

ARE YEAST CELLS OF ENDOMYCETALES HOMOLOGUES OF
CONIDIA OF EUROTIALES?

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Similarities in structure, symmetry, and size of asci and ascospores indicate a phylogenetic relationship between the Endomycetales (Endomycetes, Hemiascomycetes) and the Eurotiales and Erysiphales of the Ascomycetes. Their anamorphs which form catenate conidia from meristematic zones and which are released by disjunctive structures, are also similar. The structures in the septa of hyphal Endomycetales termed micropores or plasmodesmata, are considered to be disjunctive pegs.

The Endomycetales (Endomycetes, Hemiascomycetes) include the ascus-forming yeasts. As a rule only budding cells are present and relatively few species form septate hyphae. The Eurotiales are plectomycetous Ascomycetes with septate hyphae. Their asci and conidia-forming structures develop on or in the aerial mycelium. The asci and ascospores of typical members of the two orders are similar and peculiar within the Ascomycota. The asci are spherical or nearly so, botryose or catenate, with a thin, often evanescent wall. The ascospores are relatively small (mostly 3–7 μm), aseptate, hyaline or reddish brown and often ornamented. They are either oblate-bivalvate-saturnoid or spherical-ellipsoidal-fusiform (Fig. 1).

Redhead & Malloch (1977) suggested the yeasts with galeate (helmet- or hat-shaped) ascospores were related to *Ceratocystis*, *Ophiostoma*, and other genera of the Ophiostomataceae, which also include a small number of species with galeate ascospores (e.g. *Ceratocystis fimbriata* Ellis & Halst. and *Europhium trinacriiforme* Parker). Consequently, they classified the Ophiostomataceae within the Endomycetaceae, restricting this family to taxa with mainly galeate ascospores. The Ophiostomataceae, having dark, thick-walled ascomata with usually ostiolar beaks, have been classified in the Sphaeriales, next to the Microascaceae, or in a separate order Ophiostomatales. Their asci are evanescent at an early stage, and the small, often reniform, lunate, or allantoid ascospores are extruded in sticky droplets.

Since the Eurotiales (including Gymnoascales) have never been suspected to be related to the Endomycetales, typical members of the two orders were studied by both light (LM) and transmission electron microscopy (TEM). For comparative purposes the Erysiphales and some other Ascomycetes were also included in the study.

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MATERIALS AND METHODS

The following cultures from the CBS culture collection were studied by LM from freshly grown cultures on cornmeal and other agar media: *Briosia cubispora* (Berk. & Curt.) v. Arx (342.74), *Bysoascus striatisporus* (Barron & Booth) v. Arx (642.66), *Bysochlamys fulva* Olliver & Smith (146.48), *Cephaloascus fragrans* Hanawa (183.71), *Dipodascus australiensis* v. Arx & Barker (625.74), *Hormoascus platypodis* (Barker & Kreger-van Rij) v. Arx (4111), *Neosartorya fischeri* (Wehmer) Malloch & Cain (544.65), *Saccharomycopsis capsularis* Schiöning (5063), *Talaromyces flavus* (Klöcker) Stolk & Samson (387.48), *Triadelphia pulvinata* Maggi & al. (744.84) and *Wallemia sebi* (Fr.) v. Arx (411.77).

The following strains were studied by TEM: *Ascoidea africana* Batra & Francke-Grossmann (377.68), *Ascoidea rubescens* Brefeld (111.48), *Cephaloascus albidus* Kurtzman (389.77), *Ceratocystis fimbriata* Ellis & Halst. (740.70), *Eleutherascus tuberculatus* Samson & Luiten (389.77), *Gelasinospora tetrasperma* Dowding (880.69), *Geotrichum terrestre* (v.d. Walt & Johannsen) Weijman (6697) *Hormoascus ambrosiae* (v.d. Walt & Scott) v.d. Walt & al. (6003) and *Ophiostoma ulmi* (Buisman) Nannf. (427.71).

For TEM the strains were cultured on yeast-malt agar for 4 days at 20°C. Material was fixed in 5% glutaraldehyde and postfixed with 1% osmium tetroxide. Ultrathin sections of the material embedded in an Araldite-Epon mixture were cut with a diamond knife and stained by consecutive treatments with saturated uranyl acetate and Reynolds lead citrate solution as described by van der Walt & al. (1974).

RESULTS AND DISCUSSION

The Eurotiales include several families, including the Trichocomataceae sensu Malloch & Cain (1972), the Gymnoascaceae and the Onygenaceae. The Trichocomataceae are characterized by 'phialidic' anamorphs with conidia formed in basipetal chains and separated from each other by double septa with disjunctive structures (disjunctors). Typical teleomorphic genera are *Eurotium*, *Bysochlamys*, *Hamigera*, and *Eupenicillium*, with anamorphs classified in *Aspergillus* (including *Cladosarum*), *Paecilomyces*, and *Penicillium* (Fig. 1a, b). Several Gymnoascaceae and Onygenaceae include anamorphs belonging to the genera *Briosia*, *Coremiella*, *Geomyces*, and *Oidiodendron* (Fig. 1d–f), in which the conidia are also catenate and are also separated by double septa with disjunctors. In the species of these genera conidiogenous hyphae become septate in a meristematic zone and conidia are delimited in basipetal sequence or at random. The disjunctive structures in and between the septa of the conidia are small, but usually visible by light microscopy as central or ring-like pegs or other excrescences. In *Aspergillus* and *Paecilomyces*, the disjunctors are especially visible in young states when the double septa are formed (Hanlin, 1976; Roquebert, 1981). Such septa apparently have no central pores, which occur in the septa of the vegetative hyphae of all Ascomycetes. In *Aspergillus*, *Penicillium*, and *Paecilomyces* the meristematic, conidiogenous hyphae develop in the apex of ampulliform or obclavate-lanceolate cells (the phialides) but are often inconspicuous (Fig. 1a, b).

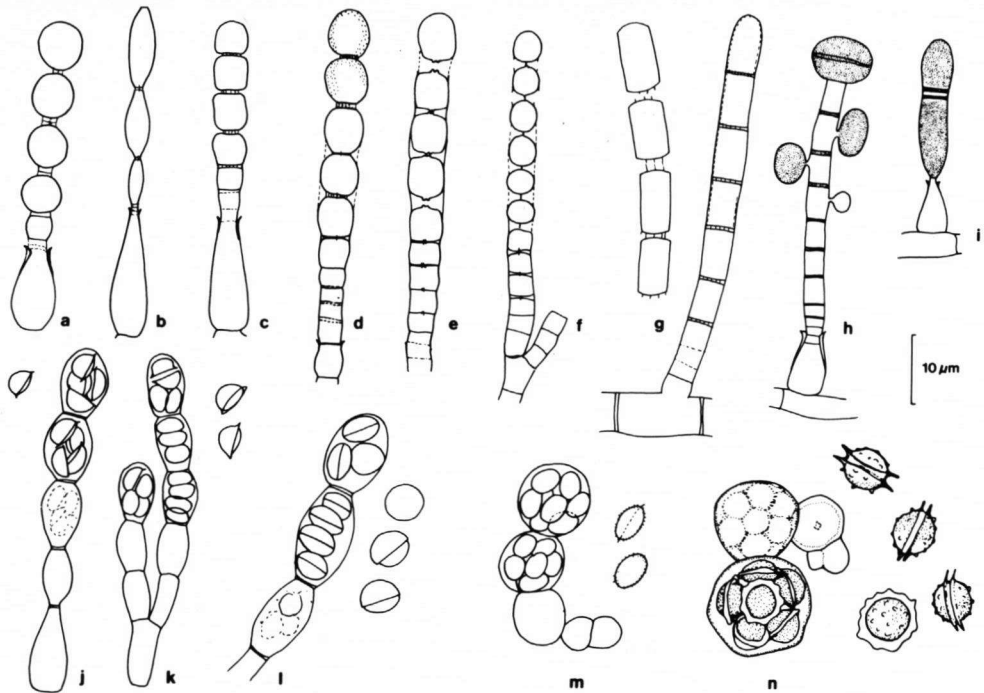


Fig. 1. Catenate conidia and catenate asci in Endomycetales and Eurotiales, and conidiogenous cells in *Arthrini* and *Triadelphia*. a. *Aspergillus* anamorph of *Neosartorya fischeri*; b. *Paecilomyces* anamorph of *Byssochlamys fulva*; c. *Wallemia sebi*; d. *Briosia* spec.; e. *Briosia* (*Coremiella*) *cubispora*; f. anamorph of *Byssosascus striatisporus*; g. *Geotrichum* anamorph of *Dipodascus australiensis*; h. *Arthrini* *sphaerospermum*; i. *Triadelphia pulvinata*; j. *Cephalosascus fragrans*; k. *Hormoascus platypodis*; l. *Saccharomycopsis capsularis*; m. *Talaromyces flavus*; n. *Neosartorya fischeri*.

Aspergillus isolates with distinct, long conidiogenous hyphae have been classified in a separate genus *Cladosarum*, which has not been accepted by subsequent authors (e.g. Raper & Fennell, 1965). Distinct ampulliform cells forming conidiogenous hyphae are absent in Onygenaceae and Gymnoascaceae.

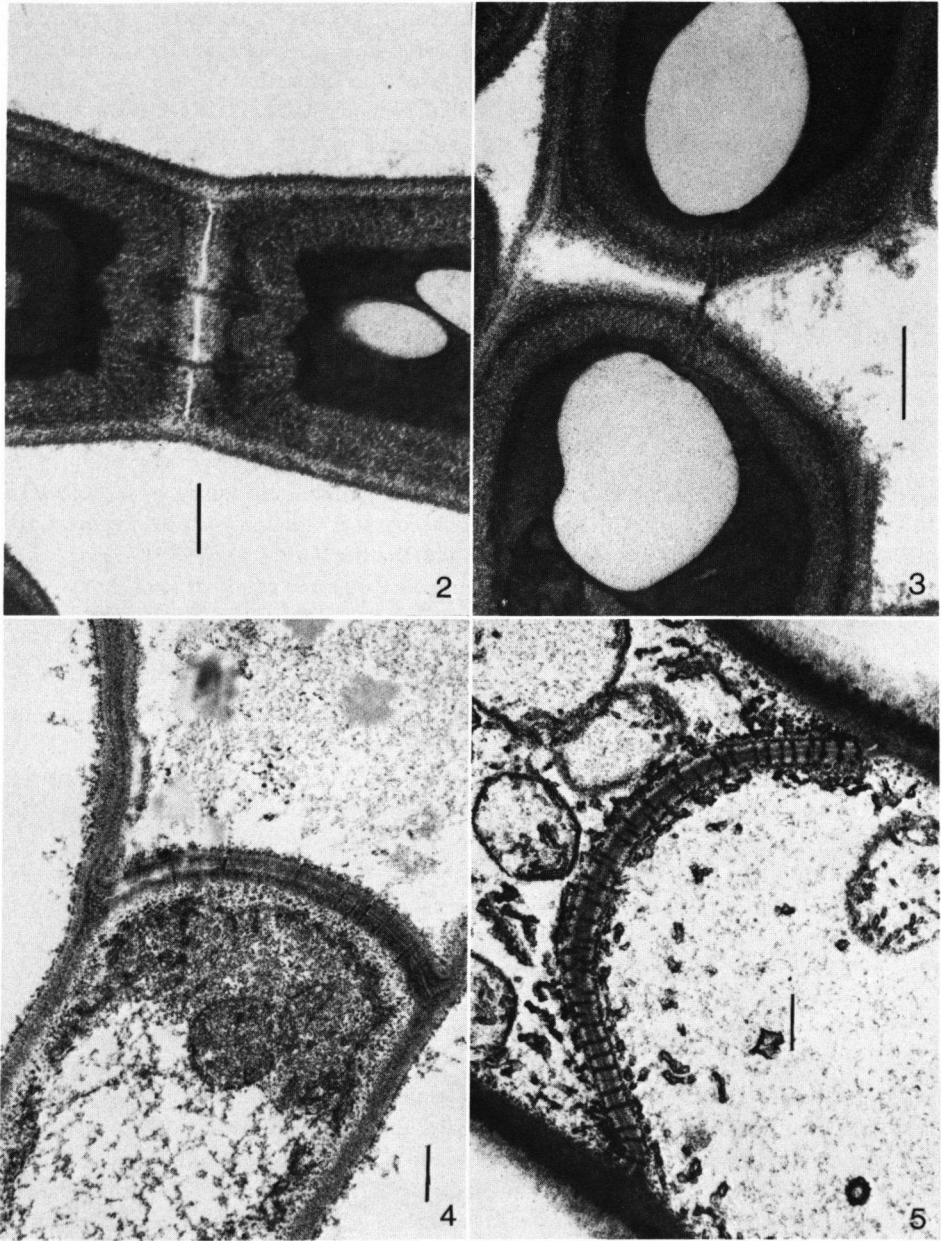
Similar releasing structures occur in filamentous Endomycetales, e.g. in species of *Ascoidea*, *Dipodascus* (anamorph: *Geotrichum*), *Saccharomycopsis*, and *Endomyces* (Fig. 1g). The releasing structures have been demonstrated by TEM in ultrathin sections of the double septa of the hyphae or connected conidia and were formerly interpreted as micropores, plasmodesmata, or closure lines. However, they never have a channel, but are visible by TEM even in young states as electron-opaque lines or pegs which apparently do not connect the lumina of neighbouring cells (Figs. 2–5). These structures were discovered in *Geotrichum candidum* Link by Wilsenach & Kessel (1965) and subsequently in several other species of *Geotrichum* and other genera of the Endomycetes

(van der Walt & von Arx, 1985). When the two septa bulge, the pegs extend (Fig. 3), the hyphal wall is broken and the cells separate. Extending pegs were previously also observed by Kreger-van Rij & Veenhuis (1973) in *Arthroascus javanensis* (Klöcker) v. Arx and in *Yarrowia lipolytica* (Wickerh. & al.) v.d. Walt & v. Arx. They were demonstrated by Cole & Samson (1979) by SEM in *Geotrichum candidum* (their figure 7.9, p. 109). They considered these structures to be connectives; we would prefer the term disjunctive (disjunctive pegs), this conforming with the classical term disjunctor (Hawsworth & al., 1983).

Several Endomycetales with septa with disjunctive pegs have ascospores which are similar in size, shape, symmetry, structure, and pigmentation, to those of Eurotiales. *Saccharomyopsis capsularis* Schiöningg, for example, has bivalvate, smooth, hyaline ascospores (Fig. 1b) as do *Narasimhella hyalinospora* (Kuehn & al.) v. Arx and *Leucothecium emdenii* v. Arx & Samson of the Eurotiales (Gymnoascaceae) and several teleomorphs of *Aspergillus*. *Leucothecium emdenii* includes an unnamed, *Geotrichum*-like anamorph with catenate, cylindrical conidia with disjunctive structures. The species of the yeast genus *Endomycopsella* (von Arx & Yarrow, 1984) have saturn-shaped, verrucose, slightly pigmented ascospores with equatorial furrows, which correspond in all characters with the ascospores of species of *Eurotium*, *Emericella*, and *Neosartorya*, all with *Aspergillus* anamorphs (Fig. 1n). The conidia of *Endomycopsella* species are not catenate but single with a truncate base and the septa have disjunctive pegs.

The ascospores of *Dipodascus geotrichum* (Butler & Petersen) v. Arx are bivalvate, walnut-shaped, relatively large, with a thick, ornamented wall and a longitudinal furrow. This species has a *Geotrichum* anamorph and is closely related to *Dipodascus australiensis* which has ellipsoidal or irregular, hyaline, sheathed ascospores lacking a furrow (von Arx, 1981). Ascospores similar in shape and structure to those of *Dipodascus geotrichum* but much smaller, are characteristic of the genus *Schwanniomyces*, which includes yeasts without hyphae. *Bysochlamys* and *Talaromyces*, two related, probably indistinguishable genera of the Eurotiales, include species with similar, ellipsoidal ascospores, but which usually lack distinct furrows (Fig. 1m). *Bysochlamys* and *Talaromyces* include *Paecilomyces* anamorphs (Fig. 1b), which often are classified in *Penicillium* subgenus *Biverticillatum* (Pitt, 1980).

Ampulliform, phialide-like cells forming meristematic conidiogenous hyphae also occur in the anamorphic states of *Physalospora*, *Apiospora* (Sphaeriales), and some related genera (von Arx, 1985). These anamorphs are classified in *Arthrinium*, *Dictyoarthrinium*, *Papularia*, *Nigrospora*, *Triadelphia*, and other genera (Fig. 1h, i). In most species the conidiogenous hyphae are narrow and thin-walled. The hyphae either form a single apical conidium or they elongate, becoming many-celled by the formation of often thick and pigmented septa and forming supplementary conidia by lateral budding. The darkened septa in the conidiogenous hyphae of *Arthrinium* or *Dictyoarthrinium* species or in the conidia of *Triadelphia* species, are reminiscent of the disjunctive thickenings of Endomycetales and Eurotiales. It may be noted that the conidia are usually bivalvate, with equatorial furrows, as are the ascospores of numerous Endomycetales and Eurotiales.



Figs. 2–5. Hyphal septa of Endomycetales. 2, 3. *Geotrichum terrestre*; 4. *Ascoidea africana*; 5. *Ascoidea rubescens*. Electron micrographs, showing septa with disjunctives (2, 3, bar $\times 0.25 \mu\text{m}$; 4, 5, bar $\times 0.5 \mu\text{m}$).

The hyphomycete *Wallemia sebi* also forms conidiogenous hyphae from ampulliform cells (Fig. 1c). The conidiogenous hyphae become closely septate and the conidia are connected by disjunctive structures. The septa of the vegetative hyphae have central, tube-like pores surrounded by a thickened wall (Terracina, 1974; Cole & Samson, 1979).

Similar central pores in the septa of the vegetative hyphae are known in the ambrosial yeast genera *Ambrosiozyma* and *Hormoascus* (Fig. 10), which are characterized by galeate ascospores (Fig. 1k) and an association with wood-attacking beetles. The thickened septa with central pores have been compared with the dolipores of the Basidiomycetes (Kreger-van Rij & Veenhuis, 1969), but are quite different in their ultrastructure. The septal pores are plugged by dark material.

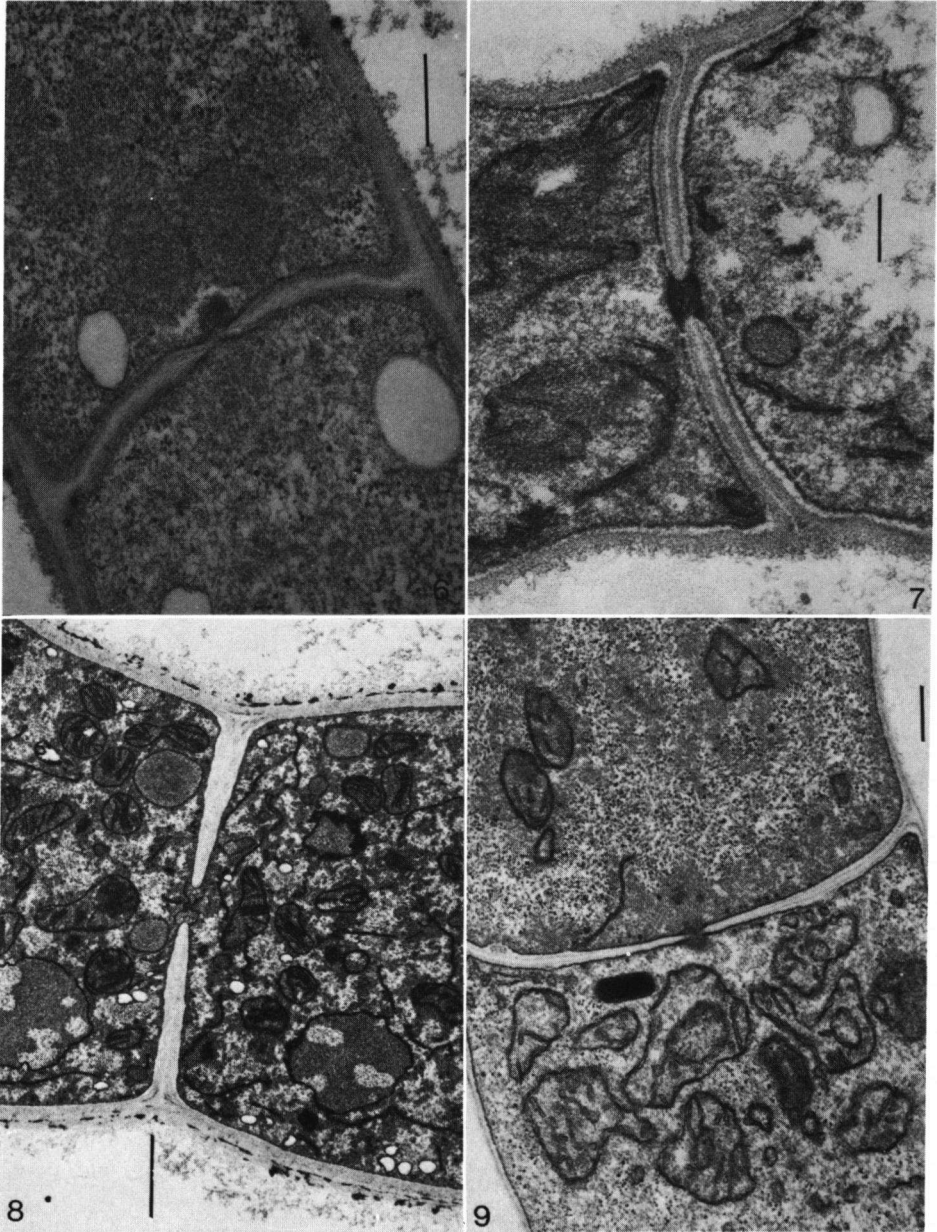
Galeate, helmet-, or hat-shaped ascospores may be considered to be asymmetrically bivalvate with a more distinct, basal brim. No taxa with galeate ascospores are known in the Eurotiales, but they are common in the Endomycetales. The genera *Hansenula* and *Pichia* are characterized by galeate or hemispherical, bivalvate ascospores. The species of *Ascoidea* have many-spored asci, galeate, ascospores and the hyphal septa have numerous disjunctive pegs. *Ascoidea rubescens* and *A. africana* form broad hyphae with septa with distinct, dark pegs (Figs. 5, 6). In *Dipodascus magnusii* (Ludwig) v. Arx the pegs are arranged in a ring near the margin of the septum (van der Walt & al., 1983). *Geotrichum terrestre* has rather thin hyphae with thick septa with one or a few pegs (Fig. 2, 3).

The classification of *Cephaloascus fragrans* (Fig. 1j) either in Endomycetales or Ophiostomatales or in separate order, is often questioned (Redhead & Malloch, 1977; Kurtzman, 1977). Its hyphae have thick septa with rather narrow central pores (Fig. 11). Two conjugating, neighbouring hyphal cells form a thick, apparently diploid hypha, on which erect, thick-walled, pigmented ascophores arise and which bear an apical brush of asci. The asci develop on an ampulliform ascogenous cell and are arranged in basipetal chains, as are the conidia in *Aspergillus* and related genera. In *Cephaloascus fragrans* the asci contain four small, galeate ascospores (Fig. 1j).

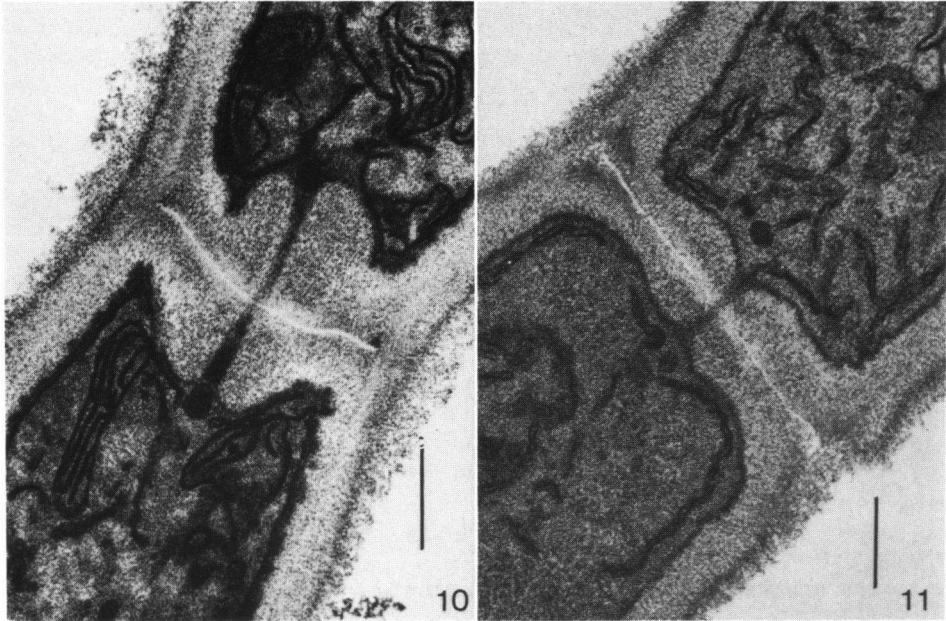
Typical genera of the Ophiostomatales are *Ophiostoma*, *Ceratocystis*, *Ceratocystiopsis*, and *Europhium*. The latter genus is characterized by non-ostiolate, dark ascomata and by galeate ascospores. The ascomata are embedded in a superficial mycelium. The *Lep-tographium* (*Verticicladiella*) anamorphs have conidiophores reminiscent of the ascophores of *Cephaloascus fragrans*.

Ceratocystis has been restricted to species with *Chalara* anamorphs, and *Ophiostoma* has been reintroduced for species which include anamorphs belonging to *Graphium*, *Sporothrix*, and some related hyphomycete genera (von Arx, 1974; de Hoog, 1974). Transmission electron microscope studies show that species of both *Ceratocystis* and *Ophiostoma* have relatively thick hyphal walls and septa with a central pore occluded by dark material (Fig. 6, 7). Some chemical characters have been introduced by Weijman & de Hoog (1975) and de Hoog & Scheffer (1984) to delimit the two genera.

Ceratocystis fimbriata is apparently the only species of the genus having galeate ascospores with a basal brim. In its *Chalara* anamorph conidia develop in basipetal sequence from a meristematic zone inside a tube-like conidiogenous cell and are cylindrical, aseptate, and hyaline. Disjunctives are apparently absent and the conidia, after release, form



Figs. 6–9. Hyphal septa of Ascomycetes. 6. *Ceratocystis fimbriata*; 7. *Ophiostoma ulmi*; 8. *Gelasinospora tetrasperma*; 9. *Eleutherascus tuberculatus*. Electron micrographs, showing septa with central pores (6, 9, bar $\times 0.5 \mu\text{m}$; 7, bar $\times 0.25 \mu\text{m}$; 8, bar $\times 1 \mu\text{m}$).



Figs. 10–11. Hyphal septa in *Hormoascus* and *Cephaloascus*. 10. *Hormoascus ambrosiae*; 11. *Cephaloascus albidus*. Electron micrographs, showing thickened septa with narrow pores (10, bar $\times 0.5 \mu\text{m}$; 11, bar $\times 0.25 \mu\text{m}$).

mucoid droplets. Some other *Chalara* species form septate conidia and the septa may be rather thick, occasionally darkened.

The Endomycetales are distinguished from the Eurotiales and from the other Ascomycetes by the absence of ascomata and specialized ascogenous hyphae. They usually develop in aqueous or very moist environments. Further distinguishing characters are the absence of septal pores and Woronin bodies in the hyphae (when present), and the absence of chitin (glucosamine) in the cell walls. In this connection it may be noted that, at least in some species of *Penicillium*, *Aspergillus*, and *Trichoderma*, the cell walls of the conidia do not contain glucosamine, but mainly mannose, galactose, and glucose. Glucosamide, in higher amounts than in the conidia, has been observed in the vegetative hyphae and in germ tubes (Martin & al., 1973; Benitez & al., 1976; Cole & al., 1979; Barreta-Bergter & al., 1981).

CONCLUSIONS

The similarity in the presence of disjunctive structures and the absence of glucosamide in the cells and hyphae of the Endomycetales and the conidial chains of the Eurotiales, suggests that these structures are homologous. Three phylogenetic lines have to be

considered. The 'aquatic' line leads to the main part of the Endomycetales, which are dependant on aqueous environments for their reproduction and dispersal. The 'aerial' line is represented by the Eurotiales, the Erysiphales, and other ascomycetes. They form superficial reproductive structures and the ascospores and conidia are dispersed by air under dry conditions. The third phylogenetic line includes fungi and yeasts primarily associated with insects and adapted to dispersal by animals. They develop in cavities, often as ambrosia fungi (Ophiostomatales, *Cephaloascus*, *Hormoascus*, *Ambrosiozyma*, and other entomogenous yeasts and fungi).

The Endomycetales, Eurotiales, Ophiostomatales, and Erysiphales may have been evolved from fungi with similar, aseptate ascospores and with spherical or obovate asci. Such species now are included in *Eleutherascus*, which was classified tentatively in the Pezizales by von Arx (1971). The genus includes four species. The asci develop singly or in small clusters from conjugating cells of the aerial mycelium and are spherical or nearly so, with a relatively persistent wall without operculum. Ascomata with a peridium are absent. *Eleutherascus lectardii* (Nicot) v. Arx has spherical, pale, spiny ascospores. It also has been classified in the Endomycetales as *Hemiascosporium spinulosum* by Batra (1973). By TEM, the hyphae are seen to have relatively thin walls and the septa to have distinct central pores, similar to those of typical Ascomycetes, e.g. *Gelasinospora tetrasperma* (Figs. 8, 9). *Eleutherascus tuberculatus* has also spherical, spiny ascospores and differs from *E. lectardii* by the formation of an anamorph with small, aseptate, hyaline conidia. *Eleutherascus cristatus* v. Emden and *E. peruvianus* Huang have pigmented, spiny ascospores with equatorial furrows.

The 'phialides' of *Aspergillus*, *Penicillium*, *Paecilomyces*, *Wallemia*, *Arthrinium*, and related genera should not be confused with the 'phialides' of *Fusarium*, *Phialophora*, *Clonostachys*, and many other genera, which do not form conidiogenous hyphae with a meristematic base and in which the conidia have no disjunctives. The conidia form usually wet, mucoid masses, but may also be arranged in 'false', often oblique chains. The 'phialoconidia' of *Aspergillus* and related genera are similar to the 'arthroconidia' of *Briosia*, *Coremiella*, and their relatives (Fig. 1). Cain (1972) and others connected the Eurotiales with the Hypocreales, which is not justified. Both differ fundamentally in the structure of ascomata, asci, ascospores, and anamorphs.

Müller & von Arx (1962) connected the Erysiphales (powdery mildews) with the Pezizales. They are also similar to the Eurotiales in that they form reproductive structures on a superficial mycelium and have non-ostiolate ascomata, spherical or obovate asci, and aseptate, hyaline or pale ascospores. The *Oidium* anamorphs also form aseptate conidia with truncate ends in basipetal chains from meristematic bases of erect conidiogenous hyphae. The conidia are separated from each other by two adjacent, bulging septa.

The catenate conidia of the Eurotiales and Erysiphales also should not be confused with the catenate conidia formed in acropetal chains, which also release by bulging scars or disjunctors (e.g. *Monilia*, *Chrysonilia*, *Cladosporium*, or *Ramularia*).

In our opinion, the Endomycetales, Eurotiales (including Gymnoascales), Erysiphales, and Ophiostomatales should be maintained in their present delimitation. An alternative classification based exclusively on the shape and symmetry of the ascospores, would be less than desirable. The shape of the ascospores, however, can be useful to delimit 'natural' groups especially within the Endomycetales and Eurotiales.

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