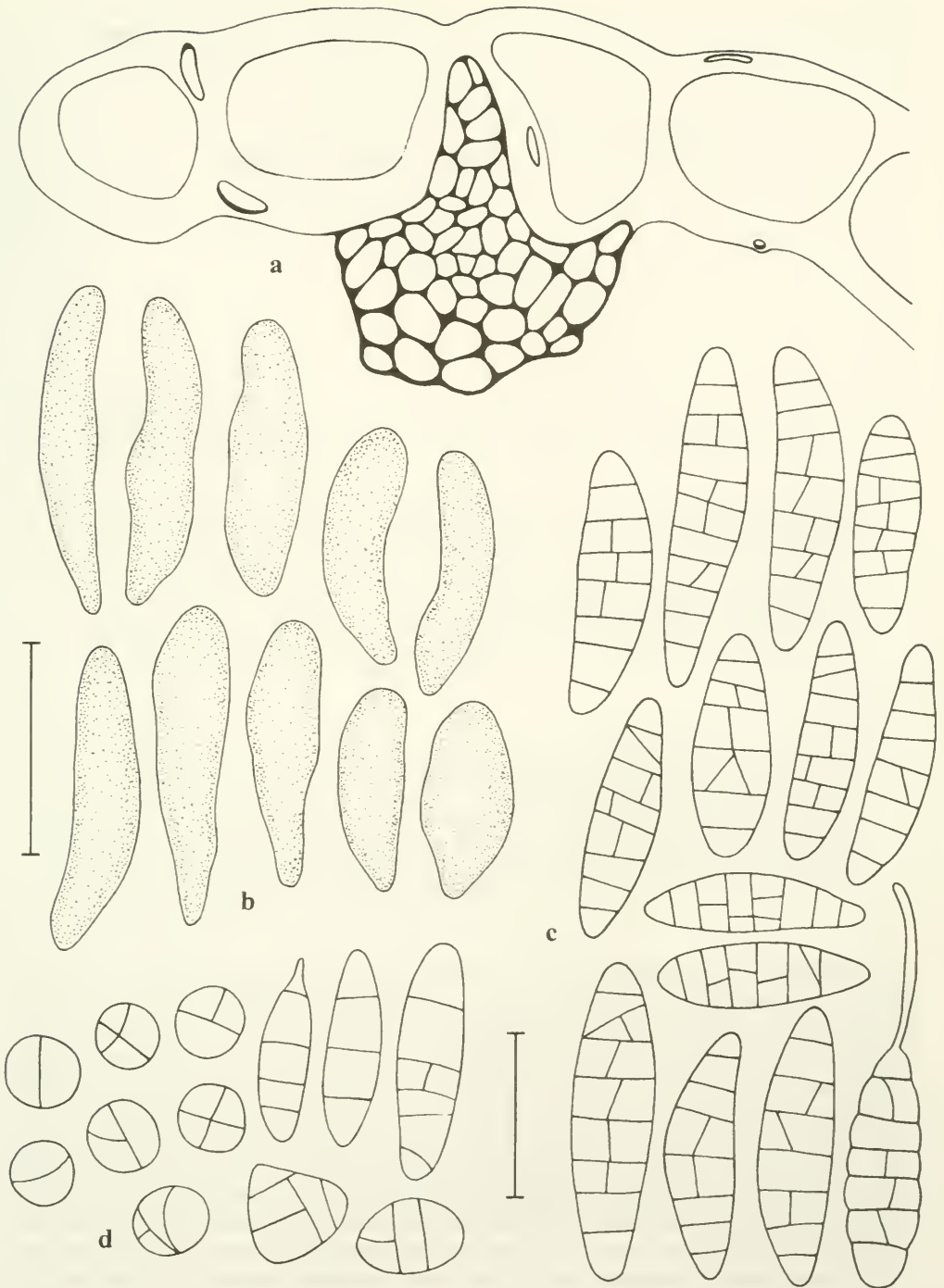


Fig. 2: *Epibryon pedinophylli*. a: Section of leaf-perforating ascocarp primordium; b: Asci; c: Spores, one germinating; d: Spores in optical transverse section, right atypical and deformed spores. Figs. a, c: holotype; Figs. b, d: Großmannshofen (M). Scale bars: a, c, d: 15 μ m; b: 50 μ m.

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