HETEROGASTRIDIALES: A NEW ORDER OF BASIDIOMYCETES[1]

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ABSTRACT

Descriptions are provided of new basidiomycetous taxa based upon the teleomorph of *Hyalopycnis blepharistoma*; the taxa are: Heterogastridiales, Heterogastridiaceae, *Heterogastridium*, and *Heterogastridium pycnidioideum*. The type species is characterized by a pycnidioid basidiocarp with an internal basal hymenium. Phragmobasidia produce sessile, digitately branched basidiospores that are released passively. Ontogeny of the basidia, basidiospores, and septal pores has been studied. The septal pores are simple, but vary morphologically during ontogeny. Hyphal cells, conidiogenous cells, and conidia are dikaryotic. The structure of the spindle pole body indicates heterobasidiomycetous affinities.

Key Words: Heterogastridiales, Heterogastridiaceae, *Heterogastridium pycnidioideum*, *Hyalopycnis blepharistoma*, Heterobasidiomycetes, gastroid basidia, pycnidia

Hyalopycnis blepharistoma (Berk.) Seeler is widely distributed and has been reported from Austria, England, Japan, and North America (von Höhnel, **1918**; Petch, **1943**; Seeler, **1943**; Tubaki, **1969**; Bandoni and Oberwinkler, **1981**). Bandoni and Oberwinkler (**1981**) studied morphology and development of the species and found sufficient characters to identify *H. blepharistoma* as a basidiomycetous anamorph. Although tetraradiate cells were also observed sporadically during that study, they were not attached to basidia when seen and were mistakenly thought to be another conidial form. Basidia were later found in substantial numbers in the pycnidioid sporocarps of one of the several strains studied.

MATERIALS AND METHODS

The strains of *H. blepharistoma* used in this study are listed in TABLE I; all are deposited in the culture collections of the Department of Botany, University of British Columbia and Lehr-

stuhl Spezielle Botanik, University of Tübingen; some also have been deposited in the IFO, Osaka, and ATCC culture collections. Cultures were maintained on malt yeast peptone (MYP, Bandoni, **1972**) and were grown on this medium, oat flake agar (OFA), potato-dextrose agar (PDA) with 10 g sucrose per liter of medium, and Difco Corn Meal Agar (CMA) fortified with 0.5 g Difco yeast extract per liter of medium. Cultures were incubated at 20 C in incubators with 12 h light/12 h dark cycles and fluorescent lighting.

We also subjected cultures to the common procedures used in stimulating sporulation in aquatic hyphomycetes in attempts to induce basidial development. The procedures included daily flooding and draining of one week old cultures on MYP or on OFA (Bandoni and Tubaki, **1985**), covering such plate cultures with a layer of sterile water, submersion of blocks of agar and mycelium in sterile, still water (Ingold, **1942**), and submersion in aerated water (Marvan *et al.*, **1979**).

All cytological and morphological illustrations shown here were obtained using a single strain of *H. blepharistoma* (CTR 66-90). Living and fixed material was examined with a Zeiss photomicroscope III, using phase optics and No-

Culture	Other nos.	Source and location
CTR 66-90	ATCC 48561	On old agaric, coll. New York, S. J. Smith No. 40782
CTR 69-137-1	ATCC 48563	On *Scleroderma aurantium* parasitized by *Sepedomium chrysospermum*, New York, C. T. Rogerson
CTR 70-135	ATCC 48560	On *Humaria hemispherica*, New York, C. T. Rogerson
CTR 78-131	ATCC 48562	On *Amanita* sp. parasitized by *Hypomyces hyalinus*, New York, C. T. Rogerson
TY 4211-C-5	IFO 8906	From rotten pumpkin harvested in Sapporo, T. Yokoyama
RJB 6063	UBC 75-6063 (1–3)	From litter of *Quercus virginiana*, New Orleans, Louisiana, R. J. Bandoni
RJB 6649	UBC 75-6649	From decaying tomato plant, Vancouver, BC, R. Bandoni

marski interference contrast optics. For transmission electron microscopy, samples were fixed in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer at pH 7.2 for periods ranging from overnight to several days. Following six transfers in 0.1 M sodium cacodylate buffer, material was postfixed in 1% OsO_4 in the same buffer for two hours in the dark, washed in distilled water, and stained in 1% uranyl acetate solution for 1 hour in the dark. After five washes in distilled water, the material was dehydrated in acetone, using 10 minute changes at 25%, 50%, 70%, 95%, and 3 × 100% acetone. The material was then embedded in Spurr's plastic (Spurr, **1969**). Series of sections were cut on a Reichert ultramicrotome using a diamond knife. The sections were mounted on Formvar-coated single-slot copper grids, stained with lead citrate (Reynolds, **1963**) at room temperature for 3–5 minutes, then washed again with distilled water. Sections were examined with a Zeiss EM 109 transmission electron microscope at 80 kV.

OBSERVATIONS

None of the experiments involving wetting or submerging mycelium of *H. blepharistoma* were successful. Plates in such tests were scanned for the presence of tetraradiate basidiospores and numerous pycnidia were examined for the presence of basidia. However, no increases in frequency of basidiospores or basidia could be detected after any treatment. Nor were increases in basidiospore production observed when strains were grown on different media. Basidia were found only in CTR 66-90, and this occurred without water treatments or changes in media. The following observations on teleomorph morphology and development thus are based only upon that strain.

Basidiomes arise from a loose hyphal network (FIG. 1) of mostly simple-septate, thin-walled, smooth hyphae, 2–3 μm in diam. Sporocarp primordia differentiate into a cluster of generative hyphae around which the sterile peridial hyphae

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FIGS. 1–5. Line drawings of *Heterogastridium pycnidioideum*. 1. Reconstructed sectional sketch of a basidiome showing internal hymenium with basidia in different developmental stages, basidiospores, conidiophores, and conidia. 2–5. Stages in basidial ontogeny. 2. Several young probasidia, showing nuclei and nucleoli, septate basidium with basidiospore initials, and one in which the basidiospores are almost mature. 3. Upper portion of a basidium showing slight asynchrony in basidiospore development and vacuolization of spore-producing cells. 4. Detail of basidial apex and developing basidiospore. 5. Portion of basidium with mature basidiospores.

FIGS. 6–12. Basidiocarps and different stages in development of basidia, basidiospores and conidia of *Heterogastridium pycnidioideum*. 6. Young pycnidioid basidiome seated on a basal network of hyphae (bar = 50 μm). Note apical divergence of neck cells. 7. Lower portion of basidiome showing internal basal hymenium (bar = 30 μm). 8. Slightly squashed hymenium showing basidia and basidiospores (bar = 30 μm). 9. Cluster of conidiophores, some conidiogenous cells of which bear conidia (bar = 20 μm). 10. Hymenium with one old basidium, several young basidia, and neighboring conidiogenous cells and conidia (bar = 20 μm). 11, 12. Detached basidiospores, two of which have anastomosed after germinating (bars = 20 μm). 11. Conidium formation after fusion of two basidiospores. 6–7. Bright-field microscopy. 8. Nomarski interference contrast microscopy. 9–12. Phase contrast microscopy.
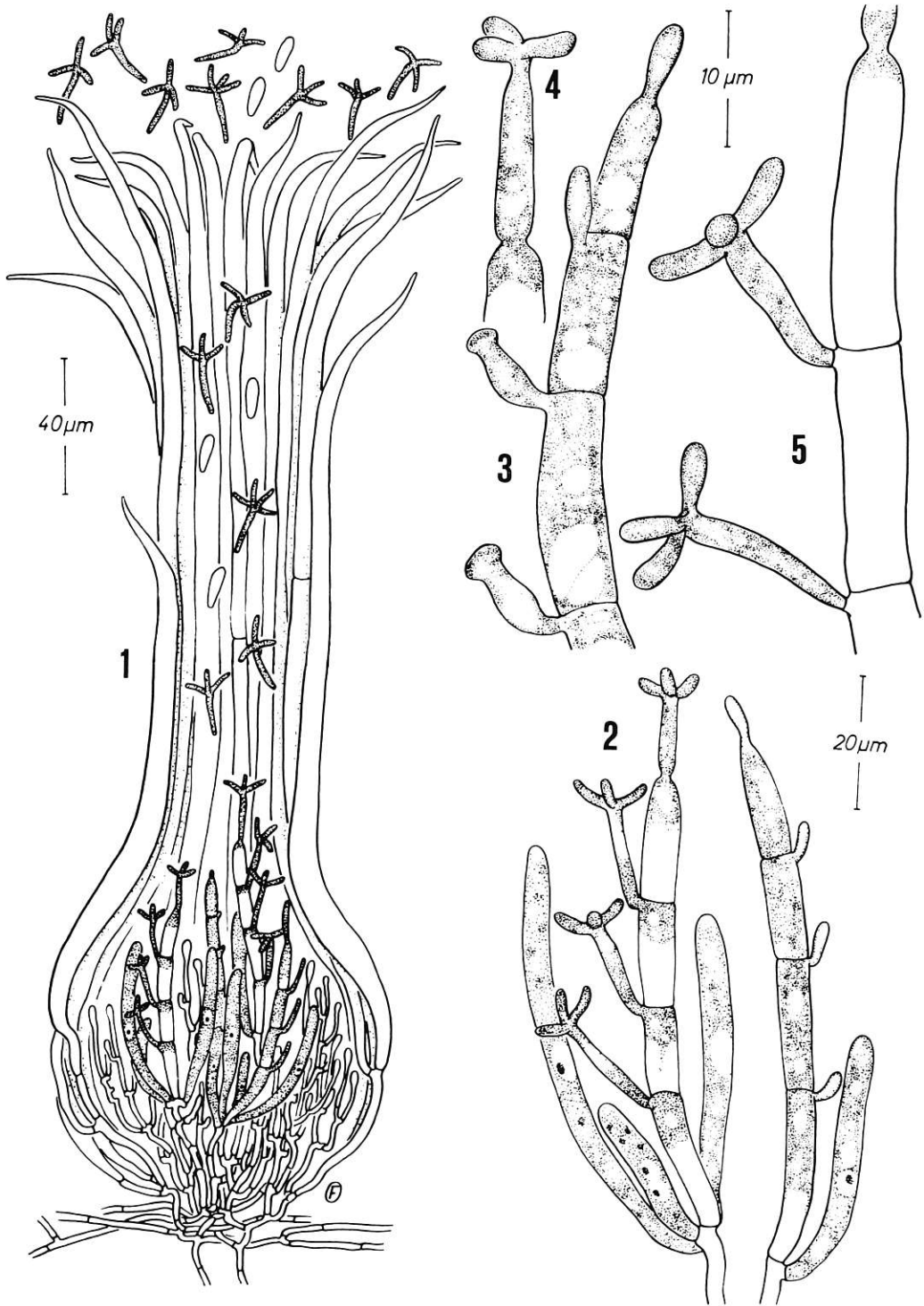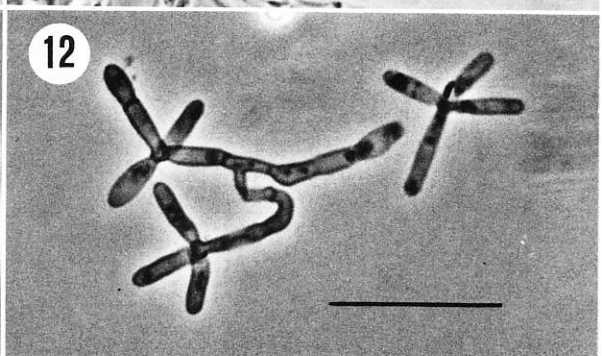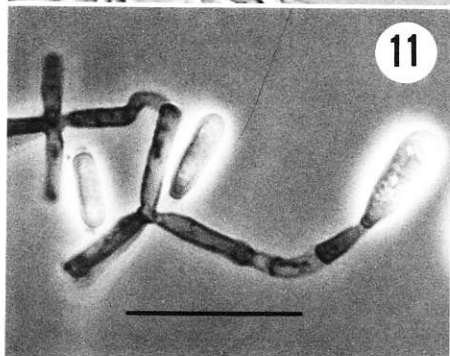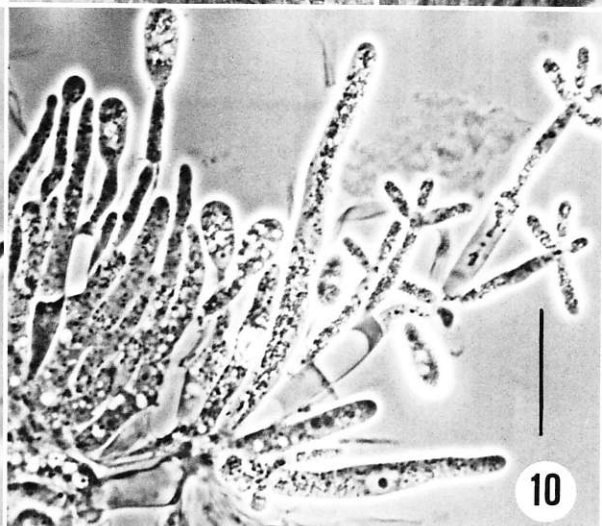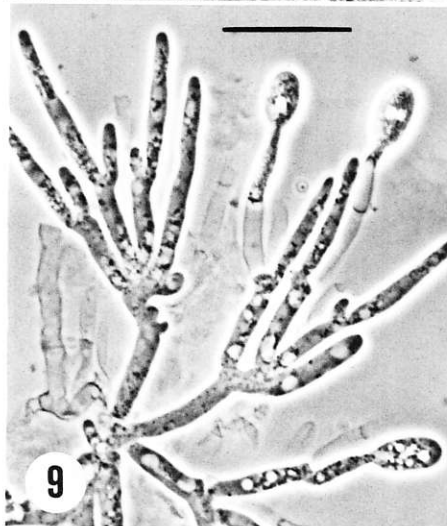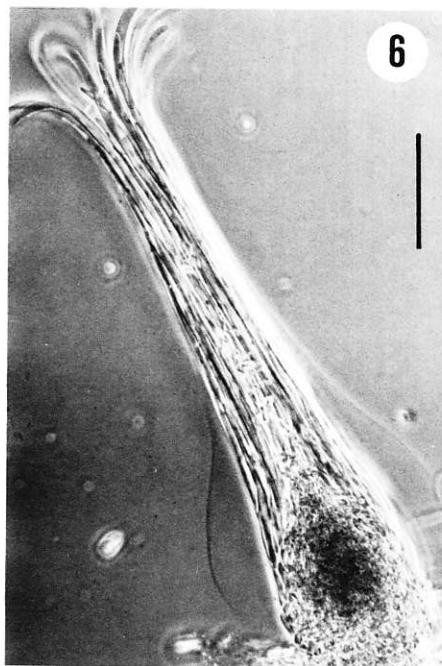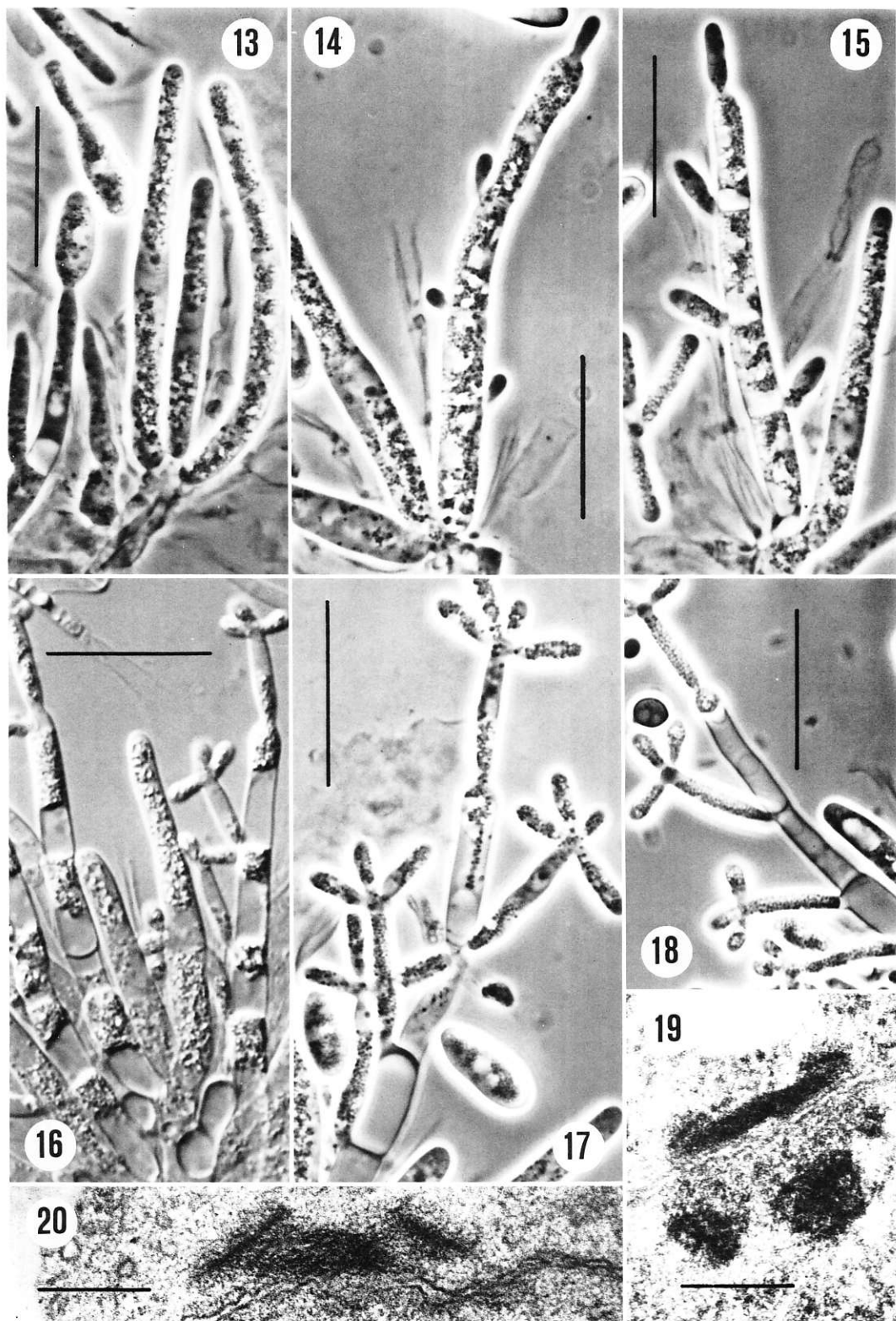
develop. A single layer of the peridial hyphae, each cell 8–15(–20) µm diam and 100–500(–800) µm long, form both the swollen base and the tapering neck of the basidiome. The neck is of variable length and 40–100 µm diam, the cells tapering gradually apically and diverging sharply near their apices (FIGS. 1, 6). The peridial cells are only weakly adherent to one another and often separate in microscope preparations. The generative hyphae form a densely interwoven basal subhymenium (FIGS. 1, 7, 8) which mostly bears a mixture of conidiophores and basidia (FIGS. 1, 10). With age, the hymenium thickens considerably by proliferative growth of generative hyphae (FIG. 1). Basidia develop successively (FIGS. 2, 10, 16).

Young basidia have diploid nuclei (FIGS. 2, 13) and are cylindrical or sometimes tapering, the cytoplasm densely and conspicuously granular. The diploid nucleus, 4–5 × 5–6 µm, and the nucleolus which is *ca* 1 µm diam are easily visible with phase contrast and Nomarski interference contrast optics (FIGS. 13, 14, 16). Post-meiotic basidia are transversely 3-septate, 5–8 × 60–80 µm (FIGS. 1–3, 10, 14–18), and each cell develops one basidiospore. The site of spore outgrowth is apical on the terminal cell and distal, *i.e.,* near the upper septum and lateral, in the remaining cells. Basidiospore development on a single meiosporangium is predominantly synchronous (FIGS. 1, 2, 4, 5, 10, 14–18), but differences occasionally occur (FIG. 3).

Basidiospore initials are at first tubular (FIGS. 2, 3, 14, 15) and, after reaching 8–12 µm long, apical enlargement occurs (FIG. 3); 3 or, infrequently, 4 radiating branches then develop (FIGS. 1, 2, 4, 5, 10, 16–18). As the spores grow, vacuoles enlarge in the basidial cells (FIGS. 2, 3, 5, 10, 15–18). Mature basidiospores are separated from basidial cells by basal septa (FIGS. 5, 18) at which time the old basidial cells are empty (FIGS. 5, 18). The predominantly tetraradiate basidiospores (FIGS. 11, 12, 17, 18) measure 8–13 × 15–

25 µm in outline, and the arms are 2–3(–4) µm diam. The basidiospores are released passively and accumulate in large quantities, generally admixed with conidia (FIG. 1), in a slime drop at the apex of the basidiome. FIGURES 6–8 show young developmental stages, the basidiomes not yet filled with spores. For the sake of clarity, only a few spores have been illustrated in FIG. 1. Basidiospores germinate by germ tube and these often fuse with other spores or germ tubes (FIGS. 11, 12). Often short hyphal outgrowths terminate by conidium production (FIG. 11).

The basidiomes examined always had conidiophores intermixed with basidia in the hymenium (FIGS. 1, 10). The presence of basidiospores and conidia is also proof of the simultaneous production of sexual and asexual propagules in the same sporocarps. The conidiogenous cells are unusual in that each produces a single conidium, *i.e.,* they are monoblastic (FIG. 9). During conidial development, as during that of basidiospores, cytoplasm empties from the sporogenous cell into the growing conidium. This type of conidial development also occurs in the basidiomycetous anamorph *Naiadella fluitans* Marvanová & Bandoni (Marvanová and Bandoni, **1987**).

Septa of *H. blepharistoma* hyphae have simple pores, the ontogeny of which has been studied in detail (FIGS. 21–30). Before reaching a minimum width of 0.06–0.08 µm, the septal pore consists of an unstructured opening in the centripetally growing septum (FIG. 21). In further development, electron-dense bodies occur on both sides of the pore (FIGS. 22–25). Such bodies are at first inconspicuous and 0.02–0.03 µm thick (FIG. 22); finally they are 0.06–0.08 µm thick (FIG. 25). These stages show mostly electron-transparent septal walls (FIGS. 21–25); only faint, electron-dense striations of wall material can be recognized (FIGS. 23, 24). Older developmental stages show thicker septal walls with multilayered electron-dense parts separated by a middle layer of electron-transparent material (FIGS. 28–

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FIGS. 13–19. Different stages of basidial development and spindle pole bodies (SPBs) in *Heterogastridium pycnidioideum.* 13. Young aseptate basidia (note nuclei and nucleoli) and associated conidiogenous cell bearing conidium (bar = 20 µm). 14, 15. Aseptate and young septate basidia, the latter with very young basidiospore initials (bars = 20 µm). 16–18. Basidia with attached basidiospores. Note correlation of vacuolation and basidial development (bars = 20 µm). 19, 20. Spindle pole bodies (SPBs) showing conspicuous middle piece and two marginal discs (bars = 0.2 µm). 19. Mitotic interphase SPB. 20. Prophase I SPB. 16. Nomarski interference contrast microscopy. 13–15, 17, 18. Phase contrast microscopy. 19–20. Transmission electron microscopy.
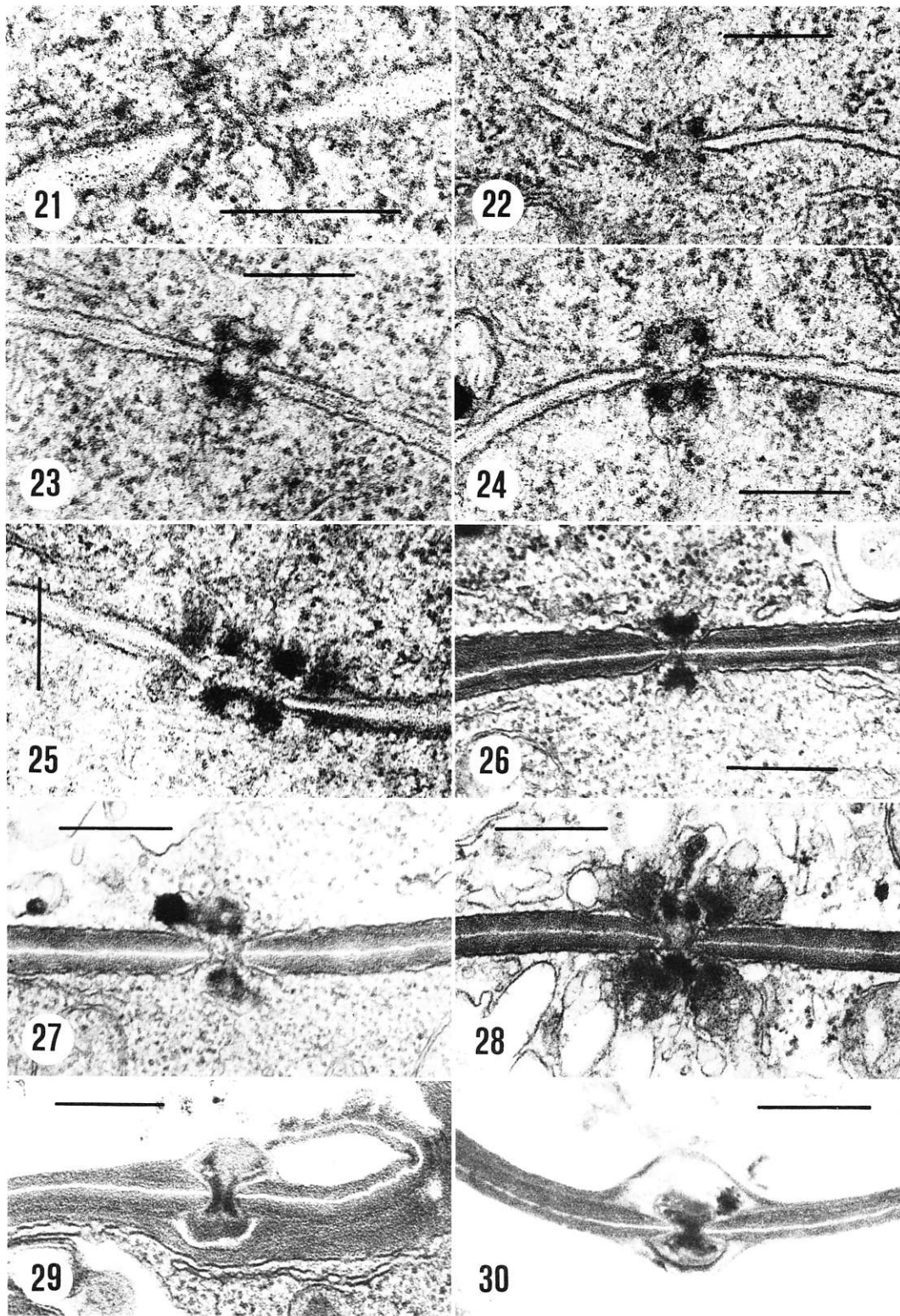
30). The electron-dense bodies fuse and occlude the septal pore. Final stages of cell aging may be recognized by large vacuoles and a thin layer of cytoplasm attached to the cell walls. The septal pores at this time are completely plugged with electron-dense material (FIGS. 29, 30) and the pore may be overgrown by additional wall layers (FIG. 29).

As viewed in longitudinal section, the interphase or prophase spindle pole body (SPB) consists of a conspicuous electron-dense middle part and two peripheral disc-like portions (FIGS. 19, 20). The discs are surrounded by electron-opaque material. The middle part is in close proximity to the nuclear envelope. Osmiophilic material is present close to the inner surface of the nuclear membrane, adjacent to the SPB.

TAXONOMY

The characteristics of the teleomorph of *Hyalopycnis blepharistoma* are unique, and they were not included in the descriptions of von Höhnel (**1918**) and Seeler (**1943**). A new genus, *Heterogastridium* Oberwinkler & Bauer, is therefore proposed to accommodate this unusual fungus.

Heterogastridium Oberwinkler and Bauer, *gen. nov.*

Genus Heterobasidiomycetum. Carposoma pycnidioideum, hyphis enodulosis parce nodulosi-septatis, distinctis, hyalinisque compositum. Septa hypharum simpliciter perforata sunt. Cystidia desunt. Basidia longa, mature transverse septata, sine sterigmatibus inde basidiosporae non modo sedentes etiam non eiectae sunt. Basidiosporae hyalinae, tenui-tunicatae, tunicis levibus, hyphas angustas germinando producunt. Plurimum fructificationibus pycnidioideis anamorphosium in cultura pura.
TYPUS GENERIS: *Heterogastridium pycnidioideum* Oberwinkler et Bauer, opus ipsum.

Heterogastridium pycnidioideum Oberwinkler and Bauer, *sp. nov.*

Fructificatio minuta, pycnidioidea, hyalina, 150–500 μm, raro ad 800 μm longa. Hyphae hyalinae, 2–3(–5) μm diam. Hyphae muri pycnidii 8–15(–20) μm diam. Basidia longi-cylindracea, 5–8 × 60–80 μm, mature transverse septata. Basidiosporae sedentes, tetraradiatae, raro pentaradiatae, 2–3 μm diam, ambitu 8–13 × 15–25 μm.
TYPUS: F. Oberwinkler 36439 (M).

DISCUSSION

Von Höhnel (**1918**) described two species of *Hyalopycnis, H. hyalina* and *H. vitrea,* but these were later considered to be identical (Seeler, **1943**). Seeler found that the species was identical to *Sphaeronema blepharistoma* Berk. The descriptions by both von Höhnel and Seeler clearly refer to fungi imperfecti, although Seeler illustrated two basidiospores and referred to these as "cruciform bud-spores." Bandoni and Oberwinkler (**1981**) described and illustrated the morphological characteristics of *H. blepharistoma* as seen by light microscopy and concluded that the dikaryotic hyphae, infrequent clamps, positive Diazonium Blue B, and chlamydospore development all indicated a basidiomycetous relationship. That assumption is now verified by basidial production in axenic culture.

Pycnidium-like pycnia or spermogonia are present as haploid developmental stages in the life histories of many Uredinales, some of which may resemble the "pycnidia" of *H. blepharistoma* morphologically. However, rust pycnia are haploid and are functionally different from pycnidia of the latter. Only a few basidiomycetes are known to produce dikaryotic pycnidioid sporocarps to date; they include *Fibulocoela indica* Nag Raj (Nag Raj, **1978**), *H. blepharistoma* (Bandoni and Oberwinkler, **1981**), *Ellula guaduae* (Viegas) Nag Raj (Nag Raj, **1980**), and *Mycaureola dilseae* Maire & Chemin (Porter and Farnham, **1986**). So far as is known, the only one of these taxa in which basidia develop in pycnidioid basidiomes is *H. blepharistoma. Heterogastridium pycnidioideum* and its anamorph, *H. blepharistoma,* have identical sporocarp wall morphologies and these differ sharply from the walls of all other pycnidioid basidiomycetes.

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FIGS. 21–30. Transmission electron micrographs showing septal pore ontogeny in *Heterogastridium pycnidioideum* (bars = 0.2 μm). 21. Early developmental stage without electron-dense bodies and the septal wall electron transparent. 22. Initial stage in development of the pore-associated electron-dense bodies. 23–25. Well developed electron-dense bodies, the septal wall electron-opaque. 26–28. Mature septal developmental stages, showing fusion of the electron-dense bodies and partial occlusion of the pore. Two electron-dense layers, separated by an inner electron-transparent layer, are visible in the septal wall. 29, 30. Old septa with completely occluded pores and with additional wall layers deposited on one side of the pore in FIG. 29 and on both sides in FIG. 30.

The stilboid, gastero-auricularioid heterobasidiomycetes were surveyed by Oberwinkler and Bandoni (**1982a**) and an order, Atractiellales, was proposed to accommodate the group. Species in the Atractiellales mostly have synnemata-like basidiomes and transversely septate basidia; aseptate clavate basidia are characteristic of *Pachnocybe* and *Chionosphaera* species. The basidiospores in this group are generally sessile, although those of *Stilbum vulgare* are briefly pedicellate. Basidial cells in species of *Agaricostilbum* and *Atractogloea* bud off numerous basidiospores; single basidiospores are produced by basidial cells in species of *Atractiella, Stilbum,* and *Phleogena* (Oberwinkler and Bandoni, **1982a, b**), as in *H. pycnidioideum*. These taxa differ markedly from *H. pycnidioideum* in numerous other features. However, there may be a parallel in spore dispersal between the two groups. Some gasteroid auricularioid taxa, *e.g.,* species of *Atractiella* and *Stilbum* resemble the "stalked spore drops" discussed by Ingold (Ingold, **1961**); in *H. pycnidioideum,* propagules also accumulate in the apical slime drop. It is likely that either arthropods or water (or both) are responsible for dispersal of spores in both groups.

Tetraradiate basidiospores occur in some basidiomycetes, *e.g.,* in *Digitatispora marina* Doguet and *Nia vibrissa* Moore and Meyers. In *D. marina* the basidia are not enclosed in pycnidioid basidiomes (Doguet, **1962**). Basidiospores of *Nia vibrissa* are predominantly 5-radiate (Doguet, **1967**), the thread-like branches originating from a swollen central body. Conidia of remarkably similar form have been described for *Cyrenella elegans* Gochenaur, a dikaryotic basidiomycetous anamorph (Gochenaur, **1981**). All of these morphologically unusual propagules can be considered as adaptations for water dispersal. *Heterogastridium blepharistoma* has been collected on various types of decaying plant material and mushrooms; isolates from Louisiana were found on oak litter that regularly is washed about by heavy rain during thunderstorms. Although the circumstances under which the *Heterogastridium* state develops are unknown to us at this time, dispersal of the basidiospores can be expected to be by water.

Heterogastridium blepharistoma hyphae were reported to have mostly binucleate compartments and simple septa (Bandoni and Oberwinkler, **1981**). Binucleate compartments have also been seen in TEM studies. Clamps are infrequent, varying with the strain and stage of development, *i.e.,* they are most commonly present in germ hyphae emanating from chlamydospores. Hyphae with clamps are not common in gasteroid heterobasidiomycetes, but they do occur in species of *Phleogena* and *Atractogloea* (Oberwinkler and Bandoni, **1982a, b**). Clamps are also present in some unstudied *Pachnocybe*—like Asian species of gasteroid heterobasidiomycetes (unpubl. obs.).

Heterogastridium pycnidioideum has simple septal pores as characteristic in the majority of gasteroid auricularioid heterobasidiomycetes (Oberwinkler and Bandoni, **1982a**) and, in fact, of most auricularioid fungi (Oberwinkler, **1985**). Species of the genera *Auricularia* (Sebald, **1977**; Moore, **1978**; Patton and Marchant, **1978**; Tu and Kimbrough, **1978**; McLaughlin, **1980**) and *Mylittopsis* (Oberwinkler, **1985**) are the only known auricularioid fungi with dolipore septa and parenthesomes. The ontogeny of *H. pycnidioideum* septal pores was studied in detail (FIGS. 21–30). It is difficult to compare these with other auricularioid fungi, since few species have been examined in detail. The periphery of the electron-dense bodies which develop adjacent to the septal pore (FIGS. 22–25) is not sharply delimited from the cytoplasm and the bodies thus appear to be distinct from Woronin bodies of Ascomycetes. Pore occlusions in mature and old septa (FIGS. 26–30) resemble those illustrated and described as "pulley wheel plugs" in certain rusts (reviewed by Littlefield and Heath, **1979**). There is also some resemblance at one stage of development of *H. pycnidioideum* pore plugs (FIG. 27) to those of the simple-pored, auricularioid fungus, *Helicobasidium mompa* Tanaka, as illustrated by Bourett and McLaughlin (**1986**, Fig. 21).

Nuclear division was not studied in detail in this investigation of *H. pycnidioideum*. However, interphase and prophase SPBs are illustrated (FIGS. 19, 20) to document structural similarities with those in *H. mompa* (Bourett and McLaughlin, **1986**). SPBs with discs are characteristic of species of the Uredinales (Heath, **1980**; O'Donnell and McLaughlin, **1981**; Hoch and Staples, **1983**; Bauer, **1987**). Additional studies of mitotic and meiotic nuclear divisions are required for a more substantial comparison of SPB developmental stages in different heterobasidiomycetous taxa.

The unique features of *H. pycnidioideum* clear-

ly indicate separation of the taxon from other auricularioid fungi. The species cannot be accommodated in any of the currently recognized families and orders of such fungi. Therefore, a new family and order are proposed for this species, as follows:

Heterogastridiaceae Oberwinkler and Bauer, *fam. nov.*

Heterobasidiomycetes fructificationibus pycnidioideis, meiosporangiis transverse septatis, Gasteromycetum modo basidiosporis non eiectis. Basidiosporae triangulares. Plerumque status anamorphosium in pycnidiis praesens est.

TYPUS FAMILIAE: *Heterogastridium* Oberwinkler et Bauer, opus ipsum.

Heterogastridiales Oberwinkler and Bauer, *ord. nov.*

Descriptio eadem familiae Heterogastridiacearum.
TYPUS ORDINIS: Heterogastridiaceae Oberwinkler et Bauer, opus ipsum.

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