

Revisiones Generum Obscurorum Hyphomycetum: *Phacellula* Syd. and *Cladosterigma* Pat.

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The monotypic genus *Phacellula*, based on *P. gouaniae*, is shown to be a teleomorphic heterobasidiomycete in the Cryptobasidiales. Structures originally described as conidiogenous cells are reinterpreted as basidia and the ‘conidia’ as sessile basidiospores (statismospores). *Cladosterigma*, based on *C. fusisporum* (= *C. clavariellum*), shares many features with *P. gouaniae*, but its systematic position is less certain because developmental stages are lacking in the type material. The cells presumed to be basidia in *C. fusisporum* occur in an amphigenous hymenium on minute clavarioid basidiomes; the micromorphological similarities suggest a relationship to *P. gouaniae*. New descriptions, based upon authentic material, are provided for both taxa, which were originally described as hyphomycetes.

Keywords: heterobasidiomycetes, Cryptobasidiales, taxonomy, Deuteromycota.

Phacellula gouaniae H. Sydow (1927) was described as a hyphomycete from leaves of *Gouania tomentosa* (sic) collected in Costa Rica. The fungus was not illustrated, and there have been neither subsequent reports of the species nor commentary on its taxonomic placement. As part of an ongoing examination of type material of obscure hyphomycete genera, authentic material of *P. gouaniae* was located in The U. S. National Fungus Collections (BPI), resulting in the reinterpretation of the fungus provided here.

This reexamination led to further reconsideration of the monotypic genus *Cladosterigma* Pat., occurring on *Eugenia* spp. in the neotropics (Patouillard, 1892). Seifert (1985) reviewed the taxonomic history of this genus and redescribed and illustrated the only species, *C. clavariellum* (Speg.) Höhnelt, as a synnematus hyphomycete. He speculated that the 3-septate conidia might

actually be deciduous basidia similar to those of species of *Mycogloea* Olive. Consideration of the heterobasidiomycetous nature of *Phacellula gouaniae* prompted us to reexamine material of *C. clavariellum*. This suggested a probable relationship of the two fungi and provided morphological evidence that these fungi are teleomorphic taxa in the Cryptobasidiales (with some reservations for *C. clavariellum*).

Taxonomic part

Phacellula gouaniae H. Sydow, Ann. Mycol. 25: 139. 1927. – Figs. 1 A, B, 2–4.

Infected areas of leaves are at first green, later necrotic, with lesions from <1 mm to 5 mm when circular, but mostly irregular and with linear extensions along veins, forming erect white tufts, these

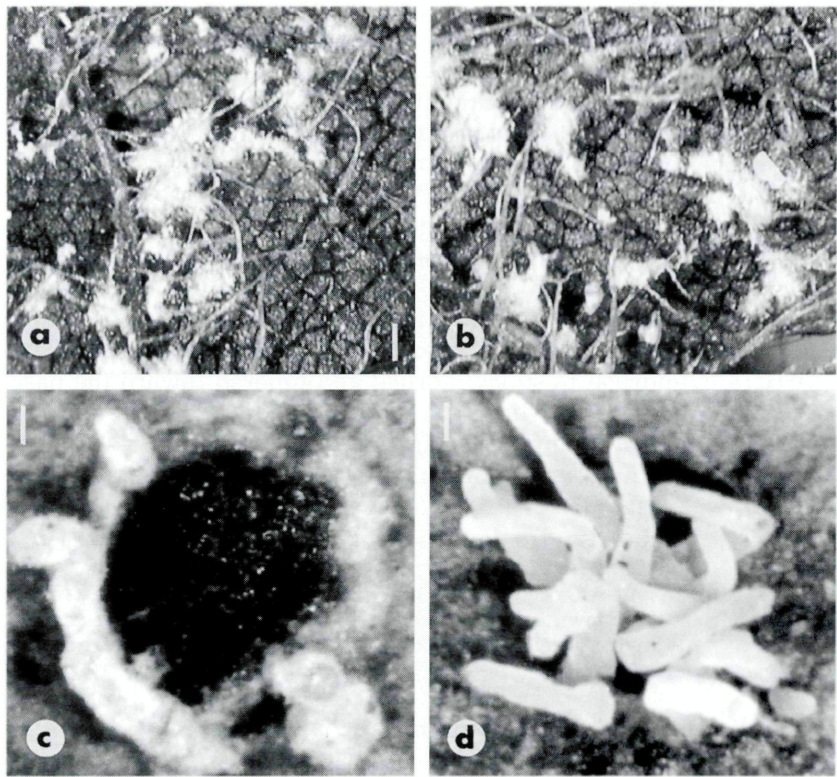


Fig. 1. – *Phacellula gouaniae* (from the type, BPI) and *Cladosterigma clavariellum* (from type, FH), habit photos. – A, B. Clusters of floccose basidiomes of *P. gouaniae*. (Bar = 500 µm). – C, D. Waxy basidiomes of *C. clavariellum* arising in both from black stromatic leaf-inhabiting fungus. (Bar = 100 µm).

ca. 0.1 mm in diam. and 0.1–0.2 mm high on the upper leaf surface, tufts both higher and of greater diam. on the lower surface, to 2 mm in diam., often anastomosing, linear along veins or with linear extensions if circular, commonest along leaf margin. – Basidiomes (Fig. 1A, 1B) are white tufts comprised almost entirely of erect basidia that arise from a thin, compact layer of hyphae on the host epidermis or extend through this layer in part; hyphae of surface layer compactly arranged, only short free segments visible, strongly adherent, the hyphae 2–4 µm diam, septate, with scattered clamps. – Basidia (35–)70–195 µm long, 3.5–5 µm diam. apically, cylindrical to narrowly clavate, most tapered toward the basal clamp but irregularly swollen in spots (Fig. 2A, 2B); 4–8 basidiospores develop synchronously at the basidial apex (Fig. 2C, 2D), each on a short denticle 1–1.5 µm long and about 0.5 µm wide (Fig. 4E), that is clearly visible and apparently occluded after basidiospore secession. – Basidiospores (statismospores) (15–)18–25 µm long, straight (Fig. 4D) to falcate or slightly S-shaped, often with an additional curvature near the base (Fig 2D, 2E; Fig. 3A, 3B,) the widest part 3–5 µm diam. (at or just above the middle), 2–4 µm apically, mostly tapering towards the base and there 1.5–2 µm, spores laterally adherent, released as a cluster, most adhering strongly even after release from the basidium, inamyloid, 1–3 septate at maturity (Figs. 2C–E, 4A–C). – Germination by germ tubes 8–10(–15) × 1–2 µm in diam., tubular to irregularly swollen, sometimes branched (Fig. 3F), or tubes lacking and sessile conidia budding directly from the spore wall or from raised loci; similar conidia developing terminally on germ tubes, or a terminal portion of a germ tube becoming separated by a septum and eventually falling away. – Conidia cylindrical to subcylindrical and tapered toward the base, or crescent-shaped to ellipsoidal or subglobose, mostly 2–4–10 × 1.5–2 µm, smooth, inamyloid (Fig. 3G). Abundant ellipsoidal to globose cells in some mounts are possibly buds from the basidiospores (Fig. 3H).

Material examined. – COSTA RICA, Rio Poas, Sabanilla de Alajuela et San Pedro, growing on living leaves of a *Gouania* species, 10 Jan. 1925 (BPI 420188). The type was recorded by Sydow as growing on *Gouania tomentosa*, but this species is unknown in Costa Rica (L. Fournier, University of Costa Rica, pers. comm.). All infected leaves examined had heavy insect damage and most had additional fungal species present.

Cladosterigma clavariellum (Speg.) Höhnelt, Sber. Akad. Wiss. Wien Abt. I, 128: 536. 1919 (as '*clavariella*'). – Figs. 1C, 1D, 5.

≡ *Microcera clavariella* Speg., An. Soc. cient. argent. 22: 222. 1886.

≡ *Cladosterigma clavariella* (Speg.) Petch, Trans. Br. mycol. Soc. 8: 214. 1922. (superfluous combination)

= *Cladosterigma fusisporum* Pat., Bull. Soc. Mycol. France 8: 138. 1892.

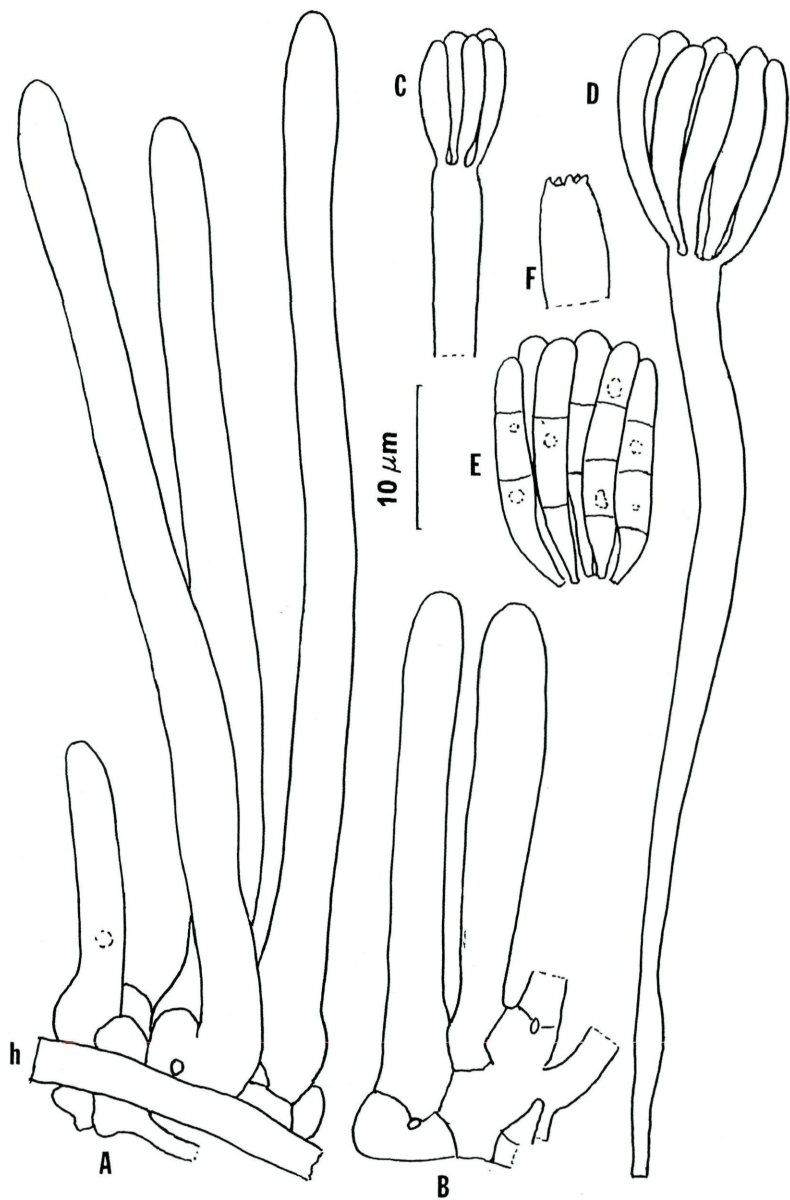


Fig. 2. – *Phacellula gouaniae* (from the type, BPI). – A, B. Early stages in development of basidia, h host hyphae. – C. Apex of mature basidium with developing basidiospores. – D. Mature basidium with apical cluster of nearly mature basidiospores. – E. Mature adherent cluster of basidiospores after secession. – F. Apex of collapsed basidial apex after spore release, showing tooth-like sterigmata. (Bar = 10 μm).

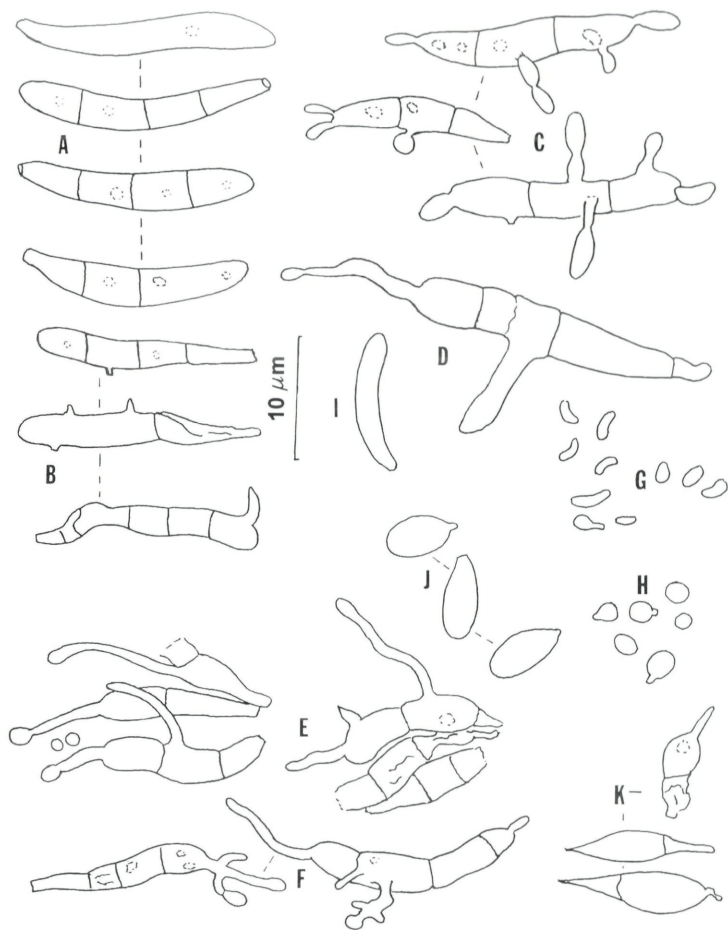


Fig. 3. – *Phacellula gouaniae* (from the type, BPI). – A. Single basidiospores before germination (Note: basidiospores appear always to be released as strongly adherent clusters; single basidiospores shown here were separated by tapping the coverslip). – B. Two basidiospores (above) with spicules probably representing budding loci, one with a single septum and a collapsed basal cell, the third basidiospore (lowermost) with a short germ tube. – C. Three basidiospores with blastic conidia developing directly from the spore or from short germ tubes. – D. A single basidiospore with one conidium arising from a long apical germ tube. – E. Two clusters of germinating basidiospores, several cells with germ tubes. – F. Two basidiospores with simple and branched germ tubes, one of the latter with a spore-like terminal cell (left, lower branch). – G. Allantoid to ellipsoidal or globose conidia, the most frequently found forms with basidiospores. – H. Budding cells associated with basidia. – I. Single representative of a type found together with basidiospores, the origin unknown. – J. Spores, the upper and lowermost of which appear possibly to be ballistospores, their origin unknown. – K. Apparently single, still cytoplasmic basidiospore cells, each with attached vestiges of emptied cells (note sterigma-like apical tube on upper example). (Bar = 10 µm).

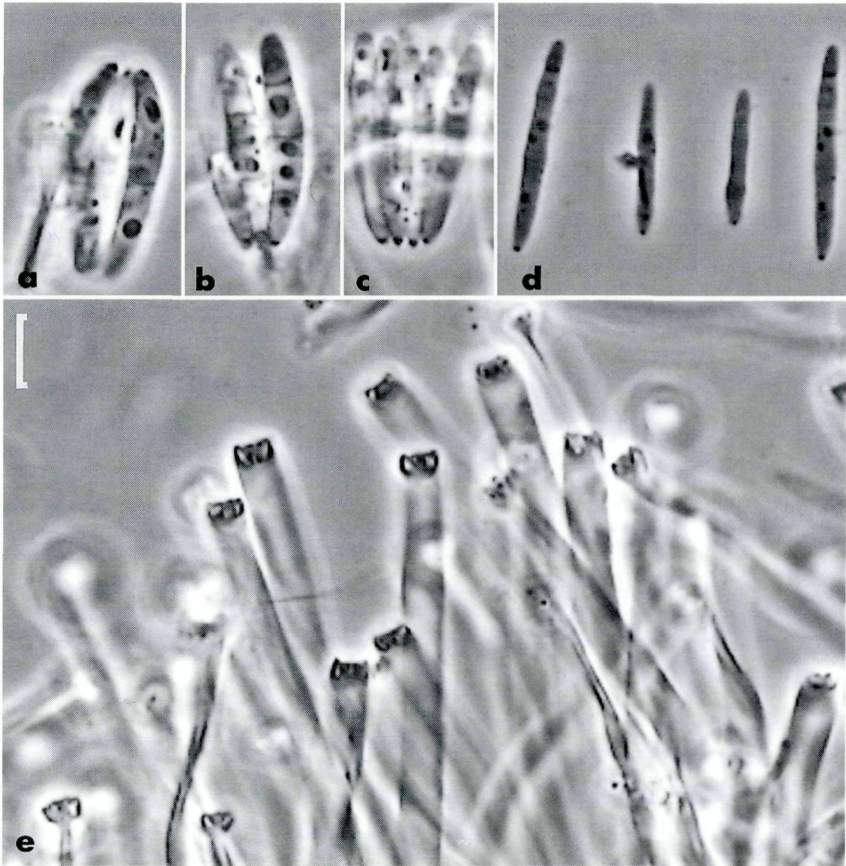


Fig. 4. – *Phacellula gouaniae* (from the type, BPI), photomicrographs in lactic acid. – A–C. Clusters of laterally adhering, seceded basidiospores. – D. Individual basidiospores released from one another by tapping cover glass, note lateral denticles or bumps, presumably sites of conidial production. – E. Apex of a caespitose cluster of basidia showing denticles remaining after secession of basidiospores. (Bar = 10 μ m).

Basidiomes epiphyllous or hypophyllous, arising singly or in groups, almost exclusively from black stromatic pycnidial structures (?host fungus) embedded in leaves, simple and cylindrical to clavate or coralloid, the dry basidiomes reaching ca. 1 \times 0.1 mm, horny translucent to opaque, the extreme base black, passing through dark brown above, the fertile part whitish to cream or pale yellow. In section, with a distinct central core ca. 50 μ m in diam. composed of compact, partially agglutinated and strongly adherent hyphae, these mostly parallel, with thickened walls; context hyphae 1.5–3 μ m in diam., thin-walled, branched, uniform to irregularly swollen in

spots, septate, sometimes appearing clamped (Fig. 5A, 5B, 5F, 5K), but this is unclear. – Hymenium amphigenous, compact, the fertile hyphae often interconnected by anastomoses (Fig. 5C). – Basidia (Fig. 5, A–F) $(9\text{--}14\text{--}19 \times 4\text{--}5.5 \mu\text{m})$, clavate to spatulate-capitate at first, later crowned by 1–4 finger-like extensions (presumably loci of basidiospore production), the extensions $2\text{--}4 \times 1.5\text{--}2 \mu\text{m}$, in a tight apical cluster; less commonly, similar basidium-like cells with spores formed singly and laterally (sympodial development; Fig. 5E). – Basidiospores $10\text{--}14 \times 3.5\text{--}4 \mu\text{m}$ (Figs. 5G, 5H), narrowly clavate to fusiform, becoming 1–3 septate, bearing conidia on short germ tubes, the latter to $4 \times 1 \mu\text{m}$. – Conidia $4.5\text{--}8 \times 2.5\text{--}3.5 \mu\text{m}$ (Fig. 5I), narrowly lacrimiform or obpyriform, thin-walled, inamyloid, germinating by budding, sometimes becoming 1-septate; other conidia (Fig. 5J) present are ellipsoidal, $4.5\text{--}5 \times 3\text{--}3.5 \mu\text{m}$, the wall slightly thickened, inamyloid both types of conidia sometimes with a minute apiculus-like extension of variable position (probable budding locus).

Material examined. – ECUADOR, leg. Lagerheim, growing on embedded (?) pycnidia in Myrtaceous leaves, Sept. 1891 (holotype of *Cladosterigma fusisporum*, herb. Patouillard, FH). For other material see Seifert 1985.

Discussion

The Cryptobasidiales is a small heterobasidiomycete order, consisting of one family with four or five genera and eight to nine species, classified in the Ustomycetes (Hawksworth & al., 1995). An additional family, *Muribasidiosporaceae* (Rajendren, 1969) appears to be unnecessary, because the single genus that it contains, *Muribasidiospora* Kamat & Rajendren, is at least superficially very similar to *Coniodictyum* Har. & Pat. The species of the Cryptobasidiales produce clavate holobasidia with variable numbers of sterigmata, and basidiospores that are not forcibly discharged (statismospores). Most members of the Cryptobasidiales produce single or tufted basidia on infected host parts or galls, with the plants generally in the *Rhamnaceae*. We suggest that both taxa considered here, originally described as hyphomycetes, *Phacellula gouaniae* and *Cladosterigma clavariellum*, might be classified in the Cryptobasidiales. Both fungi are presently known only from herbarium specimens, and therefore the location and behaviour of the nuclei during meiosis, the sequence of ontogenetic events, and the association of the various deciduous elements, can only be pieced together tentatively and by analogy to processes demonstrated in potentially related taxa.

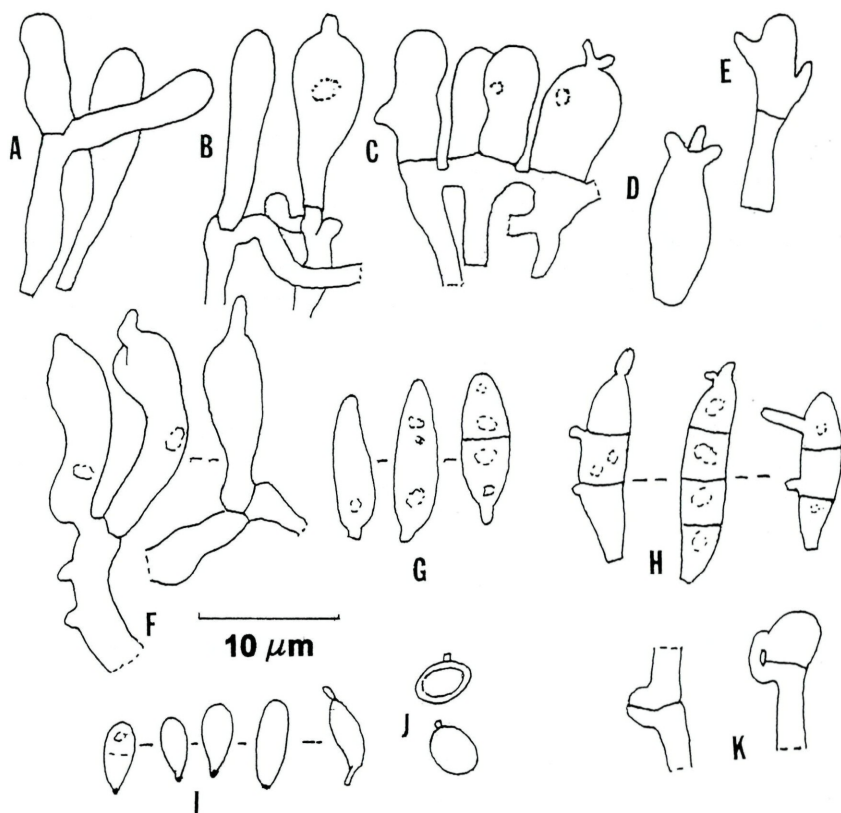


Fig. 5. A–K. – *Cladosterigma clavariellum*, from holotype of *C. fusisporum* (FH). – A–D. Young putative basidia, the septum of two possibly clamped (note anastomoses in C, and differences in arrangement of finger-like extensions that may represent sterigmata in B–D). – E. Single basidium-like cell with symphyotically arranged sporogenous sites. – F. 3 basidia, all with single apical sterigmata-like extensions, the most common form seen. – G, H. Presumed basidiospores with budding loci or tubular germ tubes. – I. Putative blastoconidia from basidiospores, that on the far right apparently budding. – J. Thick-walled spores present in one preparation, their origin unknown. – K. Two putative clamp connections. (Bar = 10 µm).

Phacellula gouaniae is characterized by clavate holobasidia and statismospores similar to those produced by taxa in the Cryptobasidiales. The necrotic lesions associated with the basidial tufts of *P. gouaniae* suggest plant parasitism, but we did not check for haustorial cells in the leaf tissue. The host plant, an unknown species of *Gouania*, is a member of the *Rhamnaceae*, in common with the hosts of other members of the Cryptobasidiales. Although additional fungi are present on the host leaves, no evidence of mycoparasitism was noted. No evidence of galls was seen, although

these are characteristically associated with many species of Cryptobasidiales and Exobasidiales. The basidia of *Laurobasidium lauri* (Geyler) Jülich (Jülich, 1982) resemble those of *P. gouaniae* in form and dimensions, and in having basal clamp connections. The basidiospores of *L. lauri* are 1–7 septate, and germinate by germ tubes or conidia. The basidiospores are in tightly adherent clusters in *P. gouaniae*, much as in *Coniodictyum chevalieri* Har. & Pat. (Cryptobasidiales), in which the spores are thick-walled. Malençon (1953), who examined germination in the latter species, commented on and illustrated the ‘promycelium-like’ development from many cells of the spore cluster (his Fig. 7 A), reminiscent of the germinating teliospore balls of some smuts.

The systematic position of *Cladosterigma clavariellum* is less certain because we were unable to find spores attached to the presumed basidia, and few spores were found on the hymenia. The basidia in the collection examined here almost all have a single terminal ‘sterigma’, which might indicate monospored basidia, asynchronous basidiospore development, or that the cells are not basidia. The arrangement seen in Fig. 5E was sometimes present, but when there was more than one sterigma-like appendage on a basidium, the pattern seen in Fig. 5D was generally evident. Very few basidiospores were found, a few with 0–1-septa (Fig. 5G), the rest with 2–3 often extremely thin septa (Fig. 5H). Very few conidia were seen attached to the basidiospores, but free ones on the hymenium had similar walls thickness and staining properties. The thick-walled spores in Fig. 5J were common in one preparation, but their origin could not be determined. The basidium-like elements in which sympodial proliferation occurs do not closely resemble basidia and we assume that the spores are formed singly, laterally, and successively. Some spores found on basidiomes (Fig. 5G, 5H) closely resemble those of *P. gouaniae* in form, septation, and germination. In both taxa, the basidiospores (if the structures illustrated in *C. clavariellum* are indeed basidiospores) bear a remarkable resemblance to the deciduous basidia in species of *Mycogloea* Olive in form, septation, and conidial production. The hyphae in the basidiomes of *C. clavariellum* are very small, slightly agglutinated and indistinct, making detection of clamps difficult. Ultrastructural examination of thin sections of a septa showed a simple septal pore of the type characteristic not only of the Cryptobasidiales, but of many rusts, smuts, and jelly fungi (figure not shown). Most members of the Cryptobasidiales produce single or tufted basidia on infected host parts or galls, unlike the minute clavarioid basidiomes of *C. clavariellum*. The copies of Geyler’s figures of *Laurobasidium lauri* provided by Jülich (1982) show single, scattered or tufted basidia arising from large clavarioid galls, but clavarioid basidiomes

are absent. The basidiomes of *C. clavariellum* develop from conspicuous pycnidial stromata embedded in leaves, rather than the leaf itself (Seifert, 1985), suggesting mycoparasitism rather than phytoparasitism.

In summary, evidence for classifying *P. gouaniae* as a member of the Cryptobasidiales is strong. It has conspicuous clamp connections, elongate basidia similar to those in species of *Botryoconis* Syd. & P. Syd., *Clinoconidium* Pat., and *Drepanoconis* J. Schröt. & Henn., and sessile, septate basidiospores, also characteristic of several taxa in the order. Although galls are lacking, parasitism of a Rhamnaceous host is also a feature shared with most other species classified in the Cryptobasidiales. What appear to be basidiospores in *Cladosterigma clavariellum* closely resemble those of *P. gouaniae*, and it is probable that they develop apically on the clavate, coronate cells resembling basidia. The basidium-like elements, which lack conspicuous basal clamps, resemble basidia only when the finger-like processes (?sterigmata) are apical. The hymenial cells of similar form and stature, but bearing spores sympodially, are possibly conidiogenous cells. The lack of developmental stages (i.e. with spores attached) for both types of fertile cells, leaves considerable doubt in this instance. The suggestion that this taxon might be mycoparasitic rather than plant pathogenic adds further uncertainty to its systematic placement. Studies of fresh material are needed to clarify development and systematic position of both taxa discussed here.

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