HERPOBASIDIUM AND ALLIED GENERA

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Morphology and taxonomy of the auricularioid fern parasites are discussed. The relationships of *Herpobasidium* and *Platycarpa* species are considered and two new genera, *Insolibasidium* and *Ptechetelium* are proposed. A new species, *Herpobasidium australe* sp.nov., is described and the following new combinations are proposed: *Insolibasidium deformans* (Gould) comb.nov. and *Ptechetelium cyatheae* (Syd.) comb.nov.

In 1881 Rostrup proposed the name *Gloeosporium filicinum* Rostr. for a fungal fern parasite. Lind (1908) showed, in a careful comparative study, that the fungus was basidiomycetous, and belonged neither with the fern rusts, *Uredinopsis* Magnus and *Hyalopsora* Magnus, nor with the auricularioid genera *Jola* Möller, *Eocronartium* Atk. and *Helicobasidium* Pat. He therefore introduced a new genus, *Herpobasidium*, to accommodate *G. filicinum*. Further, he also found that *Exobasidium brevieri* Boud. (Boudier, 1900) was not an *Exobasidium*, but was identical to *Herpobasidium filicinum*. The genus was enlarged to include a second species, *H. struthiopteridis* (Rostr.) Lind (1913). In 1939, Sydow described *H. cyatheae* Syd. from Ecuador and, with the addition of *Herpobasidium deformans* Gould (1945), the genus was extended to include angiosperm parasites. *Platycarpa*, another genus with species parasitic on ferns, was proposed by Couch (1949) for *Septobasidium polypodii* Couch

(1929) and a new species, *P. boliviensis* Couch was also described. Both taxa resemble species of *Septobasidium* Pat., but they are not associated with scale-insects.

To date, there has been no reassessment of the auricularioid fern parasites and related forms. We believe that a taxonomic re-evaluation is appropriate at this time.

MATERIALS AND METHODS

For transmission electron microscopy, living fungi were fixed with glutaraldehyde and osmium tetroxide, washed with distilled water, dehydrated in an alcohol series, and embedded in ERL according to the method of Spurr (1969). Ultrathin sections were mounted on unsupported mesh copper grids, poststained in uranyl acetate and lead citrate solutions, and examined with a Zeiss EM 9 S-2 transmission electron microscope.

KEY TO GENERA

1. Hyphae thin-walled; basidia without conspicuous basal swellings
   2. Fern parasites; haustoria coiled .... *Herpobasidium*
   2. Parasites of Caprifoliaceae and Cornaceae; haustoria lobed, branched, irregular, not coiled ... *Insolibasidium*
1. Hyphae thick-walled; basidia basally strongly swollen; parasites of ferns
   3. Parasitizing sporangial cells and overgrowing sori; probasidia formed singly, the wall relatively thin, percurrent proliferation absent. .... *Platycarpa*
   3. Parasitizing leaf cells, the hyphae emergent through stomata on lower leaf surfaces; fertile hyphae proliferating percurrently, the probasidium ensheathed by older wall layers .... *Ptechetelium*

HERPOBASIDIUM Lind, *Ark. Bot.* **7** (8): 5 (1908) emend. Oberw. & Bandoni

Parasitic on ferns; *hyphae*, growing inter- and intracellularly, the latter coiled, thin-walled, hyaline, clampless, with simple septal pores. *Generative hyphae* emerging through stomata and covering the underside of leaves to form white, irregular, corticioid patches. *Cystidia* lacking.

Basidia long cylindric or slightly clavate, straight to bent or evenly curved, one-, two- or four-celled. *Sterigmata* mostly cornute, tapered, sometimes with basal adventitious septa. *Basidiospores* thin-walled, smooth, hyaline, inamyloid, with oblique apiculi, mostly germinating by repetition.

Type species: *Herpobasidium filicinum* (Rostr.) Lind

KEY TO SPECIES

1. Spores 15–25 μm long
  2. Basidia almost straight, typically 2-celled .... *H. filicinum*
  2. Basidia at first coiled, becoming tortuous, 2- to 4-celled .... *H. struthiopteridis*
1. Spores 10–13 μm long .... *H. australe*

HERPOBASIDIUM FILICINUM (Rostr.) Lind, *Ark. Bot.* **7** (8): 7 (1908). (Figs 1, 12)

Gloeosporium filicinum Rostr. in Thuem., *Myc. Univ.* no. 2083 (1881).
Exobasidium brevieri Boudier, *Bull. Soc. Mycol. Fr.* **16**: 15 (1900).
Helicobasidium filicinum (Rostr.) Killerm. in Engl. & Prantl, *Nat. Pflanzenf.* **2**, 6: 106 (1928).

Developing in living leaves of ferns, the hyphae inter- and intracellular, with coiled haustoria. *Basidiocarps* commonly 1–3 mm broad, 100–500 μm thick, sometimes confluent, or spreading as a whitish layer on the lower surfaces of leaves; corresponding dark brown spots visible on upper leaf surface, the pigment largely residing in walls of parasitized epidermal cells and in the coiled haustoria. *Hyphae* 2–3 μm diam, thin-walled, clampless. *Basidia* narrowly clavate, tapering below, becoming 1-septate, $7–12 \times 40–120$ μm, typically bent near the base, the upper part almost straight. *Sterigmata* variable, stout, basally often walled off from the basidium by an adventitious septum, tapering to the apex. *Basidiospores* $6–9 \times 15–22$ μm, hyaline, inamyloid, obovoid to fusiform or subcylindric, sometimes slightly curved to allantoid or irregularly shaped, germinating by repetition.

Specimens examined: F. Petrak, *Mycotheca generalis* 1763. Matrix: *Aspidium filix-mas*. Germany, Branden-burg: Werneuchen, June 1917, H. Sydow (M); on *Phegopteris dryopteris*, Canada, Woods, Centreton, Ont., 5 June 1933, M. K. Nobles, det. H. S. Jackson; on *Dryopteris filix-mas* (L.) Schott, Finland, Aland, Lem-land, Nato, Sloskar, 10 July 1938, J. I. Liro & H. Roivainen; on *Dryopteris filix-mas* (L.) H. W. Schott, Germany, Bavaria: Tertiärabbruch am Inn, westlich von Marktl, westlich Braunau, 350–450 m, 22 June 1963, F. Oberwinkler FO 5137; on *Dryopteris filix-mas*. Austria,

Steiermark, Grazer Bergland: Mühlbachgraben nahe Stift Rein, Bezirk Graz Land, 500 m, 27 May 1972, leg. J. Poelt 11036; on *Dryopteris filix-mas*, Graz, May 1976, H. Teppner FO 23645.

Lind (1908) reported the occurrence of this species on *Athyrium filix-femina* (L.) Roth, *Cyst-opteris montana* (Lam.) Desv., *Dryopteris filix-mas* (L.) Schott, *Gymnocarpium dryopteris* (L.) Newm. and *Pteridium aquilinum* (L.) Kuhn. However, Reimers (1958) doubted that *Athyrium filix-femina* was correctly identified. The parasite appears to be widespread in Europe and in North America.

Two-celled basidia develop rather constantly in *Herpobasidium filicinum*. Jackson (1953), who studied the nuclear behaviour in detail, found binucleate mycelial cells, fusion of the two nuclei in the young basidium, followed by a single division. This is obviously the first meiotic division, and each of the resulting nuclei migrates into one basidiospore. Though a second meiotic division was not observed, it was assumed to occur in the first nuclear division at spore germination.

The septal pore ultrastructure of *H. filicinum* was studied by Sebald (1977). His report of rust-like simple pores has been confirmed by our studies. During ontogeny of the septum, the fine structure undergoes considerable variation (Fig. 12), but dolipore structures were not found.

The life cycle of this wide spread fern parasite is still not fully known. Parasitic mycelium develops in fern leaves and produces prominent haustoria. The hyphae grow through stomata (Fig. 1) and spread on the underside of the leaves to form whitish, thin, non-gelatinous but slightly waxy hyphal systems with scattered to densely arranged basidia. Basidiospores germinating by repetition can often be found. Further development and the infection of the host are not known. Jackson (1935) suggested that the fungus is systemic and perennial, presumably over-wintering in the rhizomes.

Fig. 1. *Herpobasidium filicinum*. Sectional view showing hyphae in *Dryopteris filix-mas*, the fertile hyphae emerging through a stoma and bearing basidia and basidiospores.

HERPOBASIDIUM STRUTHIOPTERIDIS (Rostr.) Lind, *Dan. Fungi*: 345 (1913). (Fig. 2)

Gloeosporium struthiopteridis Rostr., *Bot. Tids.* **17**: 236 (1889).

Uredinopsis struthiopteridis (Rostr.) Lind, *Ark. Bot.* **7** (8): 10 (1908), non Stoermer (1895).

Growing in living leaves of *Matteucia struthiopteridis* (L.) Tod., the hyphae inter- and intracellular, emergent through stomata and forming minute, granular, fertile pustules, these enlarging, flake-like and with abrupt margins, finally confluent and extensive, on both leaf surfaces, buff to tan. *Hyphae* 3–5(–8) μm diam, thin-walled, hyaline, without clamps, the branches mostly at right angles. *Basidia* basically narrow-clavate, but curved to tortuous, becoming 2- to 4-celled at maturity, 7–10 × (50)–80–150 μm, mostly with 1–2 prominent
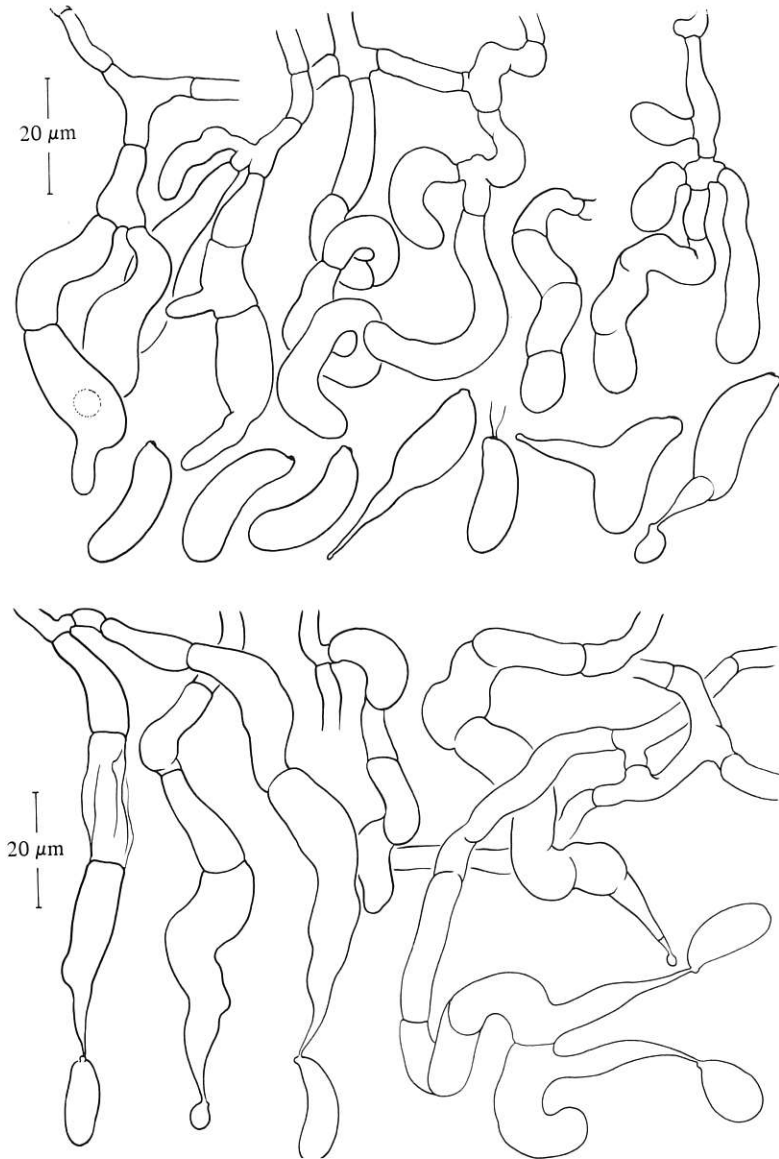
Fig. 2. *Herpobasidium struthiopteridis*. Hyphae and basidia from the underside of leaf of *Matteucia struthiopteridis*; basidiospores, some germinating by repetition.

sterigmata. *Basidiospores* 8–10 × 20–25 μm, hyaline, with thin, smooth walls, inamyloid; germination by repetition.

Specimens examined: Denmark, Copenhagen, 15 May 1890, F. Börgesen (DAOM); Copenhagen, 15 June 1891, F. Börgesen, Loc. class. (O) *Gloeosporium struthiopteridis*, Copenhagen, 19 May 1890, E. Rostrup (O).

The species is known to occur only on *Matteucia struthiopteridis* (L.) Tod. (= *Struthiopteris filicastrum* All., *S. germanica* Willd.). It has been reported from Denmark (Lind, 1913; Christiansen, 1959) and Norway.

Limited information is available on this species and we have examined only three herbarium specimens of it. It differs from *H. filicinum* in its
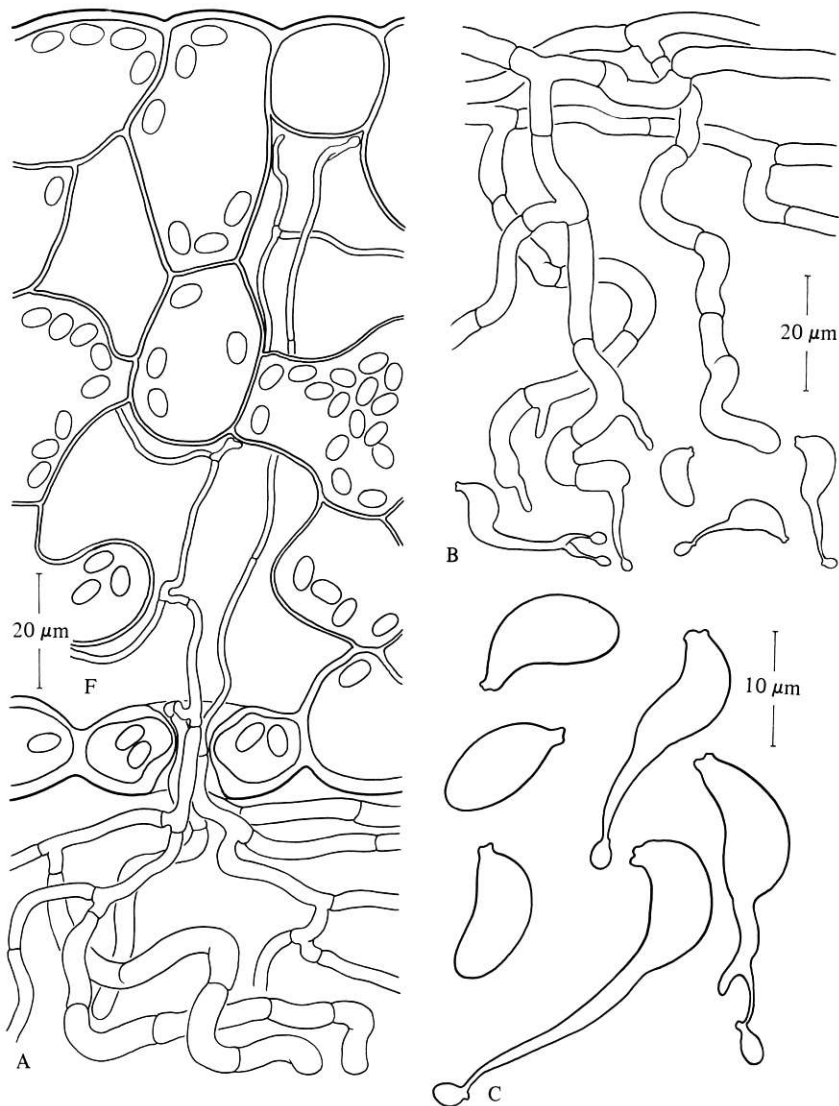
Fig. 3. *Herpobasidium australe*. (*a*) Section through leaf of *Adiantum silvaticum* showing host tissue, internal hyphal arrangement, hyphae emerging through a stoma, external hyphae and young basidia; (*b*) generative hyphae with basidia, the latter with sterigmata, basidiospores, several germinating by repetition (note one bifurcate germination-sterigma); (*c*) basidiospores, several germinating by repetition.

macroscopic featues and in the basidial structure and form. Young basidia are coiled but become distorted during development, and mature basidia are tortuous. Lind (1913) considered the characteristic deformations of the host as one of the important features of *H. struthiopteridis*. However, some deformation is at times apparent with *H. filicinum*.

Herpobasidium australe sp.nov. (Figs 3, 4, 5)

Mycelium parasiticum in frondibus vivis filicorum inter et intra cellulas hospitales crescit et per poros stomatorum prorepit. Hyphae hypophyllae maculas albas, extensas, confluentes formant; hyphae hyalinae, tenuiter tunicatae, effibulatae, in basidiis cylindraceis, curvatis vel sinuosis terminant. Basidia 6–8 × 60–80 µm, mature transverse septata, uno sterigmate vel plerumque sterigmatibus pluribus (2–4). Basidiosporae hyalinae, tenuitunicatae,
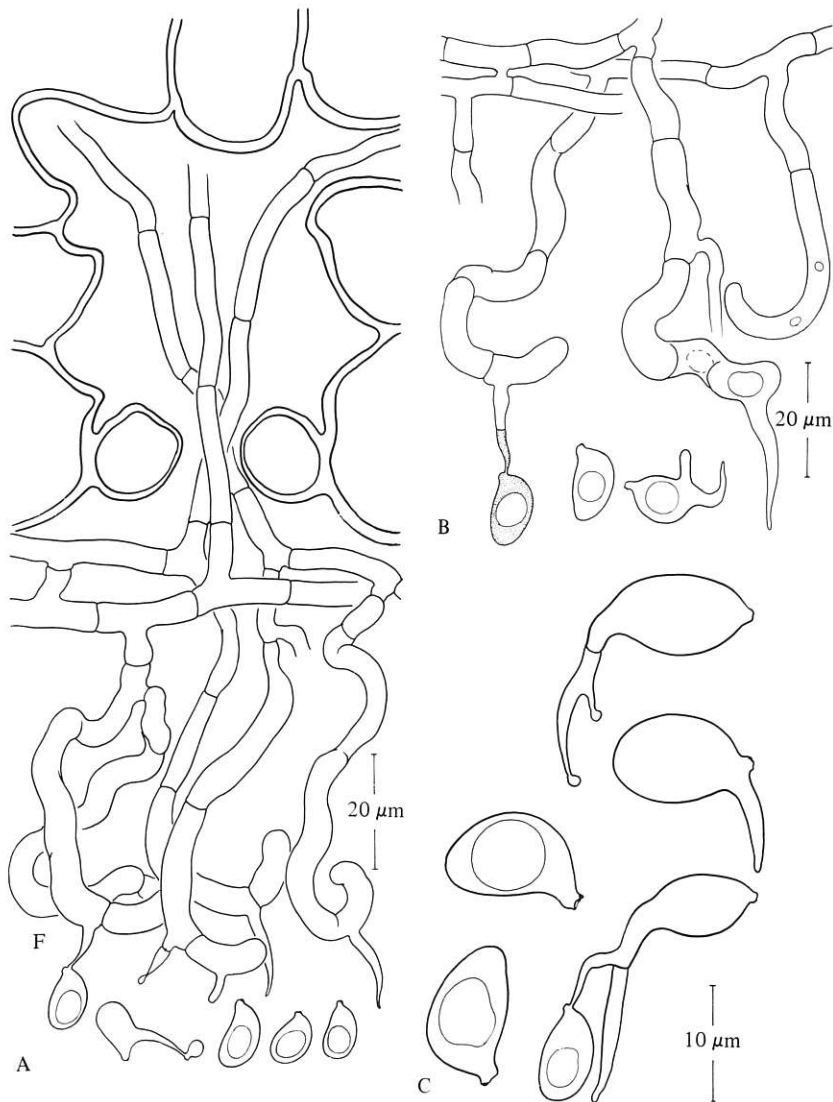
Fig. 4. *Herpobasidium australe*. (a) Stoma of the host, *Adiantum silvaticum*, with emergent hyphae, hyphal system, basidia and basidiospores; (b) generative hyphae with basidia, sterigmata, adventitious septum, basidiospores; (c) basidiospores showing different stages of germination by repetition.

tunicis levibus, non amyloideis, apiculis prominentibus, 6–8 × 10–13 μm, frequenter per repetitionem germinantes.

Herpobasidio filicino (Rostr.) Lind et *Herpobasidio struthiopteridis* (Rostr.) Lind affine, sed sporis minoribus diversum.

Habitatio: in foliis vivis *Adianti silvatici* Tindale et *Arthropteridis beckleri* (Hook.) Mett. Australia, New South Wales, Hastings Forest Reservation, prope fluvium, nomine Wilson River. Typus: FO 32274.

Parasitizing living leaves of *Adiantum silvaticum* Tindale (Adiantaceae) and *Arthropteris beckleri* (Hook.) Mett. (Oleandraceae), the hyphae inter- and intracellular. *Hyphae* 3–6 μm diam, septate, without clamps, branching at right angles, walls hyaline, smooth, thin to only slightly thickened, emergent through stomata and spreading along the underside of leaflets to form the thin, white, basidiocarp. *Basidiocarp* crust-like when dry, membranous and readily separable from the leaf

when wet. *Basidia* born on hyphae parallel to leaf surface, curved-cylindric, mostly somewhat tortuous or, alternately, strongly curved above the middle, becoming 1- to 3-septate. Mature basidia 6–8 × 60–80 μm, with cornute sterigmata, the latter often adventitiously septate. *Basidiospores* 6–8 × 10–13 μm, ovoid with a large apiculus, hyaline, the walls thin, smooth, inamyloid, the content typically including large guttules; germination by repetition, the sterigmata often bifurcate.

Specimens examined: Australia, New South Wales, Hastings Forest Reservation north of Wauchope, Wilson River Reserve, 250 m, on *Adiantum silvaticum* Tindale, 18 Aug. 1981, R. J. Bandoni, FO 32274 (Type in K; Isotypes in M, NY, TUB, UBC, UNSW); on *Arthropteris beckleri* (Hook.) Mett., 17 Aug. 1981, F. Oberwinkler, FO 32222 (M, TUB, UNSW); on the same host, 18 Aug. 1981, F. Oberwinkler, FO 32248 (M, TUB, UNSW).

The species clearly differs from *H. filicinum* and *H. struthiopteridis* in its basidiospore size; the basidial form also differs in being quite regularly hooked above the middle. *Herpobasidium australe* was collected on two different hosts; the outer appearance being similar on both ferns. The parasite causes no visible deformation of the host, but forms conspicuous, widely spreading, confluent patches on the undersides of leaflets. All collections were made during a dry period in late winter and, although the host leaves were alive, it is possible that the appearance might differ somewhat in wet weather. Although many *Adiantum silvaticum* and *Arthropteris beckleri* plants were infected in the type locality, other fern species in the area were not. These included taxa classified in the following families: Aspidiaceae, Athyriaceae, Blechnaceae, Cyatheaceae, Davalliaceae, Gleicheniaceae and Polypodiaceae.

Basidial morphology of *H. australe* resembles that of *Insolibasidium deformans* to a certain extent. However, conidia have never been reported for *Herpobasidium* species parasitizing ferns; they are lacking in our collections of *H. australe*. *I. deformans* also differs in lacking the exposed, pelliculose basidiocarp structure, and in the nature of its intracellular hyphae.

PLATYCARPA Couch, *Mycologia* **41**: 427 (1949) emend. Oberw. & Bandoni

Parasites of ferns; *hyphae* inter- and intracellular, thin- to thick-walled, hyaline, efibulate. Intracellular hyphae mostly coiled, parasitizing sporangia; generative hyphae covering the sori in whitish to cream-coloured or ochraceous patches. *Cystidia* lacking; slightly to strongly thick-walled hyphidia present, originating from generative hyphae, and intermixed with basidia, but not protruding beyond the hymenial surface. *Young basidia* basally swollen, thin-walled to slightly thick-walled, hyaline, elongating apically to form cylindric, curved, rarely straight basidia; transversely septate at maturity. *Sterigmata* short, cornute, apically tapered. *Basidiospores* thin-walled, smooth, hyaline, inamyloid, with oblique apiculi, mostly germinating by repetition.

Type species: *Platycarpa polypodii* (Couch) Couch

PLATYCARPA POLYPODII (Couch) Couch, *Mycologia* **47**: 428 (1949). (Fig. 6)

Septobasidium polypodii Couch, *J. E. Mitch. Sci. Soc.* **44**: 255 (1929).

Developing parasitically in sporangia of ferns, the hyphae inter- and intracellular. *Basidiocarps* on the underside of sporophylls, covering the sori and forming small, whitish to cream-coloured patches, 200–300 μm thick, rarely 500 μm. *Hyphae* thick-walled, strongly interwoven but not gelatinized, 3·5–6 μm diam, many terminating in the hymenium and tapering slightly to form more or less unbranched hyphidia interspersed with basidia. *Probasidia* subglobose, 12–18 × 15–30 μm, thin- to inconspicuously thick-walled, hyaline, producing apical, cylindrical, mostly curved and transversely septate basidia, 8–13 × 40–70 μm. *Sterigmata* 8–20 μm long, slightly tapering towards the apiculus. *Basidiospores* 6·5–8·5 × 19–25 μm, becoming 1-septate (fide Couch 1949); germination sterigmata often bifurcate.

Specimen examined: Jamaica, Blue Mountains, on *Polypodium* sp., June 1926, W. R. Maxon (NCU).

Apparently this species is known only from the type collection.

Couch (1929) first placed it in *Septobasidium*, apparently on the basis of the hyphal system and probasidial morphology. Boedijn & Steinmann (1931) and later Couch (1938) restricted *Septobasidium* to species associated with scale insects. A new genus, *Platycarpa*, was subsequently proposed by Couch (1949) to accommodate *S. polypodii* and a second species, *Platycarpa boliviensis* Couch. The latter is the same as *Herpobasidium cyatheae* Syd., a species that is not closely related to *P. polypodii*. A new genus, *Ptechetelium*, is proposed for *H. cyatheae*, as follows.

Ptechetelium gen.nov.

(Etym: πτυχή layer; τέλος end, 'teliospore')

Mycelium parasiticum in frondibus vivis filicorum inter et intra cellulas hospitales crescit et per poros stomatorum prorepit. Hyphae hypophyllae maculas sordide albas, ochraceas vel brunneas, plerumque minutissimas tenuis-
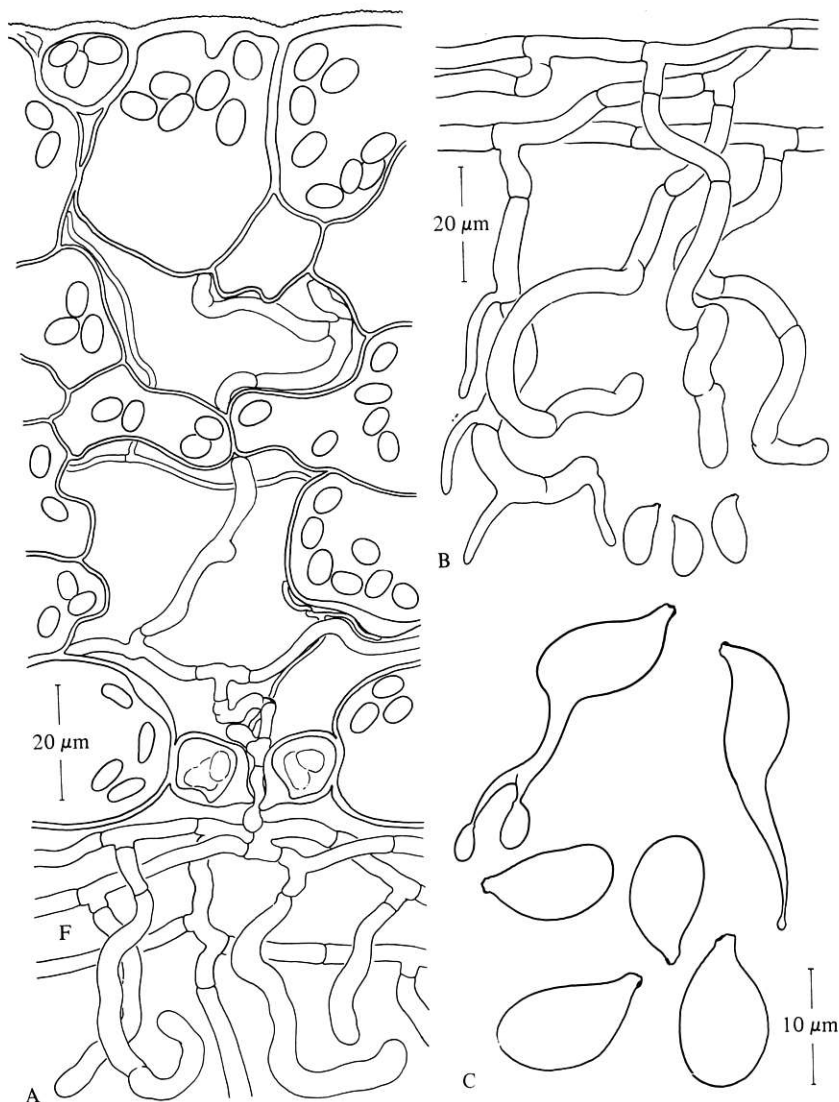
Fig. 5. *Herpobasidium australe*. (*a*) Section through a leaf of *Arthropteris beckleri* showing host tissue, internal hyphal arrangement, emergent hyphae, and young basidia outside leaf; (*b*) generative hyphae with basidia and sterigmata, basidiospores; (*c*) basidiospores, two germinating by repetition.

simasque formant; hyphae hyalinae, effibulatae, primo tenuiter, paulo post crasse tunicatae et laxe intertextae. Probasidia subglobosa vel pyriformia ad basim plerumque stipitiformiter contracta, basidiis cylindraceis per repetitionem linearem germinant; tum demum probasidia membranis pluribus constructa. Basidia mature divisa sunt in cellulas quattuor, sterigmatibus brevibus curva- tisque. Basidiosporae hyalinae, tenuitunicatae, tunicis levibus, non amyloideis, apiculis obliquis, plus minusve irregulariter falcatae, per repetitionem germinantes.

Habitatio: in foliis vivis filicorum.

Typus generis: *Herpobasidium cyatheae* Sydow

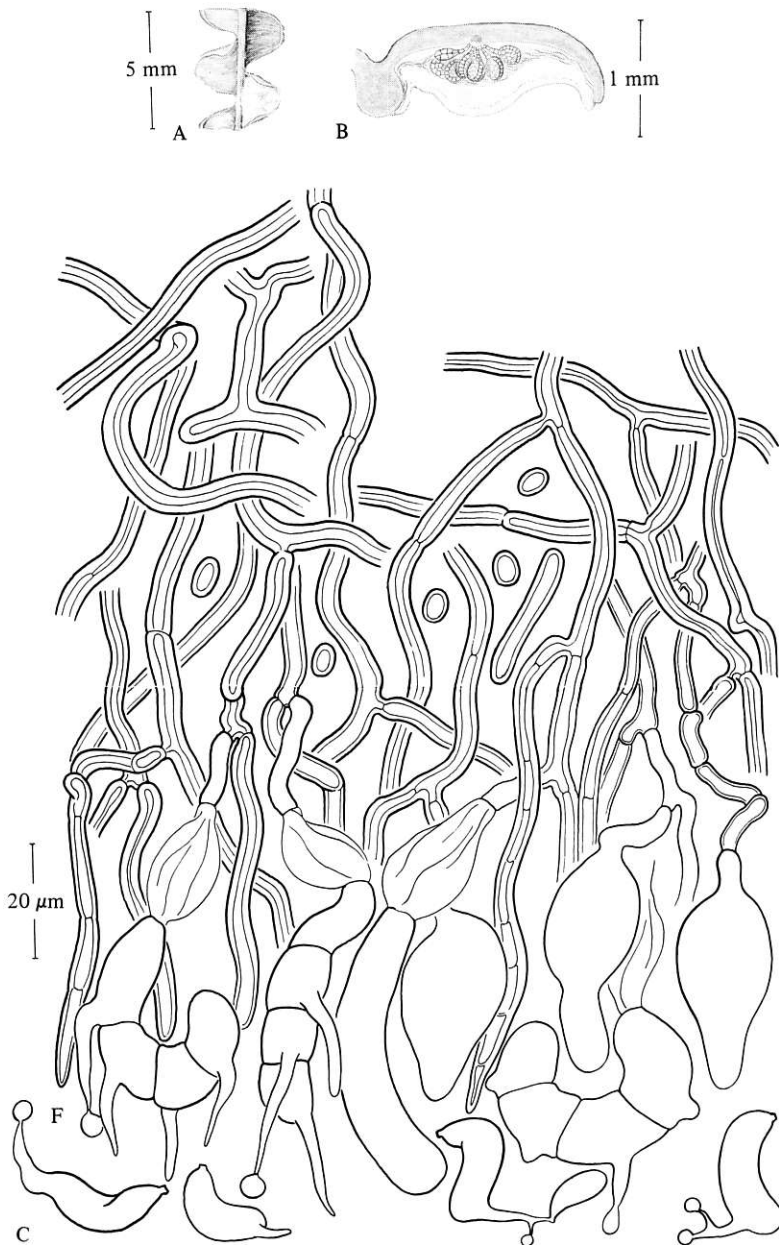Only one species is known in the genus.

Fig. 6. *Platycarpa polypodii*. (*a*) Habit sketch of *Polypodium* sp. with whitish patches of the parasite on the underside; (*b*) section of leaf with sporangial sorus, and fructification of *Platycarpa*; (*c*) section through basidiocarp showing thick-walled hyphae, probasidia, basidia in different developmental stages, and basidiospores germinating by repetition.
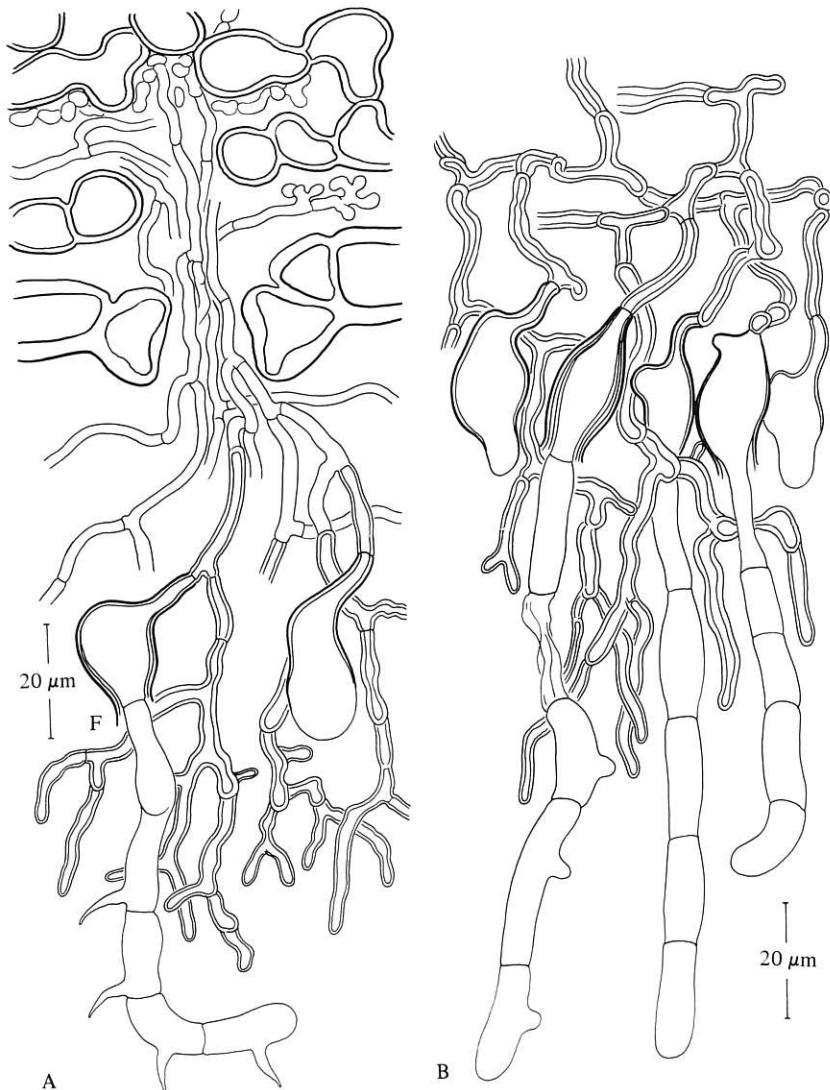
Fig. 7. *Ptechetelium cyatheae.* (*a*) Hyphae of parasite growing in host leaf (*Cyathea stuebelii*) and emerging through a stoma with dendrohyphidia, generative hyphae, probasidia and basidia; (*b*) dendrohyphidia, probasidia and basidia in different stages of development.

Ptechetelium cyatheae (Syd.) comb.nov. (Figs 7, 8)

Herpobasidium cyatheae Sydow, *Annls Mycol.* **37**: 285 (1939).

Platycarpa boliviensis Couch, *Mycologia* **41**: 429 (1949).

Developing in living leaves of ferns; *hyphae* thin-walled, inter- and intracellular; emerging through stomata and forming small, rarely confluent patches of basidiocarps, 1–2 mm diam, on the underside of green sporophylls, 100–200 μm thick, whitish to cream-ochraceous or yellowish to brownish, horny when dry, soaking cartilaginous-gelatinous. Hyphae in the leaf and those arising from them mostly thin-walled, hyaline, 2–3 μm diam; those of the subhymenium and hymenium thick-walled, 2·5–4–5 μm diam, hyaline, whitish to cream-coloured; terminating in probasidia and
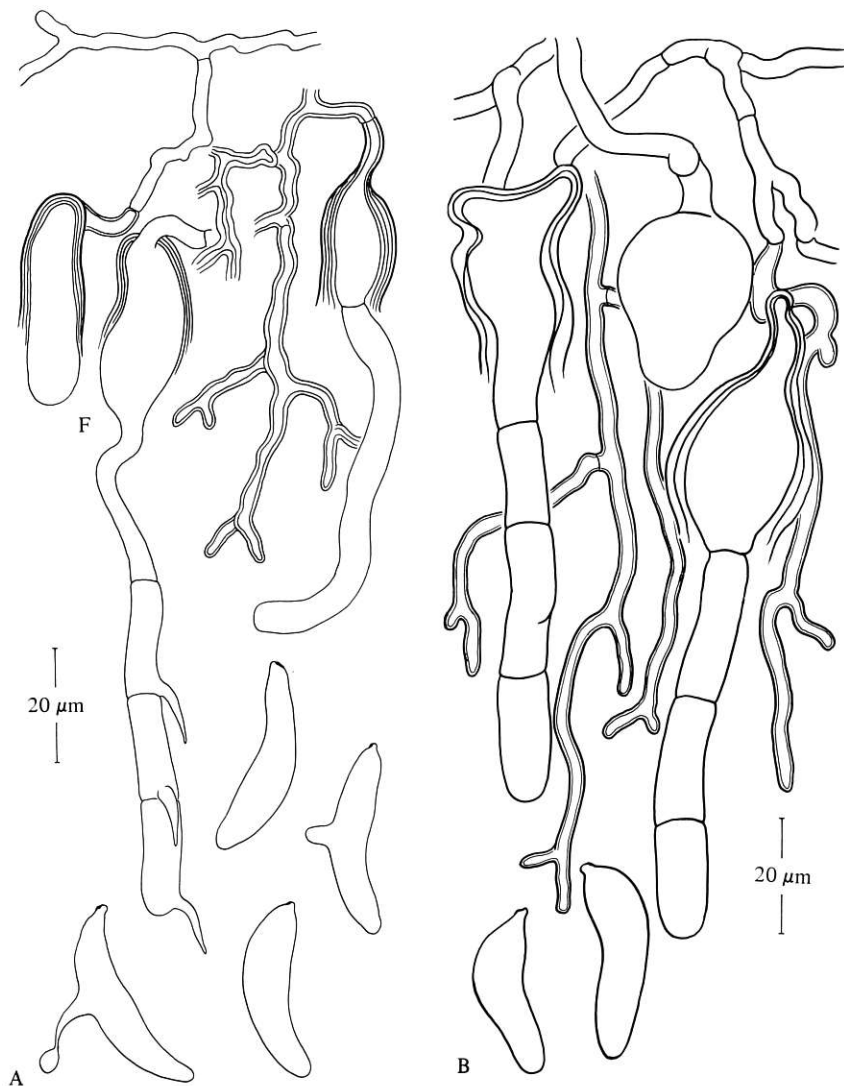
Fig. 8. *Ptechetelium cyatheae*. (*a*) Dendrohyphidium, probasidium, young basidium and basidium with sterigmata; basidiospores, one germinating by repetition; (*b*) type of *Platycarpa boliviensis*; dendrohyphidia, generative hyphae, probasidia, basidia and basidiospores.

conspicuous thick-walled, branched, light-coloured dendro-hyphidia with blunt terminations. *Probasidia* commonly stalked, globose to elongate-pyriform, $15–20 \times 20–30$ μm, thick-walled, proliferating percurrently and the wall obviously multi-layered after development of successive probasidia. *Basidia* cylindrical, straight to slightly curved, $6–8 \times 90–120$ μm, 4-celled when mature, the sterigmata cornute. *Basidiospores* hyaline, thin-walled, smooth, irregularly sickle-shaped, $6\cdot5–9 \times 30–40$ μm, with oblique apiculi; germinating by repetition.

Specimen examined: Ecuador, Puyo, Napo-Pastaza prov., on *Cyathea stuebelii* leaves, 13 Feb. 1938, H. Sydow (M).

Ptechetelium cyatheae differs from *Platycarpa polypodii* in several important characteristics: (1) The parasite develops in the leaf tissue of fern sporophylls, thus corresponding with *Herpobasi-*
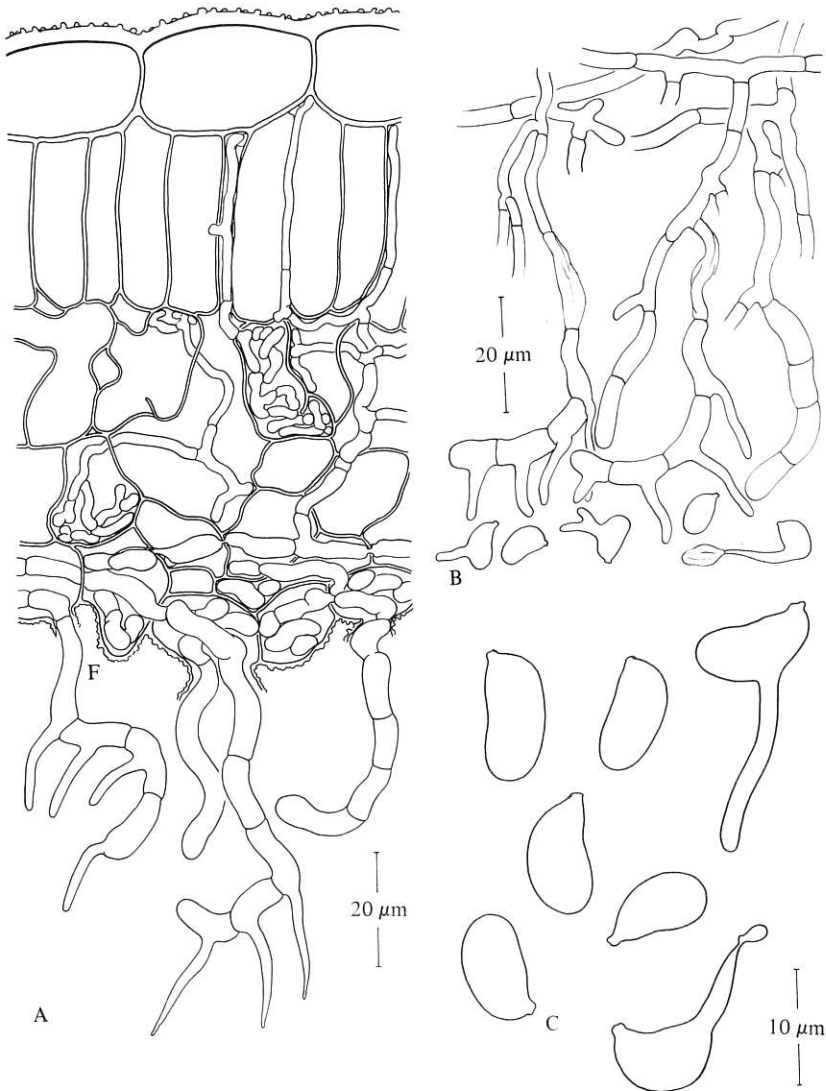
Fig. 9. *Insolibasidium deformans*. (*a*) Section through a leaf of *Lonicera tatarica* showing host tissue, internal hyphal arrangement, and basidia breaking through the lower epidermis of the leaf; (*b*) generative hyphae, basidia and basidiospores, several germinating; (*c*) basidiospores, one germinating by repetition.

dium species but deviating from *Platycarpa* which is parasitic in fern sporangia. (2) Probasidia proliferating percurrently, forming successive basidia; a multi-layered probasidial wall is thus formed. Such basidial development is unique in the Auriculariales *sensu lato*. (3) The basidiospores are slightly sickle-shaped, a form differing from that in related species, though not too strongly digressing. (4) The intercellular hyphae in mesophyll cells are

irregular masses according to Couch (1949); those of *Platycarpa polypodii* are strongly coiled and similar to haustoria of *Herpobasidium* and *Septobasidium*.

These differences clearly separate *Platycarpa* and *Ptechetelium*. Additional distinctions discussed by Couch (1949) occur in the basidiocarps, which are arid and stratose in *P. polypodii* vs. cartilaginous in *Ptechetelium cyatheae*.

Insolibasidium gen.nov.

(Etym. Insolitus, insolens – unusual, uncommon; basidium for basidiomycete; referring to the uncommon characteristics of being an auricularioid parasite on angiosperms and associated with anamorph stages)

Mcyelium parasiticum in foliis vivis Dicotyledoneis. Hyphae hyalinae, tenuitunicatae, effibulatae, inter et intra cellulas hospitales crescunt et per poros stomatorum prorepunt; hyphae hypophyllae maculas albas, tum brunneas, minutas, raro confluentes producunt. Cystidia probasidiaque conspicua desunt. Basidia cylindracea, erecta vix curvata, mature divisa sunt in cellulas quattuor. Sterigmata plus minusve cylindracea. Basidiosporae hyalinae, tenuitunicatae, tunicis levibus, non amyloideis, apiculis obliquis, breviter cylindraceis, per repetitionem germinantes. Frequenter status anamorphosium conidiis globosis, asperulis, hyalinisque praesens est.

Habitatio: in foliis vivis Caprifoliacearum Cornacearumque.

Typus generis: *Herpobasidium deformans* Gould

Only one species is known in this genus.

Insolibasidium deformans (Gould) comb.nov.
(Figs 9, 10, 11)

Herpobasidium deformans Gould, *Iowa St.Coll. J. Sci.* **19**: 317 (1945).

Developing in living leaves of *Lonicera*, possibly also *Symphoricarpus*, and *Cornus*, the hyphae inter-and intracellular, necrotrophic. *Hyphae* 2–4 μm diam, thin-walled, hyaline, clampless, those within cells irregularly lobed or branched; inter-cellular hyphae abundant, forming compact masses in substomatal chambers; fertile hyphae giving rise to single terminal basidia which protrude through stomata, then proliferating to produce a cluster of basidia; older parts of infected areas with scattered, closely adherent hyphae on leaf surface, affected areas having a thin, chalky, whitish bloom consisting mainly of protruding basidia or conidia. *Basidia* 4–6 × 20–40 μm, more or less cylindric, but curved to tortuous, 4-celled at maturity. *Sterigmata* 2–4 × 10–15 μm, hypha-like to cornute. A thin-walled, uninflated probasidial cell is present; it is empty and collapses when the basidium is fully extended. *Basidiospores* 5–7·5 × 9–13 μm, short cylindric and slightly curved or ovate-cylindric, hyaline, thin-walled smooth, inamyloid, apiculus oblique; germinating by germ-tube or by repetition, often with a bifurcate tube. *Conidial stage* (*Glomopsis*) developing after, or instead of, the basidia, the *conidiophores* 30–60 × 5–9 μm, emergent through stomata, dichotomously branched or unbranched below, septate, the walls hyaline, thin, typically giving rise

to *conidiogenous cells* apically, each conidiogenous cell producing two globose conidia, 8–17 μm diam, hyaline, thin-walled, the wall verrucose, the verruculae branched and apically 2- to 5-lobed. In addition to the terminal ones, *conidia* later develop bilaterally from the subterminal cells; these conidia are elongated, bent, bilobed, smooth at first but becoming verruculose, the verruculae more prominent than on the globose terminal conidia. At maturity of the conidia, the conidiophore collapses. Conidial ontogeny is difficult to follow in this species. Conidia are at first smooth, the inner ones first becoming warty. All conidia appear to remain attached to the conidiogenous cells and it is possible that a cluster functions as the dispersal unit.

Specimens examined: On *Lonicera tatarica*, 14 June 1956, D. J. Wit, det. J. A. von Arx, *Glomerularia* stage only, on *Lonicera involucrata*, Canada, Deception Falls, Mahood Lake, B.C., 8 July 1978, R. Bandoni 6296; On *Lonicera tatarica* L., U.S.A., Iowa City, Iowa, 23 June, 1939, leg. et fide G. W. Martin (UBC); On *Lonicera* sp., Iowa City, Iowa, 7 Nov. 1974, leg. et fide R. Bandoni 6171 (UBC).

Insolibasidium deformans is a distinctive species, parasitizing certain species of Caprifoliaceae and producing an unusual conidial phase in addition to *Herpobasidium*-like basidia. Unlike *Herpobasidium* species, *I. deformans* does not form a membrane-like, separable subiculum, nor are the haustoria coiled. Leaves at first have no superficial hyphae, only the basidia or conidiophores protruding. Even after extensive development has occurred, superficial hyphae are limited. The basidia develop mainly on the lower surfaces of infected leaves, but occasional leaves are found with basidia on the upper surface. Infection by the fungus causes necrosis and early abscission of leaves. In addition, *I. deformans* has consistently 4-celled basidia and the unusual conidial structures developing together with, or separate from the basidial stage.

Gould (1945) found that 18 species of *Lonicera* could be articifially infected with *I. deformans*. He also obtained slight infection of *Symphoricarpus albus* (L.) Blake, although there are no records of natural occurrence on this host. *Glomopsis corni* (Peck) Henderson, on *Cornus canadensis* L., has conidiomata similar to those of *I. deformans*, but has no known basidial stage. According to Gould (1945), *I. deformans* grows readily, but slowly in culture. Because of this, and the fact that it is a necrotrophic parasite, it is possible that *Glomopsis corni* is not specifically distinct from *G. lonicerae*. Collections on *Lonicera* include both entirely basidial, e.g. RJB 6171, infections and entirely conidial infections, e.g. RJB 6296.

DISCUSSION

Parasitism

The main groups of parasitic basidiomycetes are found in the Heterobasidiomycetes. Basidiomycetous fern parasites are restricted to the rust genera *Uredinopsis*, *Milesina* Magnus, *Hyalopsora* and *Desmella* Sydow, and the auricularioid genera *Herpobasidium* and *Platycarpa*. In *Uredinopsis*, probasidia develop in subepidermal host cells, and in *Milesina* and *Hyalopsora*, probasidia are formed in epidermal cells. Only *Desmella* species produce superstomatal teliospores. Many fern rusts are heteroecious, alternating between ferns and the coniferous genus *Abies*, and life cycles with pycnia, aecia, uredinia and telia are characteristic. However, autoecious species are known, e.g. in *Desmella*. None of these rusts closely resembles auriculariaceous fern parasites morphologically. Other rusts which lack teliospores, such as species of *Achrotelium* Sydow, *Chrysella* Sydow, *Chrysocyclus* Sydow, *Chrysomyxa* Unger, *Coleosporium* Lév., *Goplana* Racib. and *Ochropsora* Dietel are distinct in other features.

Basidiomycetous parasites of Caprifoliaceae and Cornaceae are predominantly species of the rust genus *Puccinia* Pers. Certainly, there is no connexion with the auricularioid *Insolibasidium deformans*. Also *Coleosporium viburni* Arth., parasitic on *Viburnum* (Caprifoliaceae), cannot be considered as a closely related species.

Gould (1945) carried out an extensive experimental study to establish the host range of *Insolibasidium deformans*. He induced artificial infection of 18 species of *Lonicera* as well as limited infection of *Symphoricarpus albus* (L.) S. F. Blake. However, 'Lonicera japonica halliana (DC.) Nichols' and *Symphoricarpus orbiculatus* Moench and a *Viburnum* sp., were not infected. Further, *Cornus stolonifera* Mich. (Cornaceae) was resistant.

The host–parasite interaction in species of *Herpobasidium* and *Platycarpa* is similar in that the haustoria are elongate, coiled, intracellular hyphae (Fig. 13). Such haustoria are common in species of the Septobasidiales (Couch, 1938). *Ptechetelium cyatheae* and *Insolibasidium deformans* intracellular hyphae are less morphologically distinctive.

Hyphae, septa and septal pores

All species examined during this study have rather simple and non-gelatinous hyphal systems. The hyphae are constantly clampless, thin-walled in species of *Herpobasidium* and *Insolibasidium*, but thick-walled hyphae occur in *Platycarpa polypodii* and *Ptechetelium cyatheae*. Such characteristics are representative for Uredinales and Septobasidiales,

and many auriculariod fungi. The ultrastructure of the septal pore apparatus has been studied only in *Herpobasidium filicinum*. Sebald (1977) found rust-like simple pores in this species, an observation we have confirmed (Fig. 12). Similar septal pores in auriculariod taxa have been reported for *Eocronartium muscicola* (Sebald, 1977; Khan & Kimbrough, 1980) and for the gasteroid auriculariod taxa of *Agaricostilbum* J. E. Wright, *Atractiella* Sacc., *Chionosphaera* Cox, *Phleogena* Link, and *Stilbum* Tode (Oberwinkler & Bandoni, 1982). However, dolipores with continuous parenthesomes have been reported for species of the *Auricularia–Hirneola* group (Sebald, 1977; Moore, 1978; Tu & Kimbrough, 1978; McLaughlin, 1980). Patton & Marchant (1978) reported perforated parenthesomes for *Auricularia mesenterica* (Dicks.) Pers. and *Auricularia polytricha* (Mont.) Sacc. However, McLaughlin (pers. comm.) found continuous parenthesomes in these two *Auricularia* species. It supports the close relationship of *Auricularia* and *Hirneola*. It appears that the auriculariod fern parasites and *Insolibasidium deformans* are thus linked to the Uredinales–Septobasidiales groups and auriculariod fungi such as *Eocronartium*.

Basidia and basidiospores

The typical basidium in species of *Herpobasidium*, *Platycarpa*, *Ptechetelium* and *Insolibasidium* is elongate, cylindric and transversely septate at maturity. Conspicuously swollen probasidia are found only in *Platycarpa polypodii* and *Ptechetelium cyatheae*. In the latter, percurrent proliferation occurs (Figs 7, 8) inside the old probasidia. Consequently, multi-layered probasidial walls are formed as in *Septobasidium alni* Torrend (Couch, 1938) and *Oliveonia fibrillosa* (Burt) Donk in the Heterobasidiomycetes. In Homobasidiomycetes, repetitive basidia can be found occasionally in species of *Galzinia* Bourd., *Hyphoderma* Fr., *Poria sensu lato* and *Hymenochaete* Lév., and commonly in *Repetobasidium* Eriks. & Hjorts. (Eriksson, 1958; Oberwinkler, 1965; Eriksson et al., 1981) and *Repetobasidiellum* Eriks. & Hjorts. (Eriksson et al., 1981).

Jackson (1935) found only the first meiotic division after fusion of two nuclei in the young basidium of *Herpobasidium filicinum*. He supposed that the second meiotic division occurred during basidiospore germination. The karyology of *Insolibasidium deformans* was studied by Gould (1945), who found a nuclear cycle similar to that of many other basidiomycetes, i.e. fusion of two nuclei, and first and second meiotic division in the basidium. The basidium (meiosporangium) becomes 4-celled and, after formation of sterigmata, each nucleus
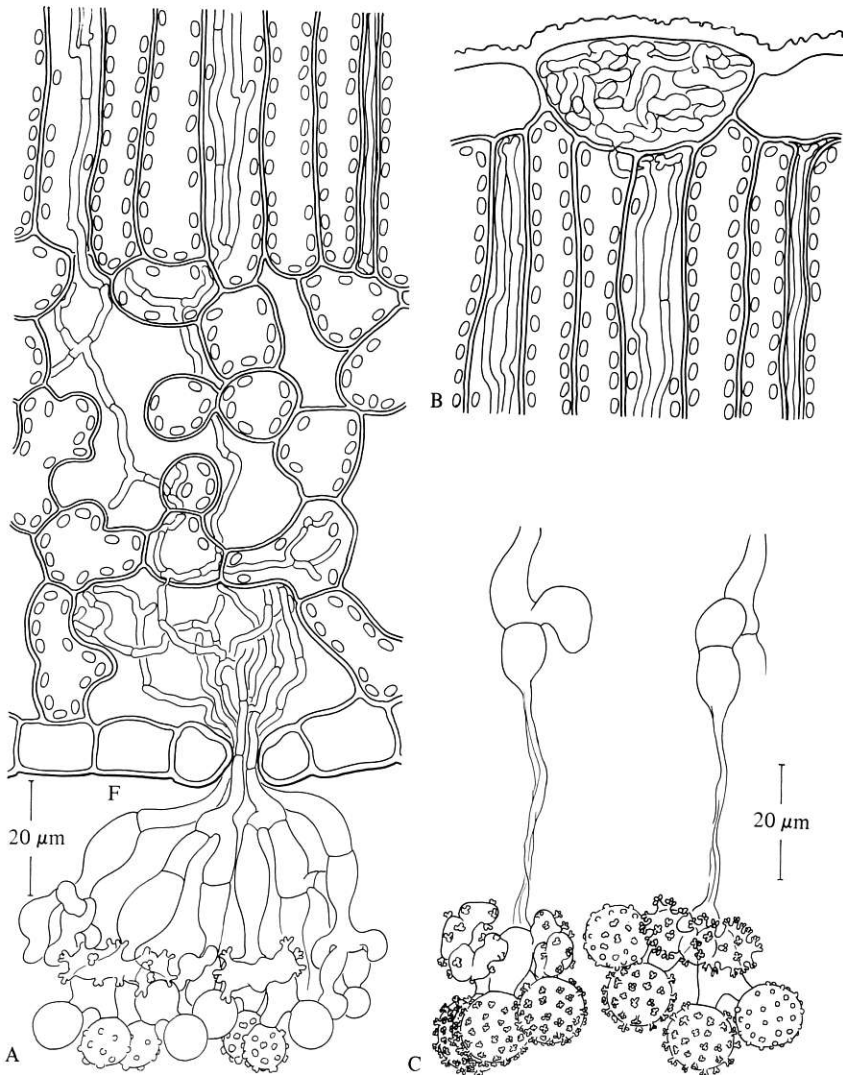
Fig. 10. *Glomopsis lonicerae*. (*a*) Section through a leaf of *Lonicera involucrata* showing host tissue, internal hyphal arrangement, and conidiophores emerging through a stoma; (*b*) upper part of the same host leaf as in (*a*) showing hyphae in palisade and epidermal cells; (*c*) mature conidial complexes with collapsed conidiophore cells.

migrates into a developing basidiospore. Jackson (1935) compared the nuclear behaviour of *Herpobasidium filicinum* with that of *Puccinia arenariae* (Schum.) Wint. In this microcyclic rust, Lindfors (1924) reported two-celled basidia and binucleate basidiospores, the latter two nuclei being the products of the second meiotic division. Jackson concluded that the fern parasite differs from *P. arenariae* in that the second division is delayed until the spore germinates. We were not able to study the

karyology of *Herpobasidium australe*, a species in which basidia are 2- to 4-celled.

Jackson (1935, Figs 4: 20, 21) observed branched sterigmata in *Herpobasidium filicinum*. Such bifurcate sterigmata are widespread in Heterobasidiomycetes and are rather common during germination by repetition (Figs 3–6, 9). During culturing experiments with *Insolibasidium deformans*, Gould (1945) found three types of basidiospore germination: secondary spores
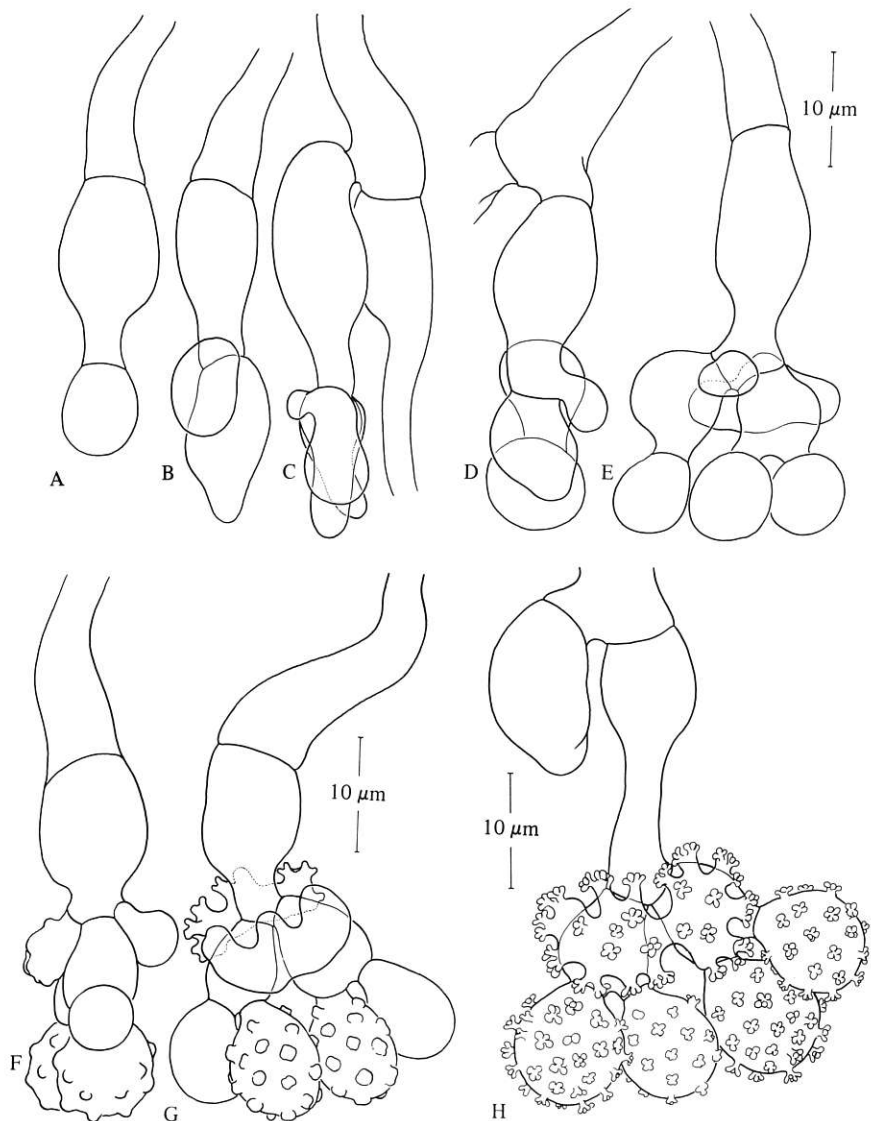
Fig. 11. Conidiogenesis in *Glomopsis lonicerae*. (*a*) Young conidiophore with single conidiogenous cell apically and swollen subterminal cell; (*b–d*) formation of additional conidiogenous cells, a single terminal immature conidium present on first-formed one; (*e*) conidiophore with three immature conidia; (*f–h*) development of verruculae on maturing conidia (note development of lateral conidia from subterminal cell in *f–h*, their unusual form, and prominent verruculae).

(ballistospores), germ-tubes and uninucleate sporidia. It is not known whether this and other species treated here have haploid yeast phases.

Anamorph stages

Of the taxa included, only *Insolibasidium deformans* has a known anamorph, the development and morphology of which is unusual (Figs 10–12). Two anamorph stages have been recognized; they are *Glomerularia corni* Peck (1885) on *Cornus canadensis* L., and *Glomerularia lonicerae* (Peck) Dearness & House (1923) on species of Caprifoliaceae. Henderson (1961) proposed a new form genus, *Glomopsis* for the two taxa, making the new

combinations *Glomopsis corni* (Peck) Henderson, and *Glomopsis lonicerae* (Peck ex Gould) Henderson. The name *Glomopsis lonicerae* Gould was thought to be a nomen nudum by Donk (1966), and was replaced by *Glomopsis lonicerae* Donk.

Sinden in Gould (1945) first discovered that a basidiomycete was associated with the leaf blight of *Lonicera*; Gould (1945) reported the connexion of the anamorph *Glomerularia lonicerae* with the newly named teleomorph, *Herpobasidium deformans* Gould. According to Henderson (1961), 'the conidial stage *Glomerularia lonicerae* is undoubtedly congeneric with *Glomopsis corni* and the two differ only in certain minor respects'. The teleomorph of *Glomopsis corni* is not yet known, but it would seem probable that it is a species of the genus *Insolibasidium*. It could, in fact, be the same species as that on *Lonicera*.

Glomospora empetri D. M. Henderson, a parasite on leaves of *Empetrum nigrum* L. and *E. hermaphroditum* (Lange) Hagerup, known from Scotland, is considered by Henderson (1961) to be the nearest relative of *Glomopsis lonicerae*. The perfect stage of *Glomospora empetri* is not yet known. Species of both genera liberate conidia in groups. It is not certain, however, that conidiogenesis is identical in both taxa.

Specimens examined: *Glomerularia corni*, on living leaves of *Cornus canadensis*, New York, Catskill Mountains, C. H. Peck 1259 (NY, type ?); *Glomopsis corni*, on *C. canadensis*, British Columbia, Mt Revelstoke Nat. Park (East Gate area), 23 Sept. 1980, S. A. Redhead, fide R. J. Bandoni (UBC).

Taxonomy

Herpobasidium species all have thin-walled hyphae growing in living fern leaves and emerging through stomata to form a loose hyphal network on the underside of leaflets. The mature basidia are cylindrical and sinuous; swollen probasidia are lacking. *Herpobasidium filicinum* and *H. australe* are specifically well separated through basidial morphology and spore measurements. In *H. filicinum*, basidiocarps are thin, most often limited in extent, and visible as circular or elliptic patches. Such patches are often associated with sori, but this association does not seem to be constant. In some instances, growth spreads from the usually restricted patches to produce an extensive pellicular growth of the type characteristic of *H. australe*. In contrast to *H. struthiopteridis*, basidiocarps of both these species are restricted to lower surfaces of leaflets.

Herpobasidium struthiopteridis differs from the foregoing species in the appearance and development of basidiocarps and in microscopic features.

In this species, the fertile structures appear first as small granules interconnected by surface hyphae; these occur on both leaf surfaces. The granules become flakelike and finally form large, confluent patches.

The host–parasite connexions are difficult to interpret. *Herpobasidium struthiopteridis* is only known from *Matteucia struthiopteridis*. This genus is currently placed in the Athyriaceae, a family which also contains the genera *Athyrium* and *Cystopteris*. Species of these genera are reported as hosts of *Herpobasidium filicinum*, which also occurs on *Gymnocarpium* spp. and *Dryopteris* spp. of the Aspidiaceae. *Herpobasidium australe* grows on species of *Adiantum* and *Arthropteris*, members of the Adiantaceae (or Pteridiaceae) and the Oleandraceae, respectively. Ten other common fern species growing in the same locality, belonging to eight other fern families, were not infected.

Obviously this pattern of 'host-selection' does not reflect natural relationships of the ferns. However, it must be kept in mind that our knowledge of these parasitic species is highly fragmentary; tropical taxa are not known at the present time.

Platycarpa is at best restricted to its type species, *P. polypodii*. This fungus parasitizes sporangia of *Polypodium* sp. and the species is well defined by conspicuous probasidia and thick-walled hymenial and subhymenial hyphae.

Ptechetelium cyatheae parasitizes fern sporophylls, but not sporangia. It possesses a hyphal system that is similar to that of *Platycarpa polypodii*, but has the unusual characteristics of percurrent proliferation. Such basidial development is known to occur in *Septobasidium alni* Torr. Because of general morphological similarities between *Ptechetelium cyatheae* and *Platycarpa polypodii* with *Septobasidium* species, we agree with the interpretation of Couch (1949) that these taxa occupy '...an intermediate position between the Septobasidiales and the Auriculariales'. However, this similarity is restricted to certain simple-pored auricularioid fungi and not the *Auricularia–Hirneola* group.

Insolibasidium deformans, growing on species of Caprifoliaceae, is certainly generically different from *Herpobasidium* and the other fern parasites. The basidia protrude from the lower leaf epidermis and do not develop from a hyphal network covering the underside of the leaf. Another unique character is the anamorphic stage with its conidial complexes. A similar, but possibly specifically distinct anamorph occurs on *Cornus canadensis* L. (Cornaceae). The teleomorphic stage of this deuteromycete is unknown. We suggest that it belongs in the genus *Insolibasidium*.

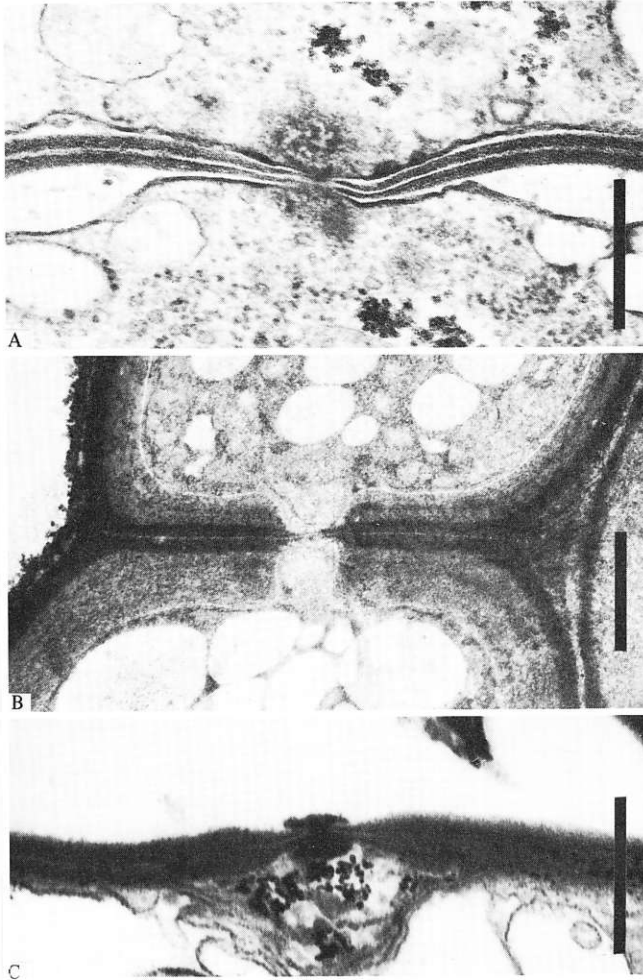Henderson (1961) considered the *Glomopsis*

Fig. 12. *Herpobasidium filicinum*, septal pore ultrastructure. (*a*) Young septum between plasmatic cells; (*b*) pore through thick-walled septum; (*c*) septum with pore between old cells lacking cytoplasm. Bars equal 0·5 μm.

anamorph of *Insolibasidium* to be the 'nearest relative of *Glomospora*', a monotypic imperfect genus occurring on *Empetrum*, a genus belonging in the small family Empetraceae (Ericales). If the closely related basidiomycetes are considered to be indicators of a natural relationship of the hosts, then Dahlgren's (1975) system can be supported. He includes Ericales and Cornales, inclusive of Sambucaceae and Adoxaceae in the Cornanae. The next taxon, Gentiananae, comprises, *inter alia*, the Caprifoliaceae as a family of the Dipsacales.

All taxa treated in this contribution share features of the Uredinales, Septobasidiales, and many simple–pored auricularioid fungi. They are parasites with clampless and simple-pored hyphae, transversely septate, 'auricularioid' basidia, and basidiospores that germinate by repetition. We consider these characteristics as taxonomically and phylogenetically most important. *Herpobasidium* and the allied genera, *Jola*, *Platycarpa* and *Eocronartium* have been considered more closely related to the Uredinales than to auricularioid fungi by some authors (Leppik, 1955). However, as Jackson (1935: 560) stated: 'It is perhaps unimportant whether one considers *Herpobasidium* a member of the Auriculariales or a simplified form of the Uredinales'. It is not clear, at the present time, whether or not the rusts constitute a natural

group, but the order Auriculariales contains two groups of only distant relationship. Transfer of *Herpobasidium* and its allies to the Uredinales therefore appears to be premature. The taxa treated here could be representative of an ancestral group from which rusts, Septobasidia and simple-pored auricularioid fungi diverged. It is interesting, from a phylogenetic point of view, that morphologically simple fern parasites still exist; they could, of course, be simple as a result of regressive evolution. The tropical fern fungi are poorly known, as yet, and additional study may yield further clues as to the evolution of such fungi.

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