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A NOVEL NEW SPECIES OF *SYNCEPHALIS*
(ZOOAGALES: PIPTOCEPHALIDACEAE) FROM CALIFORNIA
THAT FORMS HYPOGENOUS MEROSPORANGIA

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ABSTRACT

Syncephalis hypogena, a new species isolated from soil collected in southern California is described from cultures on *Mortierella bisporalis*. Salient features of its vegetative development and reproduction, both sexual and asexual, are illustrated with photographs and line drawings. The species is distinguished from all other members of the genus in typically producing merosporangia from the lower rather than the upper hemisphere of the terminal ampulla of the sporangiophore.

Key words: merosporangium, Mucorales, mycoparasite, Piptocephalidaceae, *Syncephalis*, Zoopagales, Zygomycetes, zygosporangium.

INTRODUCTION

Species of *Syncephalis* van Tiegh. & Le Monn. (1873) are a common element of the fungal biota of soil and dung where, along with species of *Piptocephalis* de Bary (1865), they develop as haustorial parasites of other fungi, mostly species of Mucorales. These genera have long constituted a separate family, Piptocephalidaceae (Schroeter 1893; Migula 1910; Fitzpatrick 1930), which has been included in the Mucorales (Benjamin 1959; Hesseltine 1955; Zycha, Siepmann, and Linnemann 1969; Hesseltine and Ellis 1973). In their mode of parasitism, vegetative development, and fruiting structures, both sexual and asexual, Piptocephalidaceae correspond in many ways with Zoopagaceae, predacious members of the Zoopagales (Duddington 1973). This resemblance led Kreisel (1969) to transfer the Piptocephalidaceae to that order, and this disposition of the family along with Cochlonemataceae, Helicocephalidaceae, and Zoopagaceae is adopted here (Benjamin 1979;¹ Hawksworth, Sutton, and Ainsworth 1983).

The most recent addition to *Syncephalis*, *S. leadbeateri* Bawcutt (1983), increased the number of named taxa in the genus to 46, not including *S. tranzschelii* Naumov (1935) which was not validly described in accordance with Art. 36 of the ICBN (Voss 1983). Zycha, Siepmann, and Linnemann, in 1969, recognized 26 species (including *S. tranzschelii*) and treated 37 of the 38 taxa ascribed to the genus up to that time. They did not mention *S. viridis* Faurel & Schotter (1965). *Syncephalis tenuis* Thaxter (1897) was included in the Dimargaritaceae as *Spinalia tenuis* (Thaxt.) Zycha (1935). Subsequent to 1969, eight additional species have been described: *S. annularis* Kuzuha (1973), *S. basibulbosa* Kuzuha (1973), *S. californica* Hunter & Butler (1975), *S. indica* Singh & Sarbhoy (1976), *S. leadbeateri*, *S. rosetta* Prasad & Mehrotra (1979), *S. vivipara* Mehrotra & Prasad (1970); and *S. trispora* Mehrotra & Prasad (1967). In 1979, Skirgiello and Zadara transferred *Acephalis radiata* Badura & Badurowa (1964) to *Syncephalis*, but their brief account of the taxon, like that of Badura and Badurowa, did not provide a

really adequate basis for evaluating the true position of this fungus in the Pip-tocephalidaceae.

Five genera that have not been generally accepted (Benjamin 1966) have been based on species of *Syncephalis*. Bainier (1882) proposed but did not formally describe three segregate genera, *Calvocephalis*, *Microcephalis*, and *Monocephalis*. Boedijn (1959) established *Syncephalopsis* based on *Syncephalis bispora* Raciborski (1909), and Badura (1963) described a new genus and species, *Syncephalidium penicillatum*, based on what doubtless was a collection of *Syncephalis depressa* van Tiegh. & Le Monn. (1873).

Not all species of *Syncephalis* have been described and illustrated with the precision needed to evaluate them from the literature alone, and there still is uncertainty regarding the status of some and the possible synonymy of others (Benjamin 1959; Bawcutt 1983). Two taxa, *S. viridis* and *S. ubatubensis* Viegas & Teixeira (1943), can definitely be eliminated on the basis of their published descriptions and illustrations. *Syncephalis viridis* was said by its authors to be a saprobe giving rise to sporophores forming elongate terminal ampullae bearing fusiform sterigmata producing chains of globoid conidia. The description and illustrations of *S. viridis* given by Faurel and Schotter (1965) were doubtless based on a species of *Aspergillus*, possibly *A. giganteus* Wehmer. *Syncephalis ubatubensis* was found on a dead insect attached to a leaf of *Psidium guajava* L. (Myrtaceae) in Brazil. This taxon, as described and illustrated by its authors, most certainly is a hyphomycete belonging to the genus *Gibellula* (compare with Morris 1963: 58 & Pl. XXIII; Carmichael, Kendrick, Connors, and Sigler 1980: 96 & Pl. 10D; and Kendrick and Carmichael 1973: Pl. 8C).

Syncephalis species, for the most part, are relatively small and inconspicuous. They are easily overlooked during routine examinations of cultures of dung or soil—unless one is specifically looking for them. Spores of the parasite that have germinated in the presence of a suitable host give rise to a germ mycelium of limited extent, which forms simple appressoria that penetrate the host wall and from which arise often branched, myceliumlike haustoria. Once haustoria have become established in the host, hyphae of the germ mycelium and haustoria give rise to cobweblike aerial hyphae that eventually become highly branched and anastomosed. These aerial hyphae form lobate appressoria from which arise haustoria that establish secondary sites of infection. Eventually, the aerial hyphae give rise to sporangiophores and, in some species, zygospores. The usually simple sporangiophores arise from a branched system of short rhizoids that may attach to any convenient surface or object. A terminal globoid or turbinate ampulla is formed by the sporophore and gives rise to a small or large number of few- to many-spored merosporangia. When mature, the merosporangia disarticulate and the head of spores typically is enveloped in a drop of liquid.

Taxonomy of *Syncephalis* is based on the nature of the sporangiophore and the merosporangium. The sporophore in most species is more or less erect and straight or only slightly curved. In a few species, however, it is strongly recurved distally, e.g., *S. adunca* Vuillemin (1903), *S. californica*, *S. cornu* van Tiegh. & Le Monn. (1873), and *S. reflexa* van Tiegh. (1878). The base of the stalk typically may be only slightly broader than the apex, although in a few species it is much swollen, i.e., *S. basibulbosa* and *S. ventricosa* van Tiegh. (1875). In *S. adunca* and *S. cornu*, on the other hand, the distal part of the reflexed stalk is conspicuously enlarged.

In all but two of the described species of *Syncephalis*, the merosporangia arise directly or indirectly (via so-called "secondary sporophores" [Thaxter 1897]) from the upper hemisphere of the ampulla and are more or less evenly spaced over its surface, even in most species having strongly recurved stalks. In several species, e.g., *S. annularis* and *S. depressa*, the sporangia are disposed in a marginal ring which encircles the barren upper surface. In *S. plumigaleata* Embree (1965) the complement of merosporangia develops somewhat unilaterally on the ampulla, and a similar kind of asymmetry is found also in *S. reflexa* (van Tiegh. 1875; Thaxter 1897).

The purpose of this paper is to describe a distinctive species of *Syncephalis* collected in southern California which differs from all others yet known in typically producing merosporangia from the lower rather than the upper or lateral surface of the ampulla. Salient features of the sexual as well as the asexual characteristics of the new species also will be discussed.

MATERIALS AND METHODS

The new *Syncephalis* was first isolated in September, 1965, from soil collected beneath an aged *Quercus agrifolia* Neé growing in a small tract of undeveloped land east of the Rancho Santa Ana Botanic Garden. It was maintained in dual culture on *Mortierella bisporalis* (Thaxt.) Björling (*RSA 1588*) on YpSs agar (Emerson 1940) for several years, but eventually it died. Subsequently, it appeared in cultures of soil collected at the same site in June, 1976, and February, 1977. It was isolated again from the latter soil collection, and it has been carried in culture on *M. bisporalis* on YpSs since that time. During many years of isolating *Syncephalis* spp. from soil, I have not encountered the new species elsewhere.

The fungus was isolated by means of a technique that I have long employed for recovering not only *Syncephalis* but also many other kinds of soil or dung-inhabiting fungi. A small quantity of soil was scattered on the surface of wheat germ agar (WG: 10 g of wheat germ cooked in 800 ml of water for 10 min, filtered, brought to 1 liter; 1 g of dextrose; 15 g of agar) in a Petri dish and observed daily for the appearance of the characteristic glistening spore drops of *Syncephalis* spp., which are easily recognized by the experienced eye. Spores were gathered by carefully touching the tip of a flamed stainless steel minuten needle held in a pin vice to a head of spores. The spores then were transferred to a premarked spot on a plate of YpSs agar. A succession of transfers was effected from separate heads until four or five spot inoculations had been made on each of several plates. A small bit of inoculum from a culture of the host was added to each point of inoculation, and those which, in a day or two, evidenced no contamination with bacteria or unwanted fungi were cut out and transferred to YpSs slants in test tubes. Successful isolation of the *Syncephalis* was indicated in about a week by the appearance of sporangiophores developing from mycelium that had contacted the walls of the test tube.

Mortierella bisporalis is the only host of several fungi tested, including *Cunninghamella elegans* Lendner, *Mucor hiemalis* Wehmer, and *M. ramannianus* Möller, that has supported growth of the new species in culture, but a definitive study of the host range of the parasite has not been carried out. This host has proved ideal, at least under the cultural conditions employed, in providing a

substrate of low profile well suited to the manipulation and observation of mounts needed for examining, photographing, and drawing the parasite. Luxuriant growth of the host was inhibited by reducing the concentration of nutrients used in Emerson's original formula for YpSs agar. The medium used, termed YpSs/5, had the following composition: water, 1 liter; K_2HPO_4 , 0.5 g; KH_2PO_4 , 0.5 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; yeast extract, 0.8 g; soluble starch, 3 g; agar 15 g.

Colonies of host and parasite were established on small squares (ca. 1–1.5 cm²) of sterile cellophane on agar in Petri dishes. These were then removed and mounted as needed to monitor spore germination, mycelial development, and the formation of haustoria, sporangiophores, and zygospores of the parasite. A cellophane square was lifted from the agar, and the culture was transferred to the appropriate mounting medium. A cover slip was added directly or after the colony had been carefully floated off the cellophane into the mounting medium. Living material was observed in dilute salts solution (DS) (0.001 M KH_2PO_4 ; 0.0001 M $MgCl_2$; 0.00002 M $CaCl_2$; KOH to pH 7 [Emerson 1958: 593; Machlis 1953: 190]). Stained whole mounts were prepared in 2% KOH containing a trace of phloxine or in lactophenol-trypan blue after fixation in 65% acetic acid. Nuclei were well stained and easily counted by means of the following simple procedure carried out at room temperature: cultures on cellophane membranes were fixed for 10 min in Schaudinn's fluid (saturated aqueous solution of $HgCl_2$, 20 cc; absolute alcohol, 10 cc; glacial acetic acid, 3–4 drops); washed in water; hydrolyzed in 5 N HCl for 10 min; washed in water; stained in a saturated aqueous solution of basic fuchsin (Matheson Coleman & Bell) for 10–20 min; washed three times in water and mounted in water. Preparations were sealed with a 50:50 mixture of beeswax and paraffin and then ringed with nail polish.

Spores to be measured or photographed were mounted in DS on thin films of 2% water agar on slides to prevent Brownian movement.

Drawings were prepared with the aid of a camera lucida on a Leitz Dialux microscope equipped with differential interference contrast optics. The same microscope was used for preparing photographs which were taken on 4 × 5 in. Kodak Technical Pan Film #2415. Film was developed in Kodak D19 or in Kodak HC-110.

DESCRIPTION

Syncephalis hypogena R. K. Benjamin, sp. nov.

Sporangiophora laevia hyalina vel luteola, (30–)40–100(–110) μm alta, ex rhizoideis brevibus ramosis robustis enata. Stipes rectus vel aliquando curvatus, apicem versus deminutus, basi 6–12 μm latus, apice 3–6 μm latus. Ampulla globosa vel subglobosa, (14–)18–32(–36) μm in diametro; 20–50 merosporangia ex hemisphaerio inferno parientia. Merosporangia 1 sporam oblongam-ellipticam, 15–20 × 5–6 μm , vel 2 sporas oblongas, 8–13 × 5–6 μm , formantia. Sporangiosporae laeves hyalinae in massa luteolae. Murus merosporangii persistens rugulosus. Ampulla et sporae in guttula liquidi ad maturitatem inclusa. Zygosporae globosae vel aliquando ovoideae, 19–30 μm in diametro; murus exosporae grosse aculeatus-verrucatus dilute brunneolus, ca. 2–3 μm crassus; murus endosporae laevis incoloratis, ca. 2–2.5 μm crassus; endospora cum 1 globulo 10–16 μm in diametro. Suspensores appositi laeves inaequales; suspensor grandis infra vestigium gametangii vesiculas simplices vel ramosas facientia; suspensor parvus septatus tipice sine vesiculis. Typus in herbario RSA (1618).

Sporangiophores smooth, hyaline to pale yellow, usually arising singly from a complex of short, branched, robust rhizoids, (30–)40–100(–110) μm high, 6–12

μm wide at the base, tapering gradually to 3–6 μm wide immediately below the ampulla. Ampulla globose to subglobose, (14–)18–32(–36) μm in diam, producing 20–50 merosporangia from its lower hemisphere, these surrounding the distal part of the stalk. Merosporangia containing only one oblong-elliptical spore, 15–20 \times 5–6 μm , or two oblong spores of variable length, 8–13 \times 5–6 μm . Sporangiospores smooth, hyaline, yellowish in mass. Merosporangial wall persistent, surrounding the spore or spores in part and forming a rugulose envelope. Ampulla and spores immersed in a liquid droplet at maturity. Zygosporangia globose to slightly ovoid, 19–30 μm in diam; the exospore wall coarsely aculeate- verrucate, pale brown, ca. 2–3 μm thick; the endospore wall smooth, colorless, ca. 2–2.5 μm thick; endospore containing a single globule 10–16 μm in diam. Suspensors apposed, smooth, unequal, the larger always forming simple or branched vesicles below a well-defined gametangial remnant which subtends the zygosporangium; the smaller typically septate and lacking vesicles, its gametangial remnant inserted laterally on the zygosporangium.

Holotype.—A dried culture (host *Mortierella bisporalis*) in the Mycological Collections of the Rancho Santa Ana Botanic Garden (RSA 1618). Isolated from soil collected 4 Feb. 1977, Claremont, Calif., U.S.A. Cultures have been deposited at the American Type Culture Collection, Rockville, MD (ATCC); Commonwealth Mycological Institute, Kew, Surrey, England (IMI), and Northern Regional Research Center, Peoria, IL (NRRL).

Etymology.—Gr. *hypo*:- under, below + Gr. *-genes*, born or produced in a certain place.

OBSERVATIONS AND DISCUSSION

Sporangiospores of *Syncephalis hypogena* vary considerably in length depending on whether or not they develop in one- or two-spored merosporangia (Fig. 1, 17, 18). Spores formed in two-spored sporangia may be nearly equal or markedly unequal in length. Mature spores are multinucleate (Fig. 2); the number of nuclei ranging from as few as four in the smallest spores to as many as 12 in the largest. Nuclei in spores of intermediate or large size typically are separated into two nearly equal groups, one near each end of the spore (Fig. 2).

In the absence of a host, a high but variable percentage of spores of *S. hypogena* germinate on YpSs/5 at 20 C. In one sample of 115 spores surveyed, 57 (49.6%) had germinated after 41 h, whereas in another sample of 206 spores only 60 (29%) had germinated after 68 h. As in other species of *Syncephalis* where spore germination has been described, the spore swells to about 1.5–2 times its original dimensions and gives rise to a single germ hypha at one or both poles (Fig. 3) (Bawcutt 1983; Benjamin 1959; Embree 1965; Hunter and Butler 1975; Indoh 1962; Kuzuha 1973). A branched germ mycelium of limited extent develops in the absence of a host, but the longest hyphae seldom exceed 200–300 μm before growth ceases.

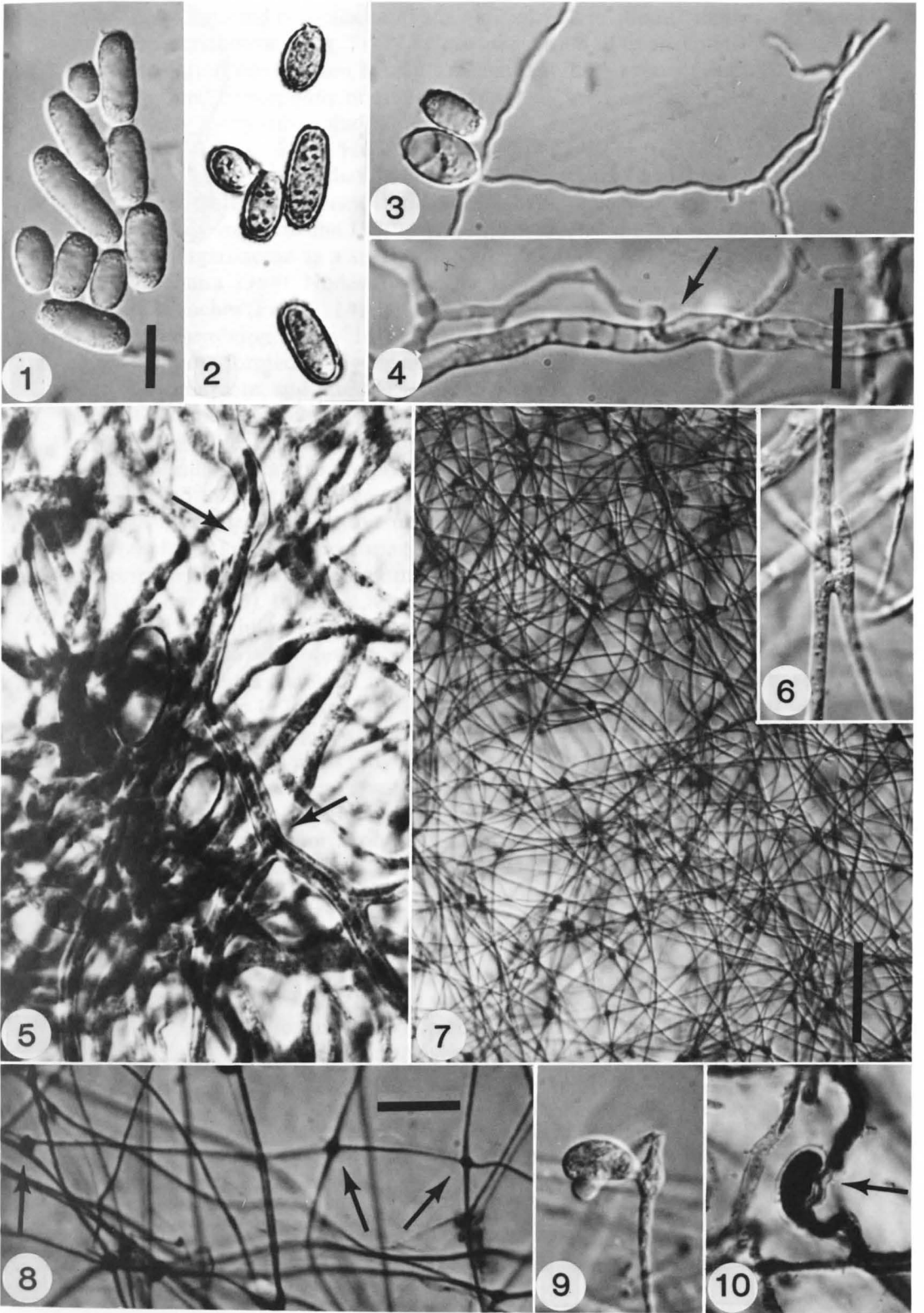
Spores of *S. hypogena* sown in the presence of *M. bisporalis* germinate within 16–24 h. In a sample of 156 scattered spores selected randomly, 99 (63%) had germinated within 17 h. Clusters of spores, representing those of heads of spores transferred in toto, had nearly all germinated, suggesting a possible stimulatory effect on one another of spores thus closely associated. The germ tubes become

more or less irregularly branched, the laterals often arising nearly at right angles to the parent hypha. Hyphae of the germ mycelium vary somewhat irregularly in width throughout their length, but are slender and ca. 1–2 μm wide. Infection of the host begins with the formation of a smallish, often only slightly enlarged, appressorium from which an at first simple haustorium arises (Fig. 4). Lobate appressoria like those developed later on the aerial vegetative hyphae are not formed by branches of the germ mycelium. The infective, intracellular hyphae rapidly invade the host and form a branched mycelium which corresponds to the branching pattern of the host (Fig. 5). Because the vegetative hyphae of *M. bisporalis* are relatively slender it was nearly impossible to trace the course of the infective mycelium within them except in stained preparations. Intracellular parasitic hyphae have a slightly greater width than hyphae comprising the germ mycelium and aerial vegetative mycelium.

Once haustoria of *S. hypogena* have been established within the host, aerial vegetative mycelium, very different from the germ mycelium, begins to develop. Hyphae of the germ mycelium, now nourished by the host, give rise to branches remarkably uniform in width, 0.5–1 μm , which elongate rapidly and extend over the substrate and into the air without themselves at first forming lateral branches. It is likely that these branches also arise from intracellular hyphae which penetrate the host cell wall (Bawcutt 1983), but because of the nature of the host used in this study I did not observe this in any of my preparations. During the course of their early development, one often can track these hyphae for considerable distances in stained preparations of cultures grown on cellophane membranes. In one instance I followed a single unbranched hypha for 1.15 cm before losing it in the confusion of other hyphae. This hypha had formed a single anastomosis with another hypha some 820 μm from its point of origin. Within two to three days in cultures where multiple infections of the host have taken place, more or less large numbers of these stolonlike, multinucleate, coenocytic aerial hyphae can be found crisscrossing one another. Where they come into contact, these hyphae appear always to anastomose (Fig. 6, 11, 12), and one hypha may anastomose with several other hyphae (Fig. 8). The number of anastomoses a hypha can make with other hyphae probably is limited only by the number of chance hyphal encounters. Within 5 or 6 days, the aerial vegetative mycelium consists

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Fig. 1–10. *Syncephalis hypogena*. All photographs are of living material unless otherwise indicated.—1. Sporangiospores after disarticulation of merosporangia.—2. Sporangiospores showing multinucleate condition (basic fuchsin).—3. Two sporangiospores, one germinating and showing polar origin of germination hypha.—4. Branch of germ mycelium that has contacted a host hypha and formed a small appressorium and haustorium (arrow).—5. Region around two germinated spores showing branched infective mycelium growing within host hyphae (arrows) (lactophenol-trypan blue).—6. Aerial vegetative hyphae showing anastomosis of two hyphae as seen in lateral view.—7. Crisscrossing aerial vegetative mycelium showing nodes resulting from frequent anastomoses (lactophenol-trypan blue).—8. Hypha of aerial vegetative mycelium crossing field of view in upper center has anastomosed with three other hyphae (arrows) (lactophenol-trypan blue).—9. Lobate appressorium arising laterally from an aerial vegetative hypha.—10. Lateral view of an appressorium showing two oppositely directed haustorial branches in a host hypha (arrow) (lactophenol-trypan blue). (Fig. 1–3, 5, 6, 9, 10, bar with Fig. 1 = 10 μm [$\times 1000$]); Fig. 4, bar = 10 μm [$\times 1600$]); Fig. 7, bar = 40 μm [$\times 400$]); Fig. 8, bar = 20 μm [$\times 650$].)



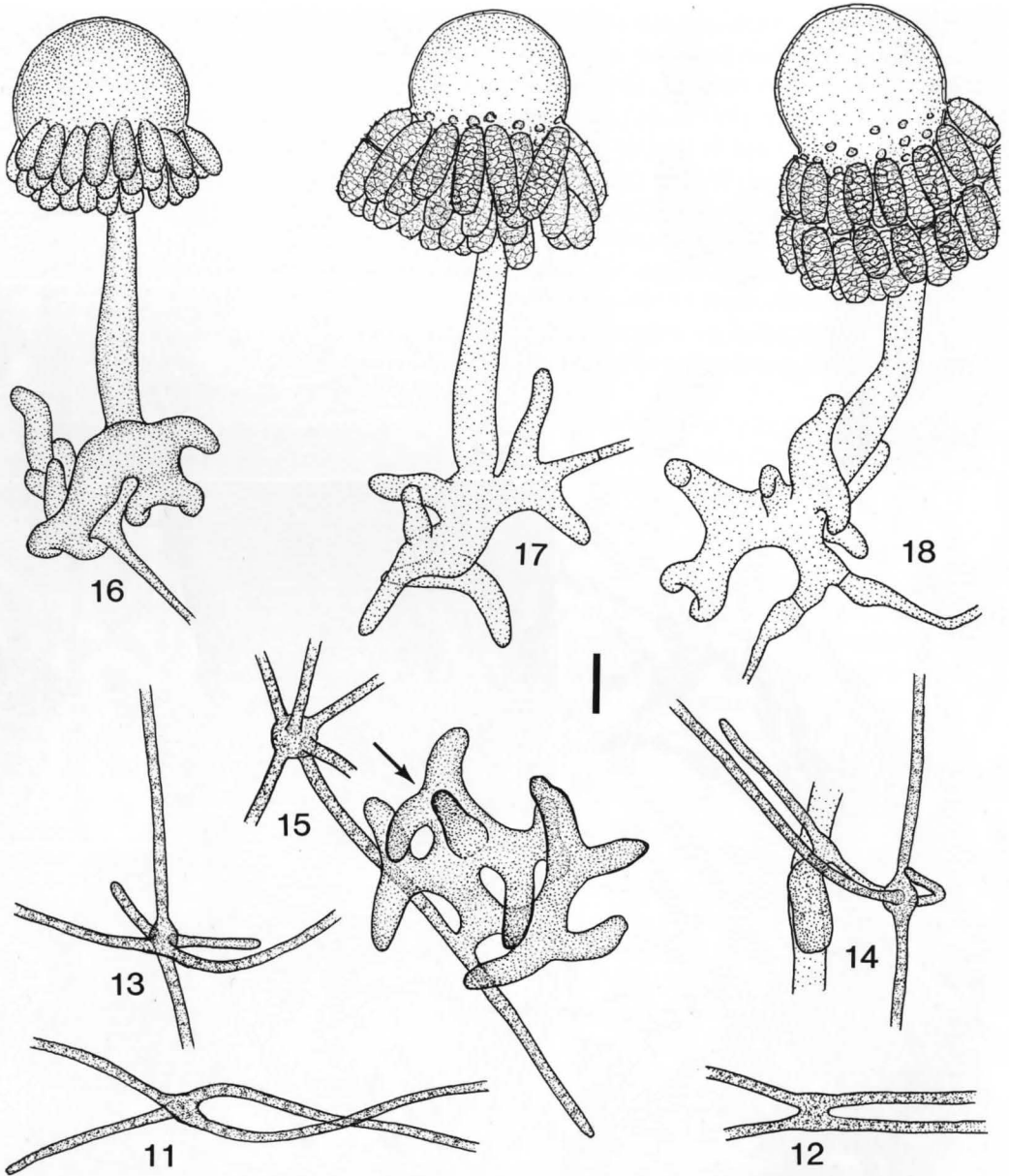


Fig. 11–18. *Syncephalis hypogena*.—11. Hyphal anastomosis as viewed from above.—12. Lateral view of a hyphal anastomosis.—13. The hypha stretching from left to right has anastomosed with the one stretching up and down; the resulting node is giving rise to two secondary branches.—14. Appressorium forming from one of two secondary hyphae that have arisen from a node developed following the head-on anastomosis of one vegetative aerial hypha with another hypha.—15. Rhizoidal system that has formed laterally on a hypha emanating from the node above and to the left. The sporophore stalk is beginning to develop (arrow).—16. Fully developed sporophore showing young merosporangia arising from the lower hemisphere of the ampulla.—17–18. Mature sporophores showing merosporangia that are beginning to separate from the ampulla. One shows mostly one-spored merosporangia, the other two-spored merosporangia. (All figures, bar = 10 μm [$\times 825$].)

of an interconnected complex of hyphae joined to one another at a multitude of points by anastomoses (Fig. 7). The close association of hyphal anastomoses and nodal formation was stressed by van Tieghem and Le Monnier (1873: 378) when they described *Syncephalis* originally, and it has been noted or illustrated subsequently by many other students of the genus (Bawcutt 1983; Benjamin 1959; Dade 1937; Embree 1965; Hunter and Butler 1975; Thaxter 1897). Formation of nodes is a phenomenon that distinguishes *Syncephalis* species from other haustorial zygomycetes, and it is a characteristic of *S. tenuis*—in addition to its distinctive zygospores (Kuzuha 1980)—that argues against the transfer of this species to the Dimargaritaceae as a species of *Spinalia* (Zycha 1935; Zycha, Siepmann, and Linnemann 1969). Nodes formed by hyphal anastomoses often give rise to ordinary branches (Fig. 13, 14), but branches also form from small spindle-shaped swellings resembling nodes. In older cultures, however, the more conspicuous nodes are those formed following anastomoses. These often are 4–8 μm or more wide, multinucleate, and more or less globoid or irregular in shape due to development of tapered extensions of their component hyphae. In age, they may be separated by adventitious septa from one or more of their attached but moribund hyphae. Similar septa also are present in ageing or dead hyphae.

Within 2.5 to 3 days, hyphae of the aerial vegetative mycelium of *S. hypogena* establish new sites of infection upon contacting the host by the formation of relatively large, lobate appressoria (Fig. 9, 10, 14) of the kind commonly observed in species of *Syncephalis* (Benjamin 1959; Embree 1965; Hunter and Butler 1975; van Tieghem 1875). Infective hyphae penetrate the host wall (Fig. 10) and form an internal mycelium like that established earlier by the germ mycelium.

Sporangiophore development in *S. hypogena* is similar to that reported in other species of the genus (Bawcutt 1983; Benjamin 1959; Dade 1937; Embree 1965; Hunter and Butler 1975; Indoh 1962; van Tieghem 1875; van Tieghem and Le Monnier 1873). Sporangiphore initials may appear within 2.5 days, but they usually are really numerous only after 4 or 5 days. Within 5 or 6 days sporangiophores with mature merosporangia may be present in small or large numbers. Development of a sporangiophore is signaled by the formation of a compact rhizoidlike system of short, robust, dichotomous branches (Fig. 15, 19) which arise terminally or laterally on the aerial vegetative hyphae. As sporangiophores mature, these rhizoidal complexes may remain free, but they more commonly encircle or adhere to neighboring objects which they have fortuitously contacted (Fig. 21), usually their own or host hyphae, or the wall of the culture chamber.

In most instances, a single sporangiophore arises from near the center of each rhizoidal system (Fig. 15, 19). The stalk elongates to its ultimate length then enlarges distally and forms a nearly globose ampulla from which 20 to perhaps 50 merosporangia, depending on the size of the ampulla, bud out from the lower surface (Fig. 16, 20). As these elongate (Fig. 21) and mature, they form a pendant aggregate encircling the upper end of the stalk (Fig. 17, 18, 22). This pattern of development is typical of the species, for it characterizes all of the larger, well-formed sporophores. However, rhizoidal systems giving rise to two or even three smallish sporangiophores are not uncommon. These sporangiophores are mostly more or less aberrant in that they often produce a small number of merosporangia which may arise on one side only or even on the upper surface of the ampulla. Spores produced in merosporangia formed on depauperate sporangiophores ap-

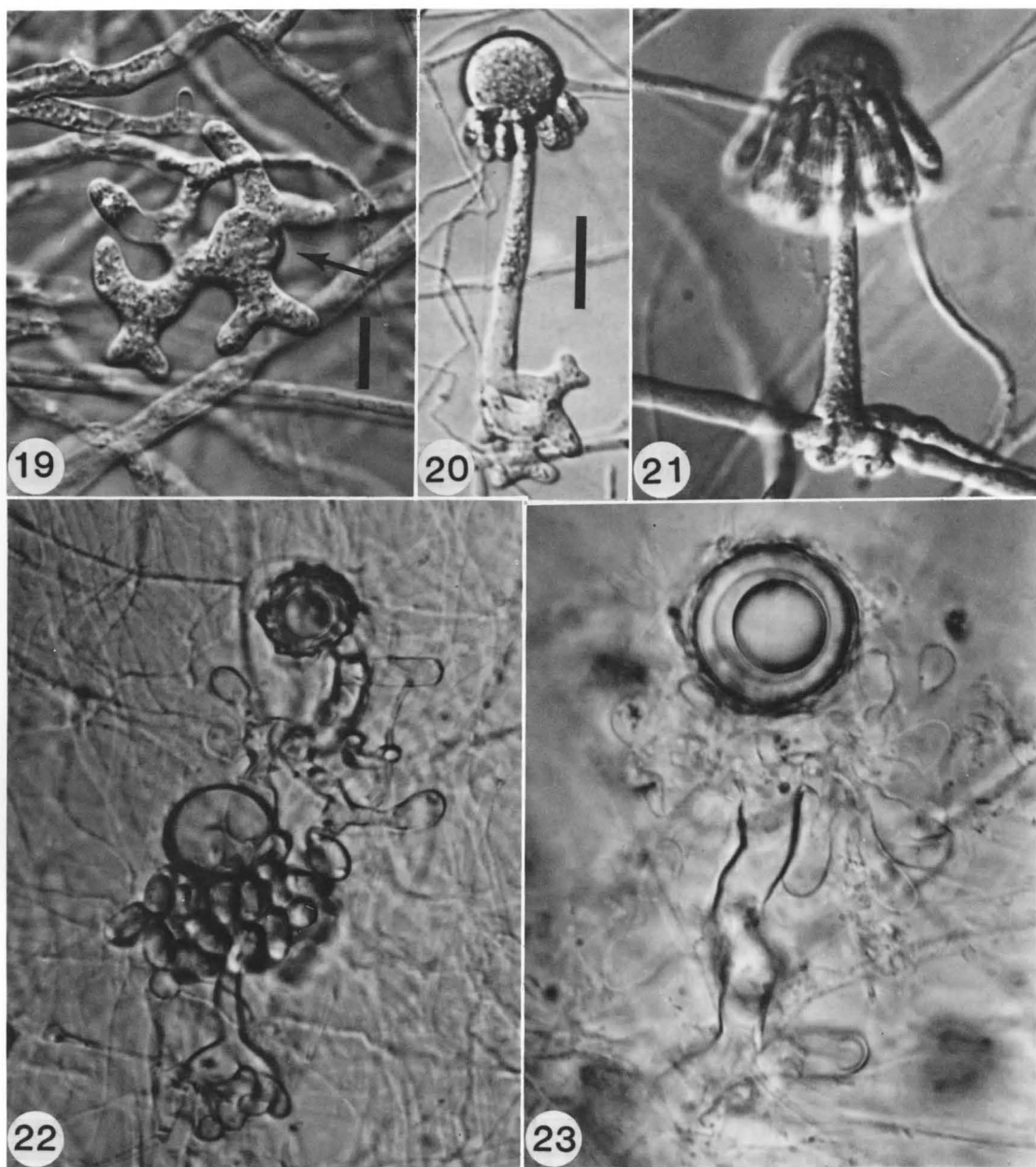


Fig. 19–23. *Syncephalis hypogena*. All photographs are of living material unless otherwise indicated.—19. Fully developed rhizoidal system from which a young sporangiophore is just beginning to emerge (arrow).—20. Young sporangiophore in lateral view showing basal rhizoids and immature merosporangia arising from lower surface of ampulla (KOH-phloxine).—21. Nearly mature sporangiophore in lateral view showing basal rhizoids clamped to a host hypha, and the complement of elongate merosporangia surrounding the upper end of the stalk (KOH-phloxine).—22. Mature sporangiophore below and mature zygospore above.—23. Mature zygospore as seen in optical section showing thick-walled endospore containing a single refractive globule. (Fig. 19, 23, bar with Fig. 19 = 10 μm [$\times 1000$]; Fig. 20–22, bar with Fig. 20 = 20 μm [$\times 650$].)

pear to be similar in all respects to those of typical sporophores, showing no cytological evidence of abnormality.

Delimitation of spores within the merosporangium of *S. hypogena* appears not to be fundamentally different from that of other species in which the process has been described (Baker, Hooper, and Beneke 1977; Bawcutt 1983; Benjamin 1966, 1979; Thaxter 1897). The developing sporangiophore and ampulla contain a large, essentially indeterminate number of small nuclei prior to merosporangial initiation. I could not decide if the several nuclei present in elongating merosporangia had entered progressively from the ampulla or were the products of division of one nucleus that had entered the merosporangial bud. In any event, the merosporangium, prior to spore formation, contains as many as 10–12 nuclei and these, as mentioned above, account for the variable number of nuclei found in mature spores. The nuclear cycle accompanying spore formation in *S. hypogena* appears to be the same as reported earlier for *S. nodosa* van Tiegh. (Benjamin 1966). In merosporangia forming two spores, the cytoplasm becomes constricted between the two presumptive spores, forming an isthmus bordered by a distinct “intermediary zone” inside the merosporangial wall like that described originally by Thaxter (1897) for an unnamed species of *Syncephalis* and observed subsequently in other species (Benjamin 1959, 1966; Bawcutt 1983). The wall at the tip of the developing merosporangium, even in those containing a single spore, is separated from the presumptive spore below by a small nonstainable zone immediately beneath a stainable terminal cap. Each merosporangium is subtended by a small, rounded ampullar projection from which it dehisces at maturity. Mature spores are separated from one another by circumscissile rupture of the merosporangial wall, which persists as a somewhat rugulose, close-fitting outer membrane.

Sporangiophores bearing only two-spored merosporangia and those with a mix of two-spored and one-spored sporangiola appear to be formed in about equal proportion. Those having only one-spored sporangiola are present in far fewer numbers, perhaps one sporangiophore in ten or even less. In a sample of 130 sporangiophores sampled, I counted 13 with only single-spored sporangia, 58 with only two-spored sporangia, and 59 with a mixture of one- and two-spored sporangia.

Zygosporangia of *S. hypogena* were found in relatively small numbers in cultures on YpSs/5 at 20 C. Early stages of development of the sexual spores were found in some cultures after only 5 or 6 days, and what appeared to be mature zygosporangia were present after 10 days to 2 weeks. The first sign of sexual reproduction is the appearance of paired, slightly enlarged branches of the aerial vegetative mycelium, which are sometimes more or less spirally entwined near the base (Fig. 24). These sexual hyphae or progametangia are unequal in size (Fig. 25) and soon become differentiated into proximal suspensors and terminal gametangia by the formation of distal transverse septa (Fig. 26). The gametangia fuse apically; the one subtended by the larger suspensor enlarges distally (Fig. 26–28) and eventually forms the body of the zygosporangium, which is subtended by a well-defined gametangial remnant (Fig. 29–30). From early stages of development of the zygosporangium, the smaller gametangial remnant assumes a lateral position on the zygosporangium wall (Fig. 27) and remains thus attached through zygosporangium maturation (Fig. 29). The suspensor derived from the slender, presumably male sexual branch usually becomes several times septate after gametangial fusion and, except for an occasional smallish,

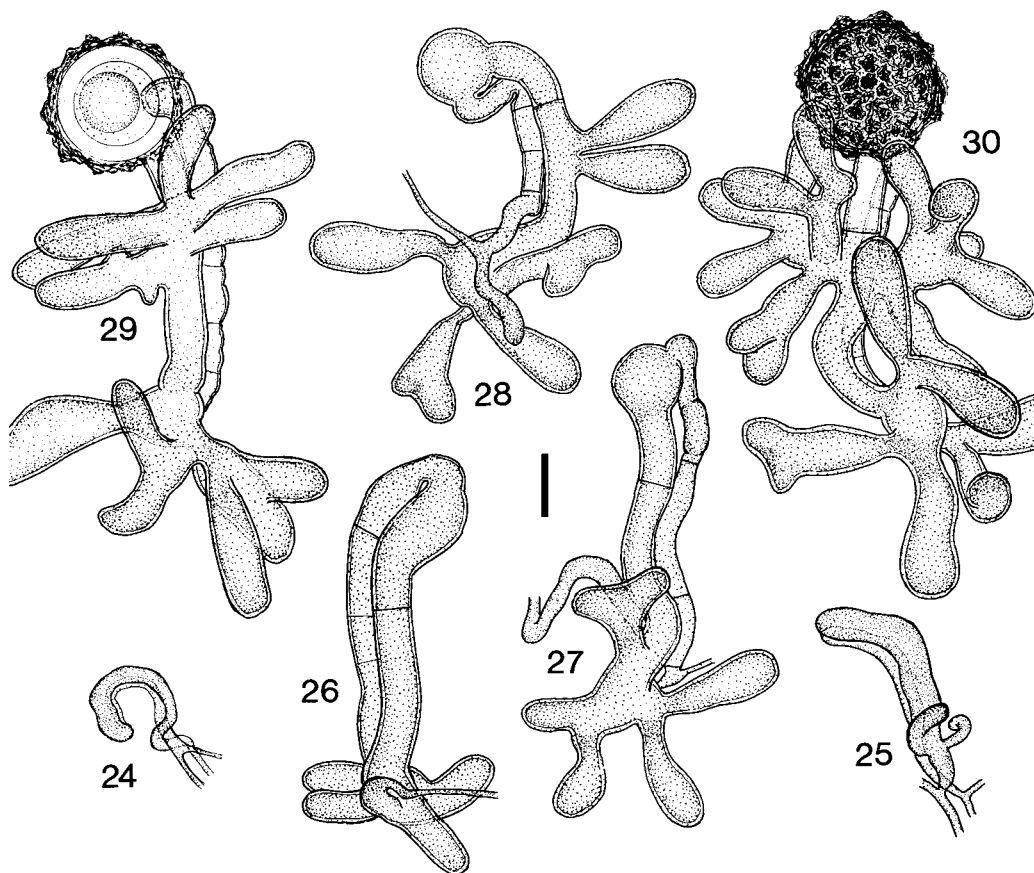


Fig. 24–30. *Syncephalis hypogena*. Stages in development of the zygospore.—24. Very young, slightly unequal progametangia.—25. Progametangia in later stage of development showing early formation of outgrowths near base of larger progametangium.—25. Apposed sexual hyphae that have delimited proximal suspensors and distal, unequal gametangia which have fused apically. Four sterile outgrowths have developed near the base of the larger suspensor, and secondary septa have been formed in the smaller suspensor.—27–28. Early stages of development of the zygospore by terminal enlargement of the larger of the two fused gametangia to which the smaller gametangium remains attached laterally. Lobate outgrowths are continuing to develop from the larger suspensor, below and above (Fig. 28). A single outgrowth has arisen near the base of the small suspensor shown in Fig. 28.—Fig. 29–30. Two mature stalked zygospores as seen in optical section (Fig. 29) and surface view (Fig. 30). Note the degree of development of lobate outgrowths from the large, zygospore-bearing suspensors, and the formation of adventitious septa in the smaller suspensors. (All figures, bar = 10 μm [$\times 825$].)

basal, lobate outgrowth (Fig. 28), is otherwise unmodified. The larger suspensor derived from the presumably female sexual branch becomes highly ornamented by the formation of more or less numerous elongate, lobate, bladderlike vesicles. The first of these develop near the base of the progametangium during the earliest stage of its enlargement (Fig. 25). During early stages of gametangial formation and fusion, other outgrowths develop near the base of the suspensor (Fig. 26–27). Soon after the zygospore begins to enlarge, additional outgrowths develop from

the upper end of the suspensor (Fig. 28). Outgrowths, many of which themselves branch, may continue to form from the upper and lowest ends of the female suspensor as the zygospore matures (Fig. 22, 23, 29, 30). The mature zygospore consists of a brownish, coarsely aculeate-verrucate exospore (Fig. 30) surrounding a smooth, colorless, thick-walled endospore—the zygote proper—which contains a single, large refractive globule (Fig. 22, 23, 29).

The pattern of zygospore development in *Syncephalis* was recently subdivided into three distinct types by Kuzuha (1980). In the first of these, represented by *S. cornu*, the gametangia form apically on apposed, nearly equal progametangia, and the zygospore enlarges more above than between the point of fusion. The mature zygospore bears two prominent, more or less juxtaposed gametangial remnants like those of species of *Piptocephalis*. One suspensor gives rise to bladderlike vesicles (Benjamin 1959; Thaxter 1897) as apparently is the case for all species of *Syncephalis* in the light of observations made up to the present. Other species having the Cornu-type of zygospore development are *S. depressa* (Christenberry 1940), *S. californica* (Hunter and Butler 1975), and perhaps *S. reflexa* (Thaxter 1897). With regard to the last-named species, Thaxter's drawing of a mature zygospore (Thaxter 1897: Fig. 15) shows a "male" gametangial remnant attached laterally to a bladderlike outgrowth. This is highly unlikely. A study of early stages of zygospore formation in *S. reflexa* is needed to clarify its developmental type. The second pattern of zygospore formation, the Nodosa-type, still is known for only one species, *S. nodosa*, in which the larger of two slightly unequal gametangia develops a lateral, budlike outgrowth which forms the zygospore. Bladderlike outgrowths develop distally on the suspensor subtending the zygospore-forming gametangium (Bainier 1883; Benjamin 1959; Thaxter 1897). The third or Tenuis-type developmental pattern was described by Kuzuha (1980) for *S. tenuis* and *S. sphaerica* van Tiegh. (1875). In both of these species the apposed sexual hyphae differ greatly in width and may be simple or much branched. As they elongate, a slender, presumably male hypha, keeps pace with a robust, presumably female, hypha. Finally both hyphae delimit terminal gametangia which fuse apically. The larger gametangium then enlarges and develops a stalked zygospore. The smaller gametangium forms a more or less inconspicuous lateral remnant on the surface of the zygospore. The branched female hypha of *S. tenuis* may give rise to 10 or more zygospores, whereas the unbranched hypha of *S. sphaerica* forms only one. Again, lobate outgrowths develop from the large suspensor below the septum delimiting the gametangial remnant. And, according to Kuzuha (1980), outgrowths also develop lower down on the suspensor of *S. sphaerica*. In the scheme of Kuzuha, the zygospore of *S. hypogena* resembles that of *S. sphaerica* and is of the Tenuis-type.

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FOOTNOTE

¹ When this paper (Benjamin 1979) was retyped by a member of the editorial staff, an error was introduced on p. 594, l. 17, which reversed the meaning of the statement given, i.e., the sentence should read, in part, "... bear great similarity to ..." not "... bear no great similarity to ..." Other errata that would not be readily apparent to the reader include: p. 575, l. 41: Fig. 23.2 Q, R not G, R; p. 580, l. 30: add I to Fig. 23.1; p. 580, l. 32: E, K not E–K; p. 585, l. 7: Fig. 23.1 J not I; p. 585, l. 10: (Ellis & Hesselatine 1974) not (1974); p. 594, l. 41: undescribed not understood.